DIPLOMARBEIT

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

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Low dissolved oxygen events in the Northern Adriatic: in situ experimental insight
into benthic responses before, during and post-anoxia

Project coordinators: Doz. Dr. Michael Stachowitsch & Ao. Prof. Dr. Martin Zuschin

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1 Introduction

In 1990, 23 % of the world´s population – an estimated 1.2 billion people – inhabited coastal areas (Nicholls & Small; 2002). The prediction is that by 2015 there will be 33 megacities (each with more than 8 million people) worldwide located near the coast (UN/DESA, 2001). This has led to direct impacts by pollution and habitat destruction. The Mediterranean coast and its shallow-water areas are also adversely affected by human activity, with documented effects e.g. on biodiversity (Danovaro & Pusceddu, 2007). One major disturbance, hypoxia and anoxia, is associated with eutrophication by riverine input, through interaction between nutrients and microbial processes (Nixon, 1995; Zhang et al., 2010). Beyond the massive run-off of nutrients, further impacts such as overfishing, introduced species, global warming and acidification have altered some productive coastal marine ecosystems into monotonous and unproductive areas (Jackson, 2008). Currently, there are more than 400 eutrophication-associated dead zones worldwide, with a total area of more than 245,000 km^2 (Diaz and Rosenberg, 2008). Dayton et al. (1995) established that coastal marine ecosystems are the world´s most endangered habitats. Over the past five to ten years, research has increasingly focused on changes in the ocean´s dissolved oxygen content (Rabalais et al., 2010). The level of dissolved oxygen in estuarine and coastal marine ecosystems is affected mainly through the process of eutrophication by chemical fertilizers, which increases productivity by an increased input of nitrogen and phosphorus. No other environmental variable than dissolved oxygen has changed so drastically in such a short time (Diaz & Rosenberg, 1995; Nixon, 1995; Diaz, 2001). This effect is predicted to be exacerbated by global warming, which increases the temperature of the sea-surface, potentially enhancing stratification. This, in turn, inhibits the exchange of oxygen-rich surface waters with deeper waters (Diaz, 2001; Schmittner, 2005; Conley et al., 2009a).

Hypoxia has been defined as oxygen levels below 2.0 ml l^{-1}. This is the point at which the benthic fauna begins to show aberrant behavior. Anoxia is defined as 0.0 ml l^{-1} (Diaz & Rosenberg, 1995; Diaz & Rosenberg, 2008). Hypoxia has adverse effects on the community structure and trophodynamics of marine ecosystems, in particular by causing fundamental changes in species composition by eliminating sensitive species but promoting certain more tolerant species (Dauer, 1993; Wu, 2002). Thus, hypoxia causes major changes in marine ecosystems (Gray et al., 2002).

1.1 Northern Adriatic Sea

The Northern Adriatic Sea is a shallow, semi-enclosed waterbody with a mean depth of 30 m, varying water column structure, and water movements with dominant seasonal influence (Justic, 1991; Malej & Malacic, 1995). Artegiani et al. (1995) defined three regions with similar physical water characteristics: 1) the shallow Northern Adriatic, which reaches a depth of maximally 100 m in the south; 2) the middle Adriatic characterized by the Pomo Depression up to the Vieste transect, and 3) the Southern Adriatic with characteristics of the open sea, extending down to the Otranto Channel. The water circulation and hydrography of the Adriatic Sea is actuated through the freshwater input, heat loss to the atmosphere, and the exchange of heat and salinity with the Atlantic Ocean through the Straits of Gibraltar (Zavatarelli & Mellor, 1995). The whole waterbody of the Northern Adriatic Sea features a seasonal thermal cycle. In spring and summer a well-developed thermocline occurs, while in autumn a significant cooling begins near the surface and the bottom water reaches the highest temperatures. In winter the entire water column cools down (Artegiani et al., 1995).

The Northern Adriatic Sea has a number of features that qualify it as a sensitive marine ecosystem (Stachowitsch, 1986), in particular with regard to seasonal hypoxia and anoxia (Stachowitsch & Avcin, 1988). It is characterized by shallow depth, soft bottoms, high riverine input mainly from the Po River, high productivity and long water residence time (Stachowitsch, 1991; Ott, 1992). Under adverse hydrographic and meterological conditions, namely calm seas and hot weather, severe hypoxia near the bottom can be expected in summer and autumn (Malej & Malacic, 1995). Decreasing oxygen conditions are also often associated with macroscopic mucus aggregates, thought to be initially produced by diatoms, which can develop into severe marine snow events (Stachowitsch et al., 1990).

In this area, long-term decreases in the bottom-water oxygen content have been observed (Justic, 1991), which is connected with changes in and mortality of benthic communities (Stachowitsch, 1984, 1991). In September 1983, for example, a rapid decrease in dissolved oxygen occurred in bottom waters in the Gulf of Trieste, which led to a large-scale anoxia. This was associated with wide-ranging mortalities (Stachowitsch, 1991). Nonetheless, the Northern Adriatic Sea is among the most productive areas of the Mediterranean (Stirn et al., 1974).

1.2 Benthic community structure

Epibenthic macrofauna communities characterize the soft bottoms in the Northern Adriatic Sea. Fedra et al. (1976) named one such wide-ranging community the *Ophiothrix-Reniera-Microcosmus* community, in short, the ORM-community, based on the most dominant organisms, the brittle star *Ophiothrix quinquemaculata* (Delle Chiaje, 1828), the sponges *Reniera* spp., and the ascidians *Microcosmus* spp.. This suspension-feeding community is aggregated into so-called multi-species clumps or bioherms. They consist of a shelly base (bivalve or gastropod shell) which is overgrown by sessile organisms (sponges, ascidians). These multi-species clumps also serve as an elevated substrate for vagile and hemi-sessile species such as brittle stars, holothurians, hermit crabs and gastropods (Fedra et al., 1976; Zuschin & Pervesler, 1996), and are also a food source for epibenthic crustaceans and fishes (Hampel et al., 2004). Such filter- and suspension-feeder communities are an important stabilizing compartment in the overall marine ecosystem (Ott & Fedra, 1977) and provide crucial ecological goods and services (Van Colen et al., 2010). Benthic communities are able to remove enormous amounts of suspended material from the waterbody and play an important role as a natural eutrophication control (Officer et al., 1982).

1.3 Impact of dredging and trawling

Commercial fishing adversely affects marine ecosystems, in particular the different types of dredges and trawls that are dragged over the sea bottom (Jennings & Kaiser, 1998). The impact of such fishing gear depends on various circumstances (weight, the degree of contact with the seafloor, trawling speed), and gear design often determines how many species other than the target species are captured (e.g. by-catch). The influence of the fishing gear also depends on the habitat in which it is used (Thrush & Dayton, 2002). Rapido trawling, for example, influences macrobenthos directly, with significant changes in community structure and mean abundance of common taxa (Pranovi et al., 2000). Altered physical characteristics of the sea bottom have been measured after beam-trawling (Kaiser & Spencer, 1996). Riemann & Hoffmann (1991) reported an increase in the oxygen consumption, the nutrient concentration and a possible promotion of phytoplankton primary production after dredging and trawling. Bottom gears clearly affect sessile epibenthic species and can change overall community structures. This includes potential long-term effects (Jennings & Kaiser, 1998).

In the Northern Adriatic Sea, Kollmann & Stachowitsch (2001) reported a negative influence of dredging and trawling on multi-species clumps. Specifically, the elevated biogenic structures important for growth were either sheared off and uprooted (e.g. *Pinna* sp. shells) or overturned and crushed. The reduction of long-lived suspension-feeding organisms is typically followed by a shift to a habitat dominated by detritus feeders: detritus-feeding groups 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 & 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 & Stachowitsch, 2001).

1.4 Recovery

The succession of benthic animals after disturbance is described by Rosenberg et al. (2002) as an increase in the number of species, abundance and biomass. Connell and Slatyer (1977) summarized that empty space generally is first occupied by “opportunist” species with rapid growth and wide distribution. Pearson and Rosenberg (1978) defined three successional stages: first there is a peak of opportunists, with few species present in large numbers; the second stage is the ecotone point, at which species abundance is low and evenness diversity high; the third stage is the transition zone, with early variation of the populations. These populations then proceed in the direction of more stable “normal” communities.

Two basic recolonization strategies exist. On the one hand, motile species can immigrate into denuded areas, in particular if the damage is rather small-scale. On the other hand, when the areas are large, colonization is mostly dependent on post-larval settlement by pelagic recruits (Günther, 1992; Pearson & Rosenberg, 1978; Whitlatch et al., 1998). The reestablishment of community structure on the soft bottoms of the Northern Adriatic requires the availability of biogenic structures. Such structures (bivalve and gastropod shells, sea urchin tests) serve as a substrate on which larvae of sessile and motile epifauna species can settle. Sedimentation influences new epigrowth considerably, and the use of bottom trawls can overturn or break apart newly established multi-species clumps (Stachowitsch and Fuchs, 1995). 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. The capacity for self-repair is reduced (Folke, 2004). Rosenberg (1971) studied the recovery time of the littoral fauna in the Saltkallefjord, Sweden, after disturbances by a sulphite pulp mill, and determined that recovery took about three years. Intertidal communities from muddy sand habitats, for example, have very slow biological and physical recovery rates (Dernie et al., 2003). According to Tuck et al. (1998), recovery of benthic communities after experimental trawling disturbances took more than 18 months (end of the experiment). In the Gulf of Trieste, Stachowitsch and Fuchs (1995) were unable to detect full recovery even after more than ten years, so recolonization was clearly a long-term process. This circumstance makes benthic communities a long-term “memory” of disturbances (Stachowitsch, 1992). Lotze et al. (2011) reviewed the optimal administrative strategies for promoting recovery. These strategies include public and political attention, legal action and realizing management plans, preservation and restoring biodiversity and ecosystem complexity, and planning for the long term.

The present work was designed to assess both the 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 (two plots measuring 0.25 m^2) by evaluating time-lapse films and by analysing photographic series. In the former, predators and scavengers were counted image by image (fishes) or every tenth image (hermit crabs and gastropods); in the latter, the area occupied by recolonizers was calculated as a measure of recovery.

1.5 The studied organisms

1.5.1 Gastropods

Muricidae

Worldwide, more than 2000 species of Muricidae have been described, making them a rich and widespread group (Poppe & Goto, 1991).

Hexaplex trunculus (Linnaeus, 1758) – Banded dye murex

The shell of *Hexaplex trunculus* (Fig. 1) is broadly conical and 4-10 cm long. It has a high spire with six to seven angulated whorls with or without small humps and spines. The siphon has a moderate length. Usually the shells have a cream colour with dark brown bands, but orange specimens also exist. The mouth of the shell is greyish-white, mostly with three brown-purple stripes. The exterior shell can be overgrown by sponges, bryozoans, polychaetes, algae or hydroids. *Hexaplex trunculus* occurs between 1 and 100 m depth and can inhabit polluted habour waters (Riedl, 1983; Poppe & Goto, 1991). According to Benovic (1997), this species is widespread in the Adriatic Sea and it is ecologically and commercially important. *Hexaplex trunculus* is fished for human consumption and in ancient times to produce a dye of lesser-quality purple (Poppe & Goto, 1991). Wurzian (1982) showed that *Hexaplex trunculus* feeds on *Arca noae* (Linnaeus, 1758), *Chlamys varia* (Linnaeus, 1758), *Corbula gibba* (Olivi, 1792), *Venus* sp. (Linnaeus, 1758), and *Ophiothrix quinquemaculata* (DelleChiaje, 1828), and it also grazed on sponges. Rilov et al. (2004) reported that *Hexaplex trunculus* has a broad diet, feeding on barnacles, bivalves, gastropods, tunicates and bryozoans.

Figure 1: *Hexaplex trunculus* with epigrowth (*Epizoanthus erinaceus*). Photo: I. Gallmetzer

Bolinus brandaris (Linnaeus, 1758) – Purple dye murex

The shell of *Bolinus brandaris* (Fig. 2) is about 7 cm in length. Some shells grow to 9 cm, and dwarf forms of less than 5 cm also occur. There is one row of spines on the siphonal canal. The shape and coloration of *Bolinus brandaris* is very variable. Usually there are two spiral rows of short spines on the body whorl, but there can also be only one or even up to four rows. Most individuals have cream coloration, but they can also be white, dark brown and sometimes even pink (Poppe & Goto, 1991). *Bolinus brandaris* is common in the Mediterranean Sea and occurs on sandy-muddy bottoms between 1 and 200 m depth (Poppe & Goto, 1991; Martin et al., 1995). In the ancient history of the Mediterranean, *Bolinus brandaris* was fished in large numbers because of the purple pigment they produced in special glands, which was used to make Tyrrhenian Purple dye. Today it is fished because of the fine taste of its meat (Poppe & Goto, 1991).

Figure 2: An aggregation of *Bolinus brandaris* on a clutch. Photo: M. Stachowitsch

1.5.2 Hermit crabs

Hermit crabs are mainly “omnivorous detrivores”. The primary nourishment is detritus, but many species feed also on macroscopic pieces of dead or living animals (Hazlet, 1981). They tend to be opportunistic feeders. Samuelsen (1970) investigated the guts of different hermit crabs and reported that the content consists of algae, foraminiferans, polychaetes, bivalves, gastropods and small crustaceans.

Paguridae

Paguristes eremita (Linnaeus, 1767)

Paguristes eremita (Fig. 3) has a reddish body with orange eye stalks and a light blue cornea. They are very common on all substrates from 4-40 m depth (Riedl, 1983). On muddy and coarse substrates from 15-30 m depth, *Paguristes eremita* is abundant in the Adriatic Sea. Depending on their size, in the Gulf of Trieste they primarily occupy *Hexaplex trunculus, Bolinus brandaris* or *Apporhais pes-pelecani* shells (Stachowitsch, 1980; Manjon Cabeza & Garcia Raso, 1999). The gastropod shells provide a substrate for epizoic growth, so the shells are often overgrown by sponges (*Suberites domuncula* (Olivi, 1792)), anemones (*Calliactis parasitica* (Couch, 1842)) or hydroids (*Podocoryna*), which in turn provide protection for the hermit crabs (Stachowitsch, 1980; Riedl, 1983). *Paguristes eremita* is described as an omnivorous hermit crab (Samuelsen, 1970; Hazlet, 1981; Wurzian, 1982).

Figure 3: *Paguristes eremita* in *Bolinus brandaris* with epigrowth on the shell (two *Calliactis parasitica*, hydroids, sponge (orange), bryozoan (red)). Photo: M. Stachowitsch

1.5.3 Fishes

Gobiidae – Gobies

Gobius niger (Linnaeus, 1758) – Black Goby

Gobius niger (Fig. 4) has a compact body with a variable coloration, including shades of yellow, brown, black or dark marmorate, with dark blotches spots on the lateral line. In general it has six changeable grey-brown horizontal stripes on a yellow-brown background, but during spawning season or aggressive encounters they turn black (Riedl, 1983; Whitehead et al., 1984). *Gobius niger* occurs on sand or mud in estuaries and inshore waters as deep as 75 m and also in sea-grass or algae. Its range includes the eastern Atlantic, the Baltic Sea, the Mediterranean and the Black Sea (Whitehead et al., 1984). This demersal fish feeds on amphipods, decapods, mysids and polychaetes (Richards & Lindeman, 1987; Stergiou & Karpouzi, 2002). Wurzian (1982) determined that more than 70% of the diet of *Gobius niger* in the Adriatic Sea consists of echinoderms.

Figure 4: *Gobius niger*. Photo: T. Makovec

Serranidae – Sea bass

The body is elongated with a thick caudal peduncle. Serranidae have an operculum that bears a spinet. They prefer the littoral zone (Riedl, 1983).

Serranus hepatus (Linnaeus, 1758) – Brown comber

Serranus hepatus (Fig. 5) has a fusiform body with one dorsal fin, which has a spiny part and a soft part, with a characteristic dark spot in between. *Serranus hepatus* has three to five dark stripes on a light background. It is demersal and very common on sand and mud, from 10 m down to deeper waters. Normally it reaches a length of 12-15 cm. It is widespread in the eastern Atlantic and the Mediterranean Sea (Riedl, 1983; Whitehead et al., 1984). *Serranus hepatus* feeds on fishes, amphipods, decapods, mysids, other crustaceans and polychaetes (Labropoulou & Eleftheriou, 1997; Stergiou & Karpouzi, 2002).

Figure 5: *Serranus hepatus*. Photo: T. Makovec

Sparidae – Porgies

Diplodus vulgaris (Geoffroy Saint-Hilaire, 1817) – Two-banded bream

The dorsal side of the body combines brown-yellow and golden colours and the ventral side is silvery. *Diplodus vulgaris* (Fig. 6) has one wide black spot on the caudal peduncle between the dorsal and the anal fin, and a second characteristic bar from the nape to the axil of the pectorals. Most teeth are crooked. During spawning season the head of *Diplodus vulgaris* turns bluish with a brown stripe on the front. This species can grow to 40 cm in length (Riedl, 1983; Whitehead et al., 1984). It is benthopelagic and feeds on fishes, echinoderms, ophiurids, crustaceans (amphipods, tanaidaceans, decapods), molluscs, gastropods, bivalves, annelids, polychaetes and algae (Stergiou & Karpouzi, 2002). *Diplodus vulgaris* is common in the Mediterranean and occurs on rocky or sandy bottoms to 70 m depth (Whitehead et al., 1984).

Figure 6: *Diplodus vulgaris*. Photo: T. Makovec

Pagellus erythrinus (Linnaeus, 1758) – Common Pandora

This species has a slim, oval body with a small mouth. The body is silvery with a light pink tinge and a bluish and metallic shimmer along with long pectoral fins. The head is nearly straight and somewhat convex (Riedl, 1983). It reaches lengths of 60 cm. *Pagellus erythrinus* (Fig. 7) occurs in inshore waters and inhabits rocky, sandy or muddy bottoms to 200 m depth in the Mediterranean (Whitehead et al., 1984). This benthopelagic fish feeds on fishes, echinoderms, ophiurids, gastropods, bivalves, cephalopods and other molluscs, crustaceans (amphipods, decapods, isopods, mysids, isopods), annelids and polychaetes (Stergiou & Karpouzi, 2002; Fanelli et al., 2011). According to Wurzian (1982) the main part of its diet consists of crustaceans.

Figure 7: *Pagellus erythrinus*. Photo: T. Makovec

2 Material and Methods

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. 8).

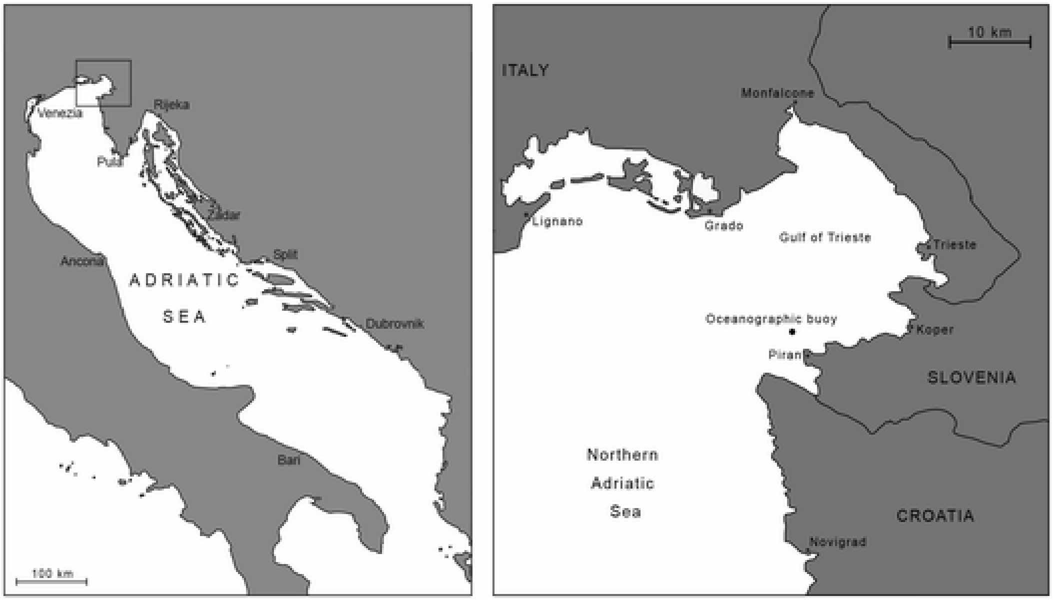

Figure 8: Study site; 1) the Northern Adriatic Sea (left), 2) Piran in the Gulf of Trieste (right) (map taken from Haselmair, 2008).

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 avoid disturbance and damage by commercial fisheries. The soft bottom here is dominated by macro-epibenthic communities consisting of brittle stars, sponges and ascidians. The investigated community has been named the ORM-community based on the biomass dominants *Ophiothrix quinquemaculata*, a brittle star, the sponges *Reniera* spp. and the ascidians *Microcosmus* spp. (Fedra et al., 1976). These species are aggregated in so-called multi-species clumps (Fig. 9), which develop on hard structures such as shells of bivalves or gastropods. These shells are overgrown by sessile organisms, which in turn provide a habitat for hemi-sessile and motile species including holothurians, gastropods and hermit crabs (Zuschin et al., 1999).

Fig. 9: Typical multi-species clump: sponge, ascidian and brittle star, from right to left: ascidian *Phallusia mammillata* (Cuvier, 1815) with brittle star *Ophiothrix quinquemaculata*, unidentified sponge and anemone (dark brown). Photo: I. Gallmetzer

2.2 Experimental set-up

The experimental anoxia generating unit (EAGU) is an underwater device (Fig. 10) that is positioned over selected multi-species clumps. It experimentally creates and documents anoxia. There are two different configurations. The first is the open configuration, in which the camera is positioned on a frame to observe behavior under normoxic conditions. The second is the closed configuration, which creates anoxia by sealing a 50 x 50 x 50 cm volume off from the surrounding water with plexiglass walls. The EAGU consists of a 2-cm-thick aluminium-profile frame (L x W x H = 50 x 50 x 50 cm) with four removable tapered metal tips to stabilize the device in the sediment. Centrally, on a lid on top of the frame, a camera housing with a time-lapse camera is positioned. The camera is flanked by two exchangeable battery packs, and the lid also bears two flashes. These batteries, combined with a specially designed electronic control circuit, enable the equipment to be operated for about 72 h.

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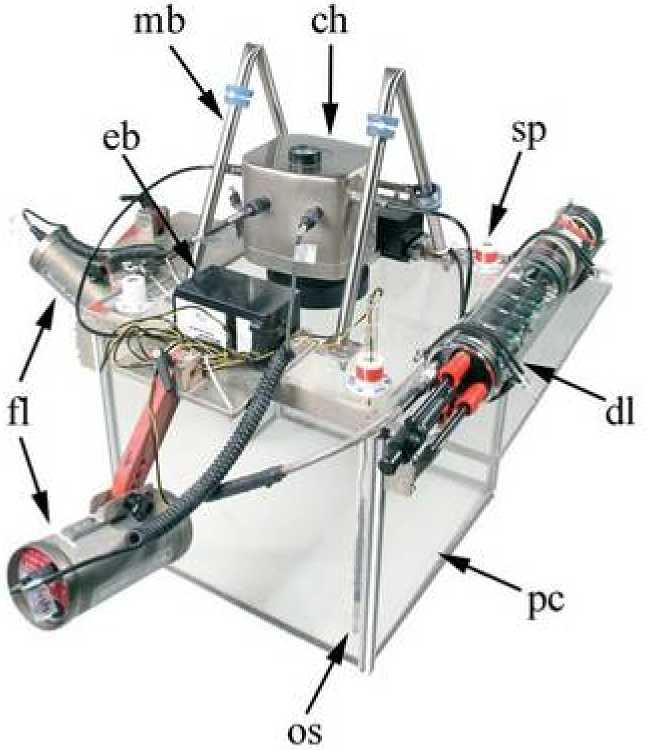


Figure 10: Experimental Anoxia Generating Unit (EAGU) with the instrument lid positioned on top of the plexiglass chamber. One sensor is visible (center, bottom) and is connected to the datalogger and inserted through a sensor port. **Ch**: camera housing, **dl**: datalogger, **eb**: external battery, **fl**: flashes, **mb**: metal brackets for protection and handling, **os**: oxygen sensor, **pc**: plexiglass chamber, **sp**: sensor port (Stachowitsch et al., 2007).

In both configurations the instrument lid is placed on top of the aluminium frame. The lid comprises the complete instrumentation for the documentation. This includes a digital camera (Canon EOS 30D, 8.2 MP) with a zoom lens (Canon EFS 10-22 mm, f/3.5-4.5 USM), a Canon Timer Remote Controller (TC-80N3) and a 1 GB flashcard. The two underwater flashes (“midi analog” series 11897; Subtronic, Germany) are fixed with PVC-swivel arms on two contiguous sides. Finally, a datalogger unit (PA3000UD, Unisense, Denmark), two battery packs (9Ah Panasonic, Werner light power, Unterwassertechnik, Germany) and four sensors are placed on the lid (for a full description see Stachowitsch et al., 2007).

The present recovery experiments involved the following deployment protocol. The EAGU was initially positioned under normoxic conditions (aluminium frame) over a multi-species clump on the sediment for about 24 h. Thereafter, a switch was made to the closed configuration, i.e. the lid was briefly lifted and the open frame replaced by the plexiglass chamber. After 72 h the plexiglass chamber was again 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 Data analyses

2.3.1 Short-term predation and scavenging – Presence analyses

This thesis evaluates two experiments. In the first experiment the images were taken commencing on 15.08.2009 (10:35 am) until 18.08.2009 (10:05 am) ("August" experiment). The second experiment extended from 14.09.2009 (03:25 pm) until 17.09.2009 (10:49 am) ("September" experiment). 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. For both experiments the open configuration (Fig. 11) after the closed configuration (anoxia) was evaluated. The three most abundant predator and scavenger groups were fishes, hermit crabs and gastropods. The fishes were analysed image by image. 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 every analysed image the present predator and scavenger species were recorded in excel-sheets. For the hermit crabs and the gastropods, the different substrates they were on were also recorded. Figure 20 (preferred substrates/prey), includes sponges, sediment, the two ascidians *Microcosmus* spp. and *Phallusia mammillata* (summarized as "ascidians"), and "others" (including the frame and all other substrates).

Individual specimens of the different species could rarely be differentiated because coloration and sizes were typically very similar. Thus, in the present contribution, the number of fish, gastropod and hermit crab individuals refers to the number of specimens 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 of time. It does, however, capture the role that an individual or individuals played because they were present and exerted a scavenging or predatory influence.

For the predators and scavengers, the time and sequence of arrival/departure and the maximum number of individuals were observed. Day/night activity of the hermit crabs and the gastropods, and the substrates they were on, were analysed. We equate the substrates chosed by the organisms with their preferred prey item. Day/night activities were based on the time of sunrise and sunset (Tab. 1; www.sun.exnatura.org).

Table. 1: Time of sunrise and sunset (www.sun.exnatura.org)

Date	Sunrise a.m.	Sunset p.m.	Sunlight hours
15.08.2009	04:04	06:14	14:09
16.08.2009	04:05	06:12	14:06
17.08.2009	04:06	06:10	14:04
18.08.2009	04:08	06:09	14:01
14.09.2009	04:41	05:19	12:38
15.09.2009	04:42	05:17	12:35
16.09.2009	04:43	05:15	12:32
17.09.2009	04:44	05:13	12:29

2.3.2 Longer-term recovery

The longer-term recovery experiments were conducted on the same two 0.25 m² plots used for the short-term time-lapse camera study. For this aspect, the surface area occupied by living sponges and ascidians, as well as by other hard structures and lebensspuren, was measured inside the closed chamber and days to years after anoxia with CorelDraw9. The objects were classified into seven categories: 1) sessile fauna (living), 2) sessile fauna (dead), 3) anemones (the latter three summarized as sessile fauna (living/dead)), 4) shells of bivalves, 5) shells of gastropods (the latter two summarized as shells), 6) little pieces of shells and areas covered with many tightly packed shells (termed coquina) and 7) lebensspuren. We also documented new colonizers.

The experiments started on two different months and the images were taken at various times. The various times when the images were taken were categorized into corresponding timeframes so that the data of both experiments could be compared (Tab. 2). For reasons of simplification, 7-13 days is termed “10-days” in the following text. The logarithmic x-axis for the long-term recovery figures uses the mean value of the respective days of both experiments.

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

Table 2: Days after anoxia (removal of the chamber) of both experiments; same day as chamber removal is termed 0.

Experiment August 2009	0	4	6	7
Experiment September 2009	2	3	6	13
Average used in figures	1	4	6	10

2.4 Statistical analyses

The distinct sequence of the arrival of predators and scavengers and the preferences for certain prey items (“preferred substrates”) were documented on Excel sheets (Microsoft). To define the residence time of gastropods and hermit crabs in the plots, time series analyses and cross-correlations were calculated with Past. To determine the difference in the substrates chosen by gastropods and hermit crabs and between the experiments, a Chi² test was calculated with Past.

3 Results

3.1 Short-term scavenging after anoxia

Image analyses

Moribund and dead sponges and ascidians attracted fishes, hermit crabs and gastropods in a rapid and distinct sequence. Figure 11 shows the originally enclosed part of the macrobenthic community 19.5 h after the chamber that created anoxia was removed (August experiment). The open frame (no plexiglass walls and therefore normoxic conditions restored) surrounds the dead multi-species clump. The sediment was still darker colour inside the frame than outside, reflecting the H_2S development (maximum in August experiment 23 µM, maximum September 30 µM during the anoxia.

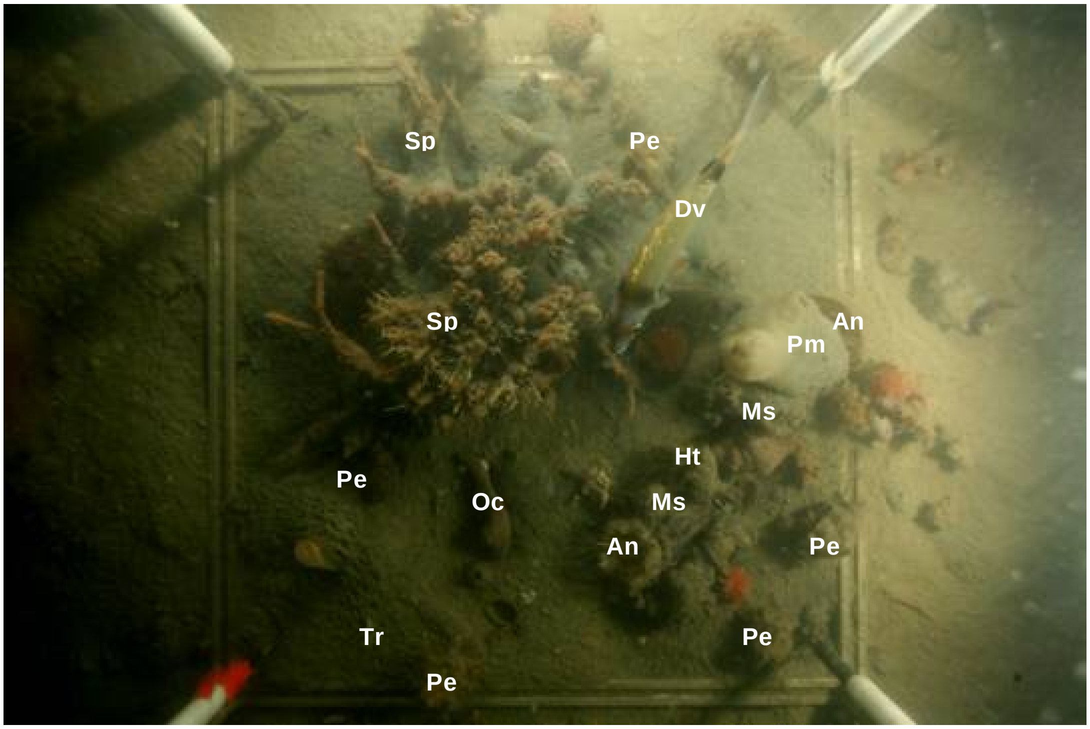


Figure 11: Open configuration, experiment August 2009, film number 1, 16.08.2009, image 8345; multi-species clump approximately 19.5 h after anoxia. Note darker sediment colour inside frame (max. H_2S: 23µM). Organisms: **An**: anemone, **Dv**: *Diplodus vulgaris*, **Ht**: *Hexaplex trunculus*, **Ms**: *Microcosmus* sp., **Oc**: *Ocnus planci*, **Pe**: *Paguristes eremita,* **Pm**: *Phallusia mammillata*, **Sp**: sponge, **Tr**: track of *Paguristes eremita*

Numerous fishes arrived very quickly 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 (Figs. 12 & 13), with a slow increase of individuals. In the second experiment (September 2009), 7 *Hexaplex trunculus* survived the anoxia (Fig. 18) and were present and visible from the start. One *Hexaplex trunculus* arrived after 30 min, but 3 left after 1 h. Only then did the number of individuals begin to increase with time. In the first experiment (August 2009), several *Paguristes eremita* dragged off (about 11 cm in 53 h) and consumed the ascidian *Phallusia mammillata* (Fig. 14).

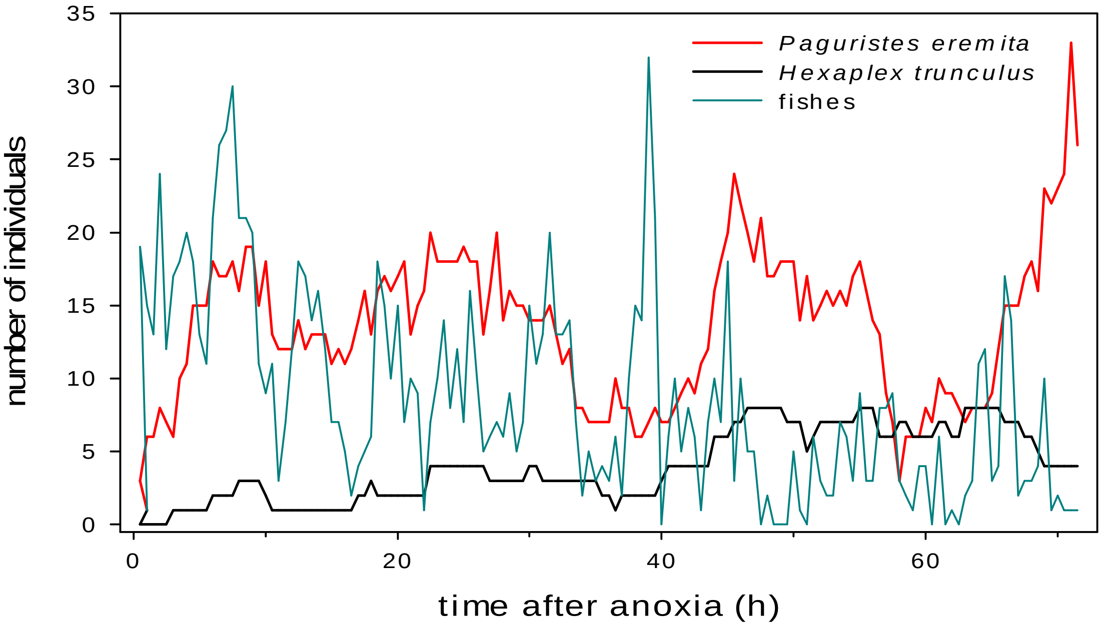


Figure 12: Arrival and presence of predators and scavengers: fishes, hermit crabs and gastropods after anoxia (August 2009 experiment).

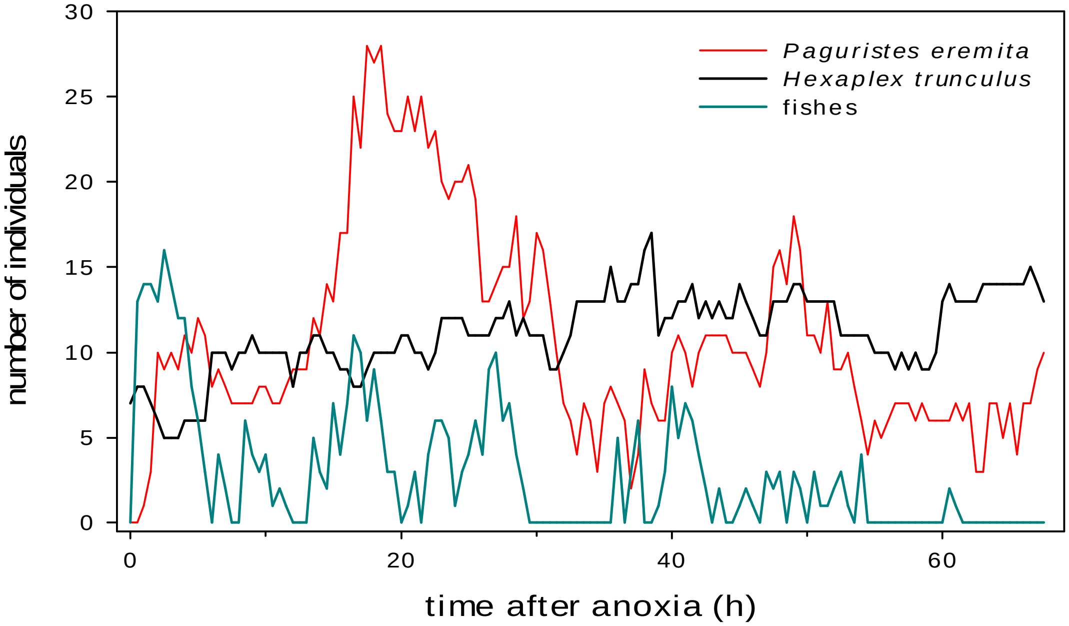


Figure 13: Arrival and presence of predators and scavengers: fishes, hermit crabs and gastropods after anoxia (September 2009 experiment).

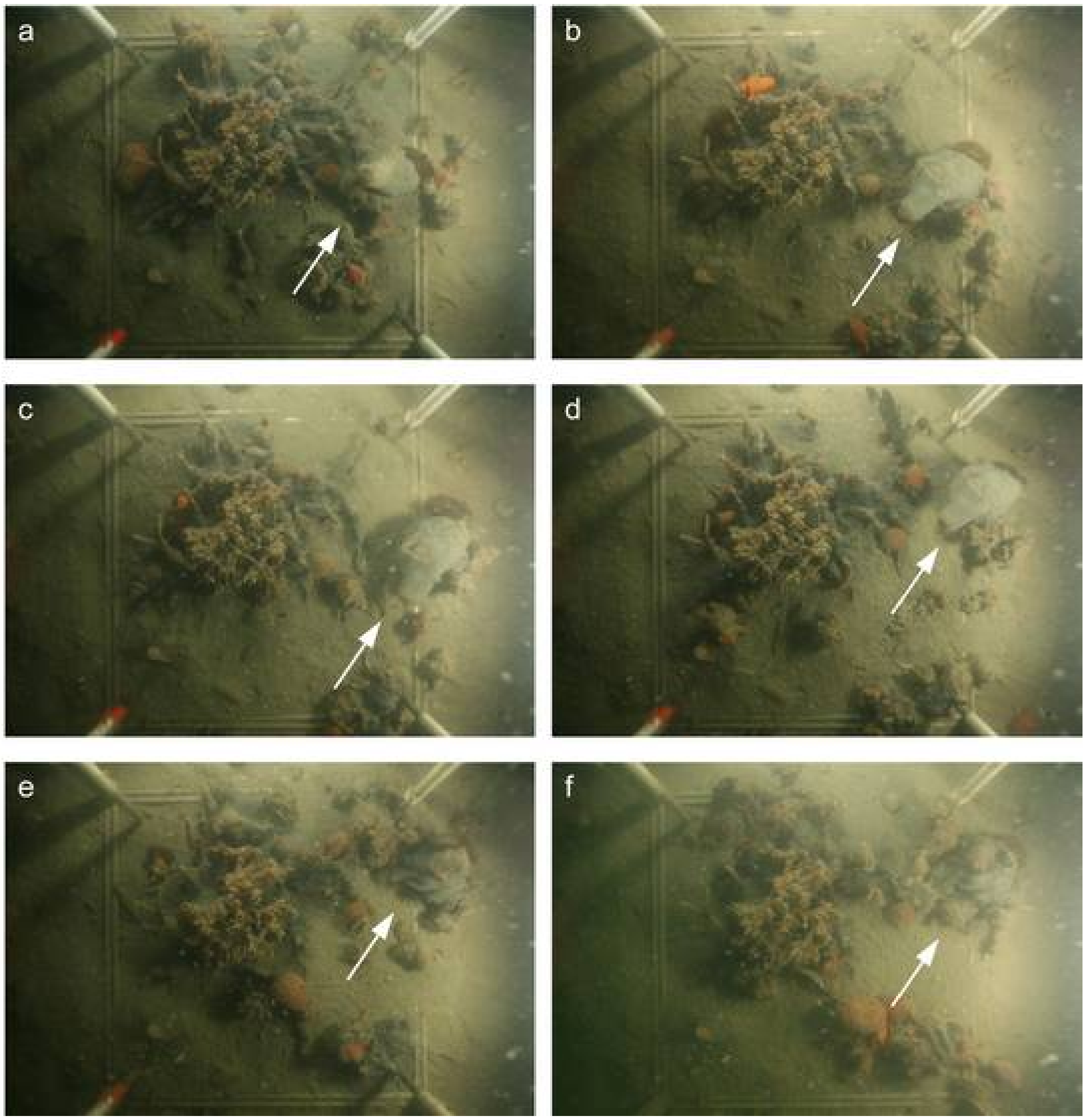


Figure 14: Hermit crabs carry away *Phallusia mammillata* (white arrow) after anoxia. Duration from top left to right bottom approx. 53 h, distance displaced about 11 cm (Experiment August 2009).

3.1.1 The fishes

In the August 2009 experiment we observed three different species, *Diplodus vulgaris*, *Serranus hepatus* and *Gobius niger*, and in the September 2009 experiment additionally *Pagellus erythrinus*. The individuals present were summarized in 6-h steps. In both experiments, all species were present in the first six hours in the largest numbers (Figs. 15 & 16).

Gobius niger had the most individuals and showed a slowly decreasing trend. The other species decreased rapidly with time to very low numbers. All species were never together in one image.

In the first 6 h of the August experiment, all three species were present: *Gobius niger* with 83 individuals, *Diplodus vulgaris* with 35 and *Serranus hepatus* with 26 individuals. The two latter species subsequently decreased to very low numbers. *Gobius niger* also decreased with time, but never fell below 22 observed individuals per 6 h (i.e. total number visible over this time period, not necessarily different individuals, see Material and Methods) The maximum number of *Gobius niger* (103) were observed from 6 to 12 h after anoxia. (Fig. 15). In the September experiment, all four species were initially present (in the first 6-h time step) and then decreased to a low number of individuals, including *Gobius niger*. The maximum number of *Gobius niger* (80) were observed during the first 6 h. *Diplodus vulgaris*, *Serranus hepatus* and *Pagellus erythrinus* were by far most frequent in the first 6 h (Fig. 16).

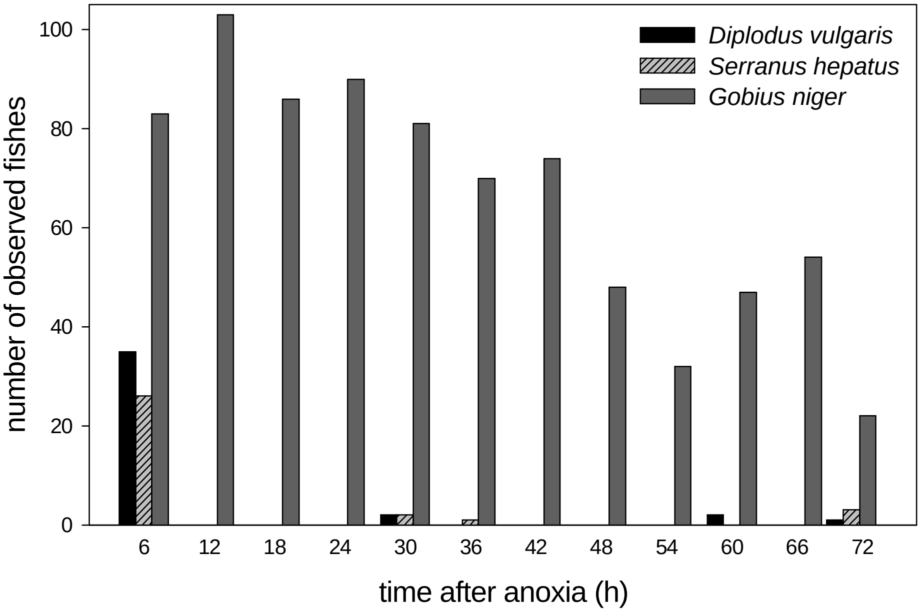


Figure 15: Post-anoxia fish abundance in August 2009 experiment. Counts summarized in 6-h steps.

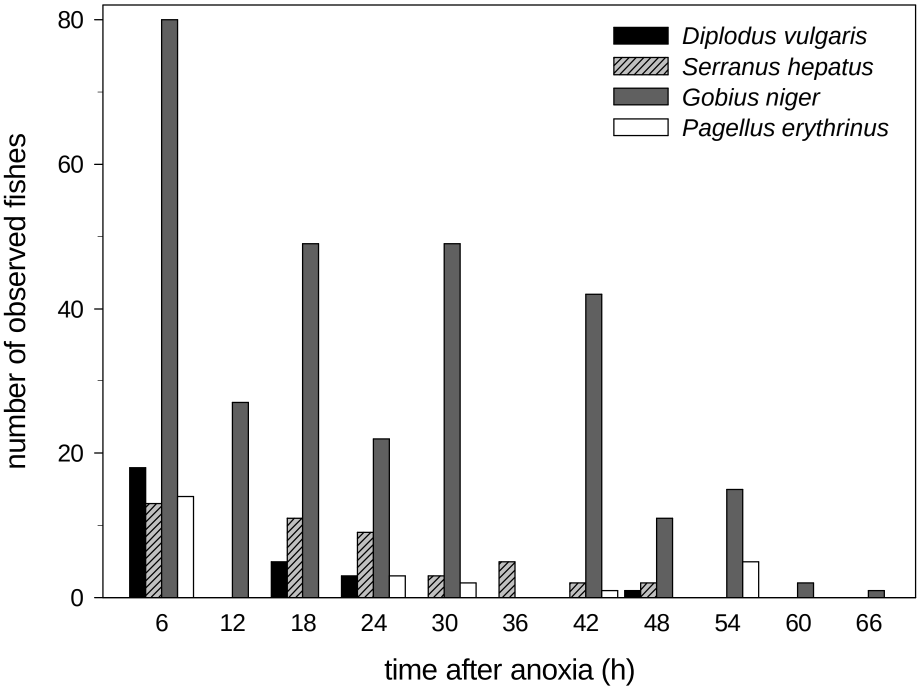


Figure 16: Post-anoxia fish abundance in September 2009 experiment. Counts summarized in 6-h steps.

3.1.2 The first 12 hours: 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 the August experiment, 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. 17).

The first *Paguristes eremita* in the September experiment appeared after 1 h, and hermit crab numbers then increased up to 12 after 6 h, decreasing again after 6 h and 30 min. As noted above, seven *Hexaplex trunculus* survived the anoxia. After 30 min the first new gastropods entered the frame (Fig. 18). From the opening of the chamber until 2 h and 30 min afterwards, the number of gastropods decreased to 5 Individuals. Thereafter, the number increased steadily.

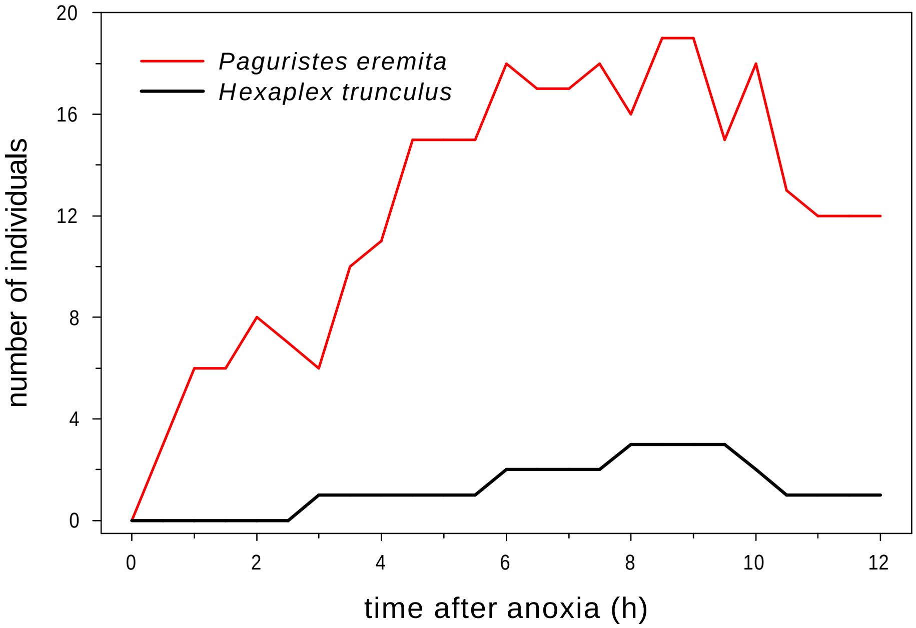


Figure 17: Presence of *Paguristes eremita* and *Hexaplex trunculus* within the first 12 h after anoxia (August 2009 experiment).

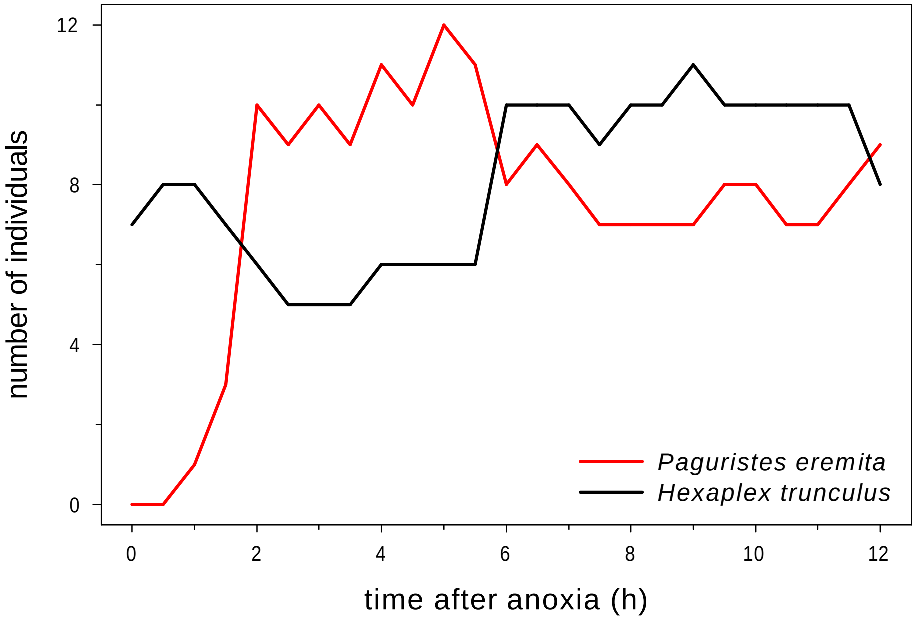


Figure 18: Presence of *Paguristes eremita* and *Hexaplex trunculus* within the first 12 h after anoxia. Seven *Hexaplex trunculus* survived the anoxia and were present from the onset (September 2009 experiment).

3.1.3 Day/night activity of hermit crabs and gastropods

In both experiments the number of *Paguristes eremita* varied considerably. The values decreased in all three nights examined and increased conspicuously during daylight hours (Fig. 19). During daylight hours the number of individuals in August increased to 24 after 45.5 h and to 33 after 71 h. During the night hours, values decreased to 6 after 38 and 38.5 h and to 3 after 58 h. In September, the highest number of individuals was observed during daylight hours, peaking at 28 individuals 17.5 and 18.5 h after the artificial anoxia. The fewest hermit crabs were observed during night hours: only 2 individuals after 37 h and 3 after 62.5 and 63 h. In contrast, *Hexaplex trunculus* showed a relatively slow but constant increase with no day/night rhythm (Fig. 19). The maximum number of this gastropod was 8 individuals after 46.5-49 h, 55-56 h, and 63-65.5 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) *Hexaplex trunculus* were still present in the plots.

The time series analyses of the residence time show a highly significant (p=0.01) peak at 21 h and a significant (p=0.05) peak at 12 h for *Paguristes eremita* in August (Appendix, Fig. 27 & Tab. 5). For September, the analysis yielded somewhat different results. The first highly significant peak for *Paguristes eremita* is at 54 h, the second at 28 h. Another peak is recognizable at 11 h, but is just below significance (Appendix, Fig. 28 & Tab. 6). The residence time of *Hexaplex trunculus* in the plot indicates a 9 h, respectively a multiple of 9 h rhythm (Appendix, Fig. 29 + 30 & Tab. 7 + 8).

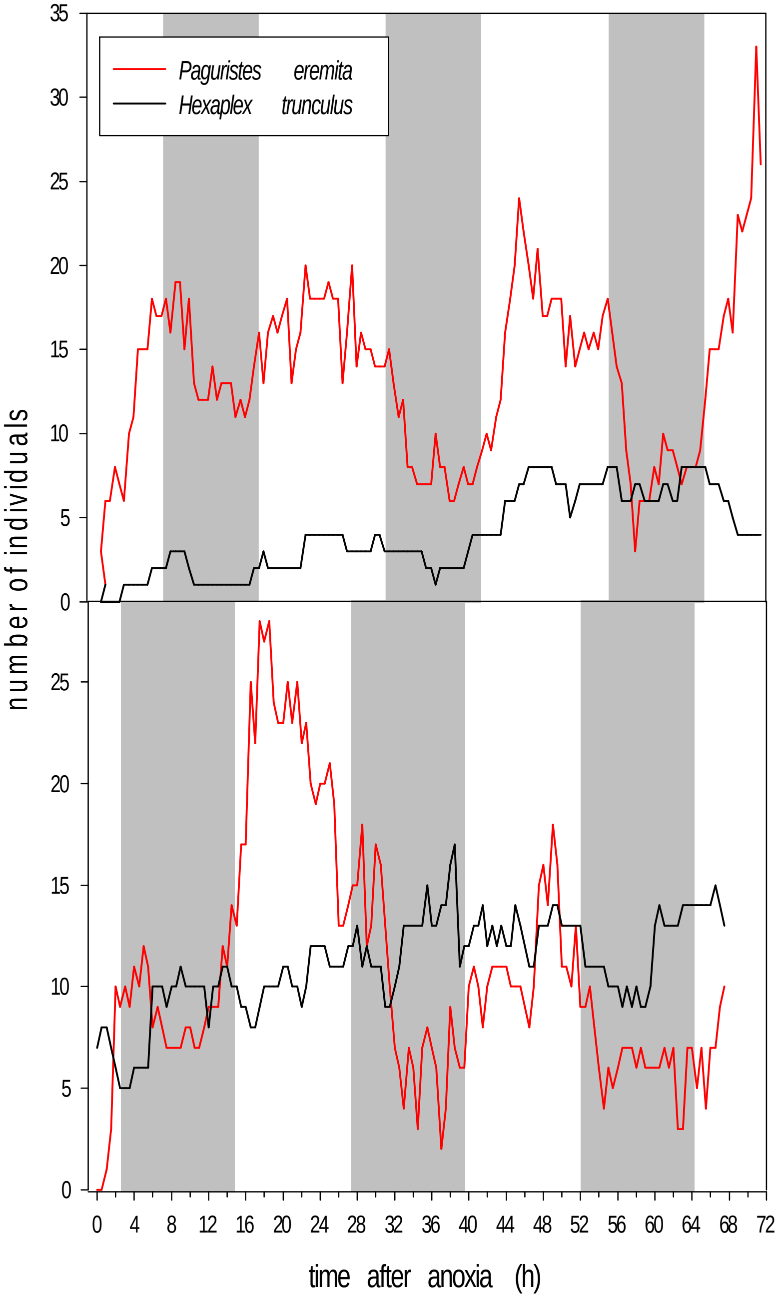


Figure 19: Day/night activity of *Paguristes eremita* and *Hexaplex trunculus* after anoxia. White bars mark daylight hours, grey bars night hours. Above: August 2009 plot, below September 2009 plot. Night is about 1 h 30 min longer in September.

3.1.4 Preferred substrates/prey items

The substrates that *Paguristes eremita* and *Hexaplex trunculus* chose were different, and the results were similar in both experiments. We equate the (moribund/dead) organisms on which these two species were observed with their preferred prey. Hermit crabs were observed on the sediment, on sponges and on ascidians, whereas *Hexaplex trunculus* occurred mainly on ascidians and to a lesser extent on the sediment (Fig. 20). All categories (i.e. compared species-experimental month pairs) are significantly different from each other. Nonetheless, there are bigger interspecific than intraspecific differences, i.e. the differences between the species (*Paguristes eremita* in August and September versus *Hexaplex trunculus* in August and September) are bigger than between the months (*Paguristes eremita* in August versus September and H*exaplex trunculus* in August versus September) (see Chi² values, Tab. 3).

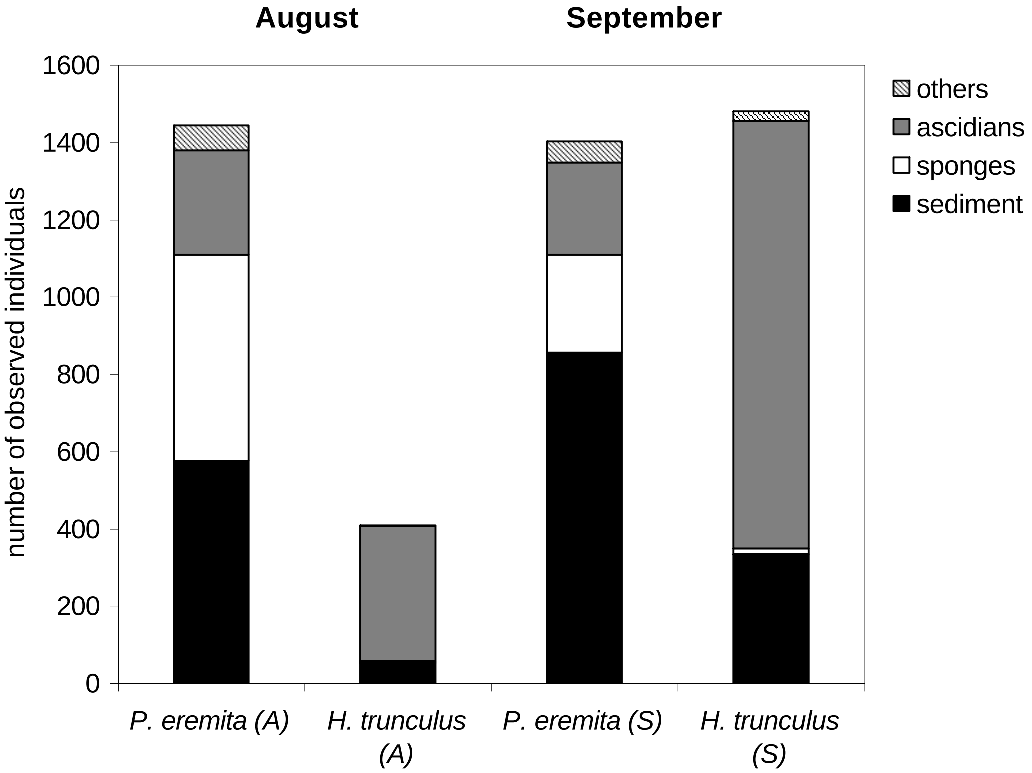


Figure 20: Substrates/prey chosen after anoxia by *Paguristes eremita* and *Hexaplex trunculus* in the August 2009 (A) and September 2009 (S) experiments.

Table 3: Statistical analysis of the Chi² test. Differences between categories of chosen substrates/prey by *Paguristes eremita* and *Hexaplex trunculus*.

	Chi²	p
P. eremita Aug09 vs. ***P. eremita*** Sept09	156.75	7.28E-33
H. trunculus Aug09 vs. ***H. trunculus*** Sept09	24.779	5.57E-05
H. trunculus Aug09 vs. ***P. eremita*** Aug09	660.55	1.21E-141
H. trunculus Sept09 vs. ***P. eremita*** Sept09	1010.2	1.12E-218
P. eremita Aug09 vs. ***H. trunculus*** Sept09	1084.1	2.07E-233
P. eremita Sept09 vs. ***H. trunculus*** Aug09	687.74	1.57E-147

The duration of the stay of 9 *Paguristes eremita* and 9 *Hexaplex trunculus* individuals was calculated (Tab. 4). The individuals were randomly chosen, whereby clearly recognizable individuals (e.g. with epigrowth such as sponges) were preferred. This duration averaged 5 h and 19 min for *Paguristes eremita* and 12 h and 9 min for *Hexaplex trunculus*. Thus, on average, the gastropods stayed nearly 7 h longer than the hermit crabs.

Table 4: The duration of the stay after anoxia. *Paguristes eremita* n=9; *Hexaplex trunculus* n=9

	Paguristes eremita	***Hexaplex trunculus***
Mean value	5 h 19 min	12 h 09 min
Standard deviation	0.263	0.177

3.2 Anemone

The sea anemone *Cereus pedunculatus* (August experiment), which was positioned in the sediment next to a sponge, began to crawl away 66 h and 15 min after the end of the artificial anoxia (opening) (Fig. 21). At the end of the short-term evaluation (71.5 h) the anemone was still positioned inside the frame. During the longer-term evaluation the anemone was visible on the images of 18 and 22 August (post-anoxia days 0 (day of chamber removal) and 2). Two days later the anemone disappeared from the images.

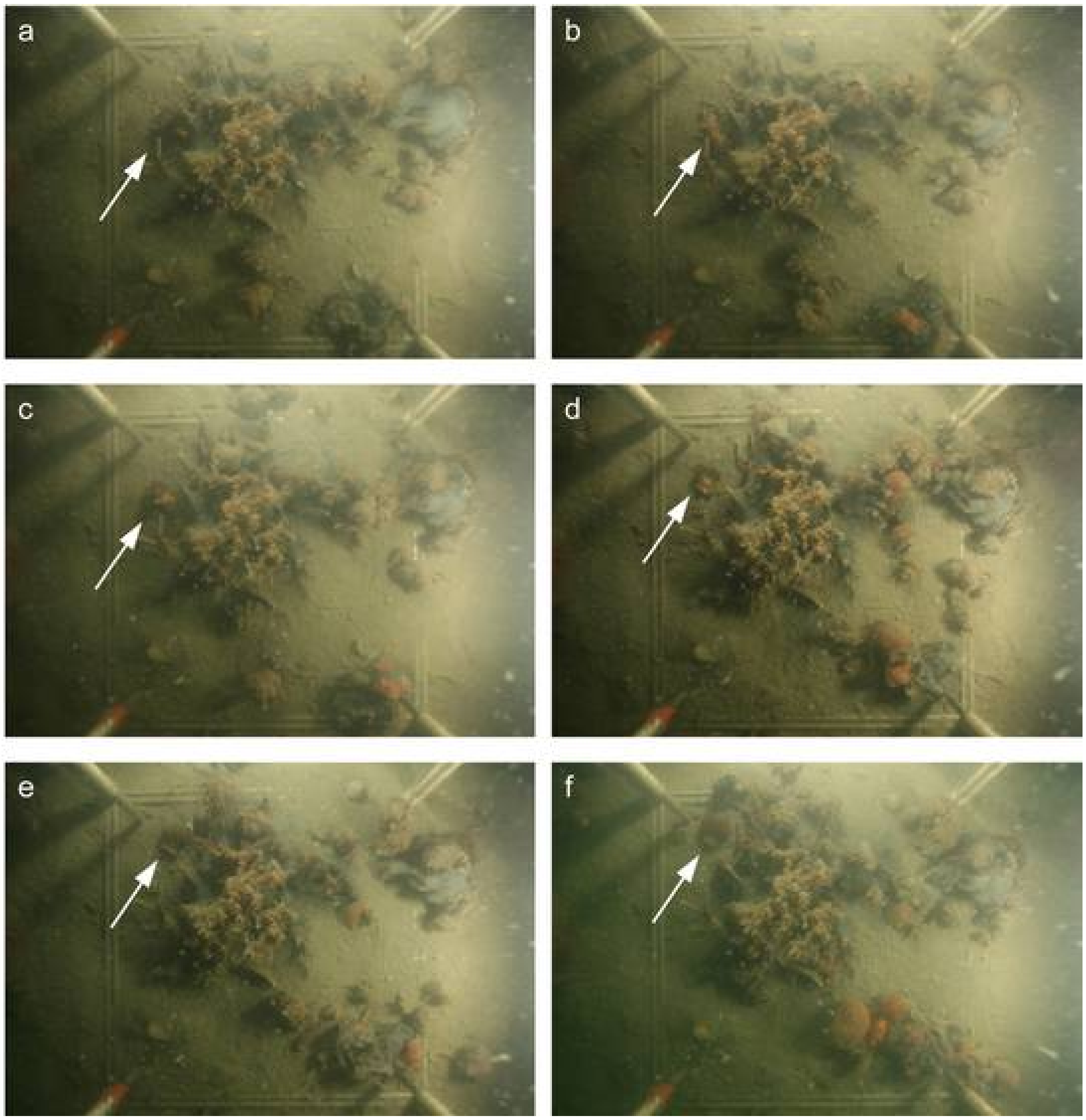


Figure 21: Moving *Cereus pedunculatus* (Pennant, 1777) 62 h after anoxia in the August 2009 experiment. Time from first (top left) to last image (bottom right): 5 h and 24 min.

3.3 Longer-term recovery

The surface area of each experimental plot was 2500 cm². At the start of the experiment (inside the chamber, measured as the baseline) in 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). Within the first 6 days, both the sessile and the vagile fauna decreased. The sessile fauna coverage decreased to 12 cm² (0.5%) and the vagile fauna to 155 cm² coverage (6%) (Fig. 22, top). In the September experiment, the initial coverage of sessile fauna was 631 cm² (25%) and of vagile fauna 663 cm² (26.5%). As in August, both fauna groups decreased drastically. After 6 days, the coverage of sessile fauna fell to 286 cm² (11.5%), that of vagile fauna to 154 cm² (6%) (Fig. 22, bottom). In the "10-day" category, nearly the whole fauna was removed (sessile) or had crawled away (vagile). In both experiments the trends in the coverage of the vagile fauna paralleled that of the sessile fauna. Both 1 and 2 years after the start of the experiment, no macroscopic sessile epifauna was observed on either plot. The exception was one anemone in the September experiment: it survived the artificial anoxia and was still present in both following years.

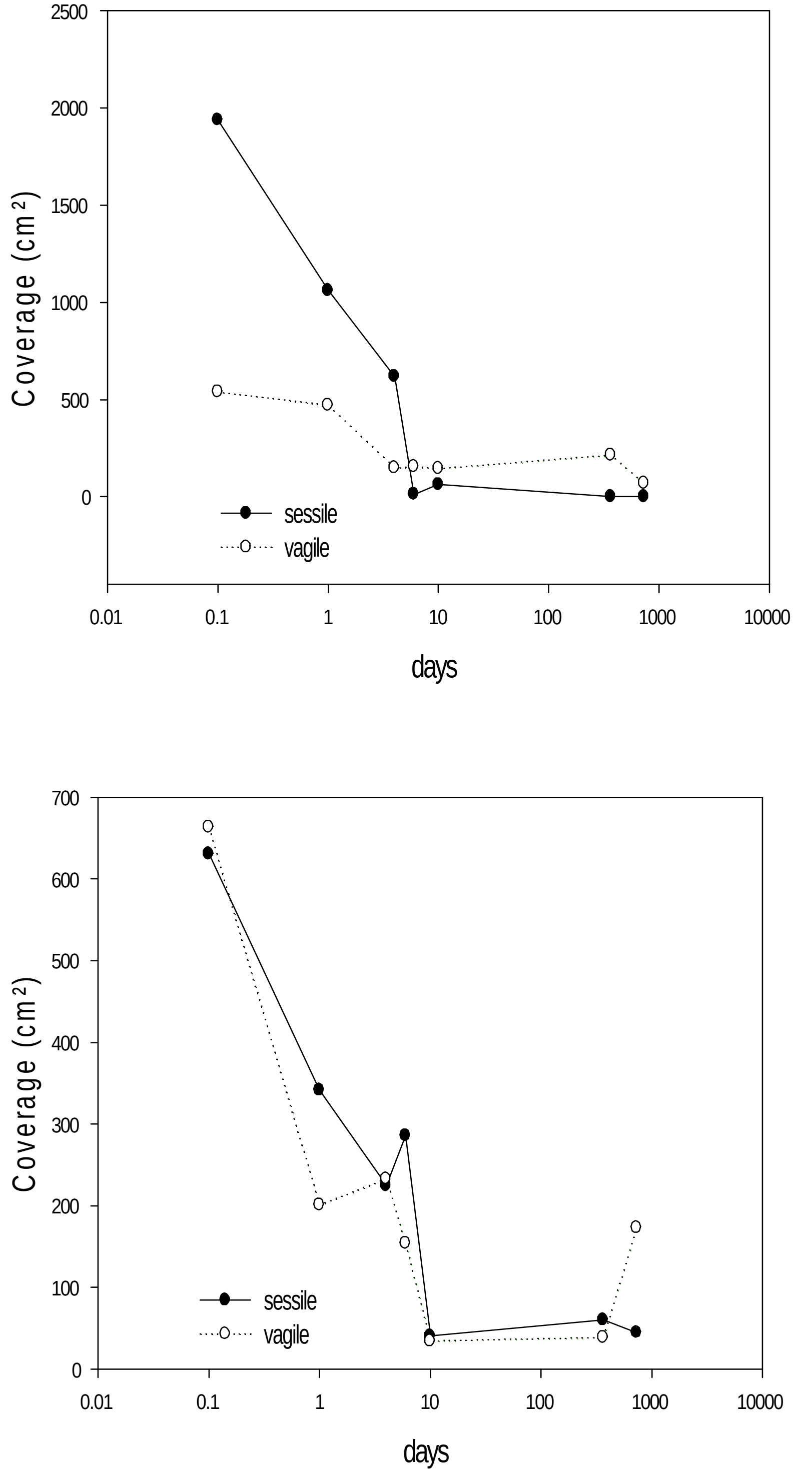
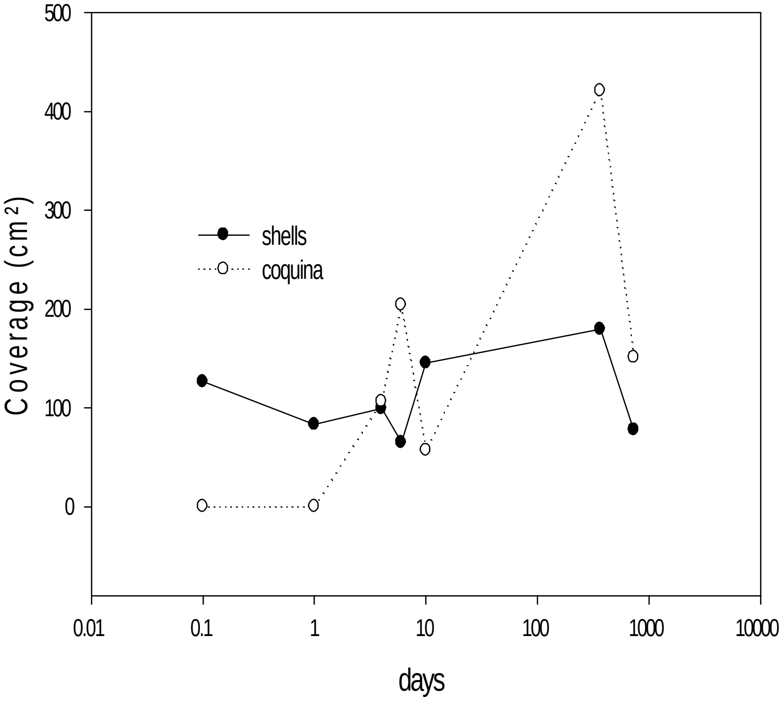


Figure 22: Coverage of sessile (dead and living) and vagile fauna after anoxia of the August 2009 (above) and September 2009 (below) plot. Note different scales on y-axis. Start of experiment defined as 0.1 and measured inside closed chamber (original coverage).

The coverage of the plots by shells increased in both experiments within the first “10-days”. At the start of the August experiment, no coquina was observed, but after 3-4 days the coverage increased. After “10-days” it decreased to 57 cm^2, followed by a peak of 421 cm^2 after 1 year (Fig. 23, top). In the September experiment, the coquina coverage was considerably higher than in the August experiment. Within the first 2 days the coverage decreased, but afterwards it steadily increased, with a peak of 948 cm^2 after 2 years (Fig. 23, bottom). In both experiments the coverage of shells remained similar within the first “10-days”. After 1 year the value increased to 180 cm^2, with a drop after 2 years to 78 cm^2 in the August experiment. In the September experiment, shell coverage decreased 1 and 2 years after the anoxia, with a minimum of 56 cm^2 after 2 years.



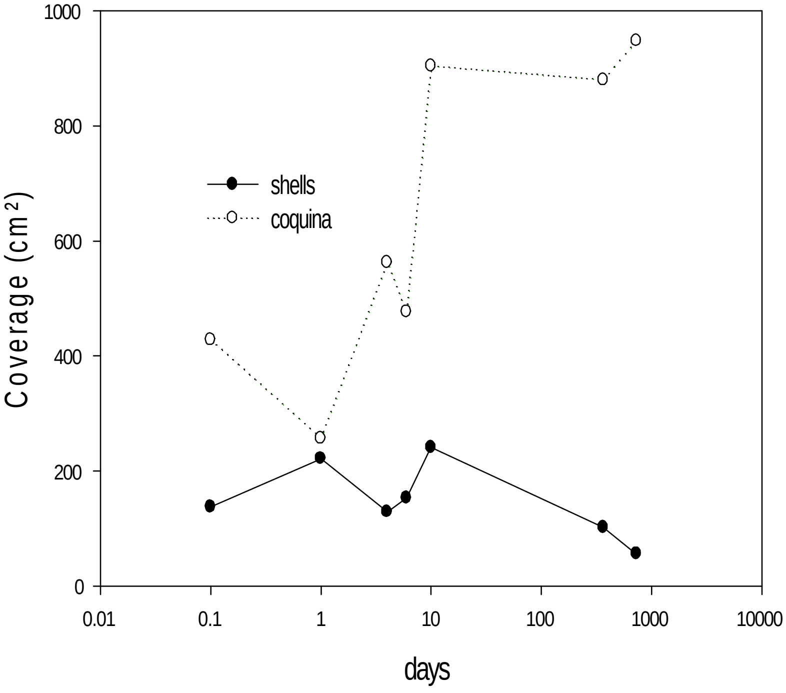


Figure 23: Coverage of shells and coquina after anoxia of the August 2009 (above) and September 2009 (below) plot. Note different scales on y-axis. Start of experiment defined as 0.1 and measured inside closed chamber (original coverage).

Between 1 year (365 days) and 1 year + 10 days (375 days) a drastic increase of coquina was recorded. The coverage increased from 0 to 842 cm² in the August experiment and from 261 to 1499 cm² in the September experiment (Fig. 24).

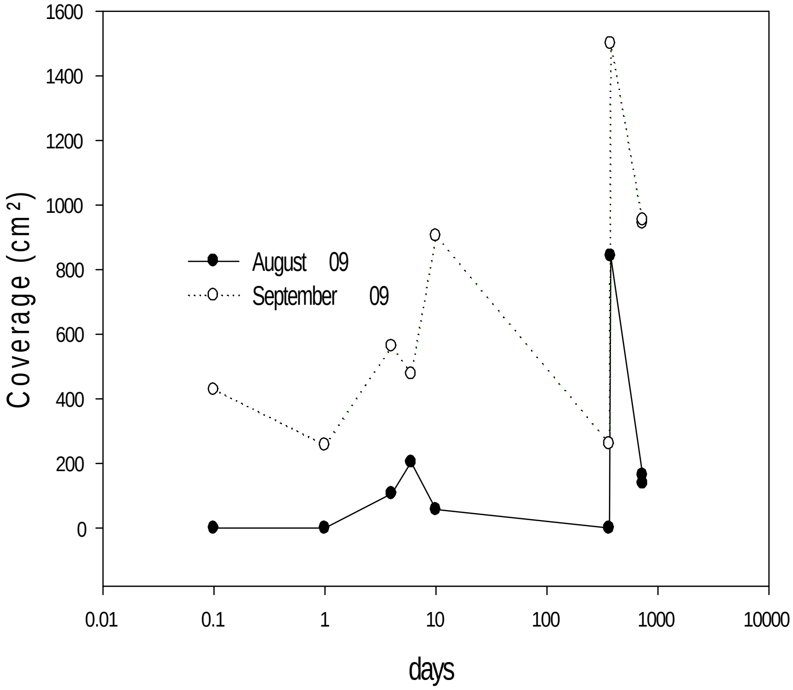


Figure 24: Coverage of coquina after anoxia. August 2009 versus September 2009 plot. Start of experiment defined as 0.1 and measured inside closed chamber (original coverage).

At the start of both experiments, shell coverage was 127 (August) and 138 cm² (September). Both values strongly fluctuated, in August between 65 and 145 cm² and in September between 56 and 241 cm² (Fig. 25).

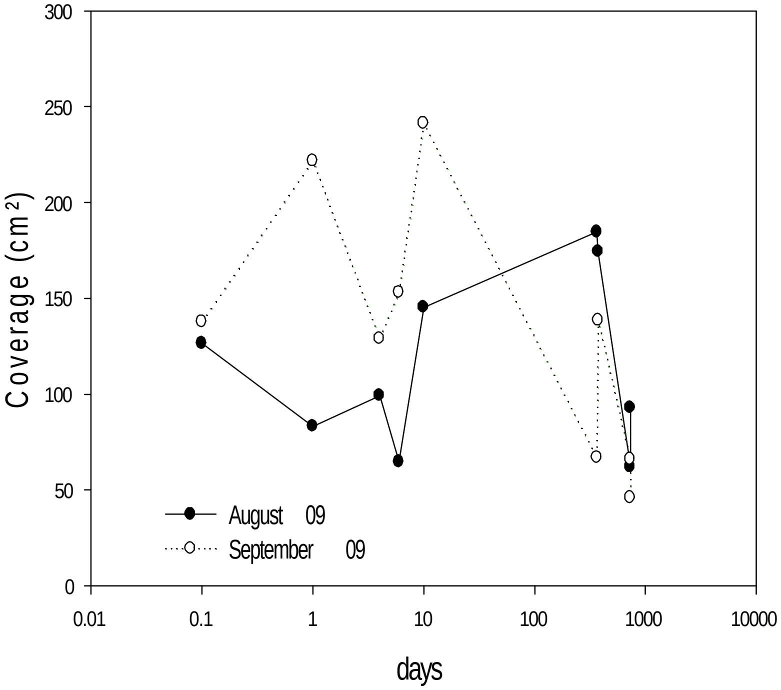


Figure 25: Coverage of shells after anoxia. August 2009 versus September 2009 plot. Start of experiment defined as 0.1 and measured inside closed chamber (original coverage).

The coverage by lebensspuren (vagile fauna, endofauna burrow openings etc.) in the September experiment ranged between 418 and 1360 cm² (Fig. 26). Insufficient visibility prevented evaluating lebensspuren on one date (6 days after removing the chamber) in September. The August experiment could not be evaluated because of poor visibility during the first 7 days after chamber removal.

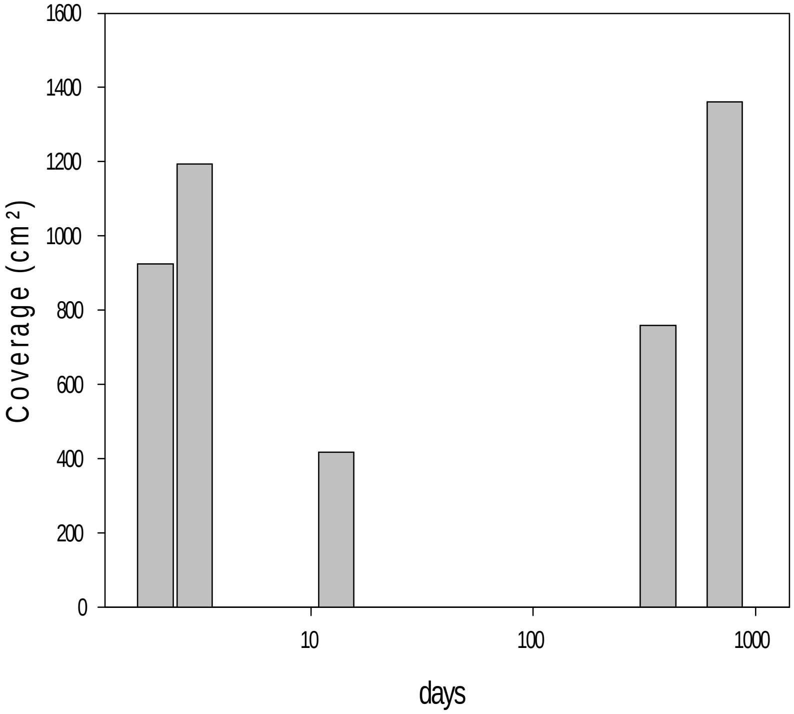


Figure 26: The coverage of lebensspuren after anoxia during the September 2009 experiment (no value on day 6 due to poor visibility).

4 Discussion

Coastal habitats are probably the marine ecosystems worst affected by hypoxia/anoxia due to human impacts. The numbers of affected areas has increased very rapidly worldwide in recent decades (Diaz & Rosenberg, 2008). 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 ecosystem (Ott & Fedra, 1977). Recolonization of such benthic communities in the Gulf of Trieste is very slow (Stachowitsch, 1991) and recovery of marine ecosystems with slow successions could take 40 years or even longer (Jones & Schmitz, 2009).

The present study extends prior investigations on the behavioral responses to artificial anoxia induced by the EAGU (Stachowitsch et al., 2007, Riedel et al., 2008a; Riedel et al., 2008b; Haselmair et al., 2010; and Pretterebner et al., 2011) and helps fill in the gap between ecosystem collapse and full 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 evaluation of the images revealed a clear sequence of predators/scavengers (Figs 12 & 13). The arrival of fishes as the first predators/scavengers after the artificial anoxia (removal of the EAGU chamber) is attributed to their swimming speed. Clearly, the speed of the earliest arrivers (e.g. *Diplodus vulgarise*: 12.3 cm.s^{-1}; Planes et al., 1997) is 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* is apparently the slowest of these three species. Erlandsson and Kostylev (1995) calculated the speed of another marine gastropod, *Littorina* *littorea*, to be 2.88-4.47 cm.min^{-1}. Hence, the speeds of the hermit crabs and gastropods may be similar. In such cases, the arrival times would also depend on the densities of the respective species, whereby more abundant species would have a greater probability of having individuals closer to the experiment plots. In the ORM-community in the Northern Adriatic Sea, *Paguristes eremita* has a density of 2.4 individuals m^{-2} (transect method: Pretterebner et al., 2011), which is slightly higher than in an earlier quadrat sampling (1.9 individuals m^{-2}; Stachowitsch, 1977). *Hexaplex trunculus*, in 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. Detached mussels are therefore abundant directly under the buoy. Accordingly, the density of *Hexaplex trunculus,* which feeds on such mussels, is also very high around the buoy. Without this bias, we would expect the gastropods to arrive in significant numbers at a much later date.

Fishes were conspicuously abundant in the first six hours after opening the chamber. At this time, the most food items were available, including smaller soft-bodied organisms emerging from the sediment and from sponges and other multi-species clumps. The fishes were dominated by *Gobius niger*, which feeds on polychaetes, amphipods, mysids and decapods (Richards & Lindeman, 1987). *Pagellus erythrinus* mainly preys on benthic organisms such as polychaetes, brachyuran crabs and benthic crustaceans (Fanelli et al., 2011). *Serranus hepatus* feeds on invertebrates, mainly decapods (Labropoulou & Eleftheriou, 1997). Finally, in the Adriatic Sea, *Diplodus vulgaris* prefers benthic echinoids such as *Echinocyamus pusillus* (O. F. Müller, 1776) and *Psammechinus microtuberculatus* (Blainville, 1825), but also consumes decapods and bivalves (Pallaoro et al., 2006). In the experiments, *Paguristes eremita* and *Hexaplex trunculus* apparently mainly fed on material that remained after the fishes had already been present for several hours. Based on the positions of the crabs and gastropods, this was mainly ascidians and sponges. The time-lapse camera approach was unable to provide direct evidence that the fishes fed on sponges or ascidians, i.e. the act of feeding was never captured in an image, although in many cases the fish were positioned in an oblique angle with the mouth facing down. Ascidians rely on chemical (Lindquist et al., 1992; Pawlik et al., 1993) and physical defences (tunic spicules, Lambert & Lambert, 1987 and tunic toughness, Koplovitz & McClintock,

2011) against predation, but the efficacy and strategies vary greatly between species (Tarjuelo et al., 2002). Both mechanisms may still be partly effective in freshly dead individuals, as in our experiments. Young (1989b) observed ascidians being eaten by gastropods, which insert their proboscis into a siphon of the ascidians and consume them. The present time-lapse evaluation showed some *Hexaplex trunculus* on the siphon of *Microcosmus* ssp., but other individuals were also positioned on other parts of the ascidians.

To better determine which food sources *Paguristes eremita* and *Hexaplex trunculus* prefer, we evaluated the different substrates on which they positioned themselves. We equate the (moribund/dead) organisms on which these two species were observed with their preferred prey. Our experiments show that, while both species feed on sponges and ascidians, *Hexaplex trunculus* was much more frequently positioned on *Microcosmus*. Thus, the interspecific differences were greater than intraspecific differences, i.e. the differences between the species are bigger than between the two experiments. Nevertheless all categories (*Hexaplex trunculus* – August, *Hexaplex trunculus* – September, *Paguristes eremita* – August, *Paguristes eremita* – September) are significantly different from each other. The time-lapse observations in August also showed *Paguristes eremita* dragging off and consuming an ascidian (*Phallusia mammillata*) (Fig. 14). *Hexaplex trunculus*, in contrast, crawled up the ascidians and typically remained there for several hours: on average, the gastropods stayed within the frame about 7 h longer than the crabs. This would confirm the results of Sawyer et al. (2009), who documented 10.5 h, 5.2 h and 2.9 h for feeding and manipulating the prey in three selected specimens of *Hexaplex trunculus* individuals in the same community. Stachowitsch (1979) observed the activity behaviour of *Paguristes eremita* in the Gulf of Triest and recognized two types of interruption of movement: 1) short stops related to feeding and investigation of structures on the sediment and 2) longer pauses during the night hours reflecting a resting period.

The time series analyses indicate an almost 12 h rhythm with regard to residence time (respectively a multiple of approx. 12 h) for *Paguristes eremita*. Stachowitsch (1979), examining movement and activity of *Paguristes eremita* in this community, determined that these hermit crabs move much more during the daytime than at night. An explanation for the fewer individuals in the plot at night versus day, however, is more difficult to explain. One explanation 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.

For *Hexaplex trunculus* the time series analyses indicate a 9 h rhythm with regard to residence time (respectively showed a multiple of about 9 h rhythm), which is more difficult to explain.

Molluscs in general are considered to be more tolerant to hypoxia than many other invertebrate groups (Vaquer-Sunyer & Durate, 2008). Individuals of *Hexaplex trunculus* are able to survive 5 to 6 days of artificial anoxia initiated by the EAGU (Riedel et al., 2008). Accordingly, seven *Hexaplex trunculus* survived the oxygen depletion during the September experiment and were evaluated right from the start.

The sea anemone *Cereus pedunculatus* (August plot) crept away from its original position 66 h and 15 min after artificial anoxia (Fig. 21). Anemones, although normally firmly attached to a substrate, are known to be able to move. Mc Clendon (1905), for example, observed an anemone (*Metridium marginatum*, nomen dubium) that crept up (similar to gastropod creeping motion) the glass in an aquarium to reach a different position. Another well-known case involves hermit crabs. Ross & Sutter (1961) showed that the hermit crab *Dardanus arrosor* (Herbst, 1796) can detach the anemone *Calliactis parasitica* (Couch, 1842) mechanically by using specific behaviors. In the present experiment, the movement of *Cereus pedunculatus* cannot be explained by a symbiotic interaction, as in the case of *C. parasitica*. Nonetheless, the high density of feeding hermit crabs may have disturbed the anemone and caused it to release the attachment, emerge onto the sediment surface, and move. An alternate explanation would be that the adjoining dead sponge caused unfavourable conditions. Accordingly, the disturbance this anemone experienced after the return of normoxic conditions was apparently more severe than the effects of anoxia: in none of the many other EAGU experiments did anemones ever move away during severe hypoxia, anoxia or H_2S conditions, although they showed a series of severe stress reactions including body contractions, rotation and extension (Riedel et al., 2008).

4.2 Coverage and Recovery

Even 2 years after anoxia, no macroepibenthic recovery was observed in either of our experimental plots. Two fundamental types of benthic recolonization can be recognized, whereby their relative roles depend on the scale of habitat being recolonized. One process is larval settlement, which is necessary for the recovery of extensively damaged areas. The second process is immigration by vagile organisms, which may be more important for small-scale recovery (Günther, 1992; Pearson & Rosenberg, 1978; Whitlatch et al., 1998).

The lack of solitary individuals or colonies, much less of the characteristic aggregations of sessile sponges and ascidians (multi-species clumps), points to the difficulty in restoring community structure and function. Jones and Schmitz (2009) reported that recovery from human disturbances took longer than from natural disturbances. Based on the known historical occurrences of anoxia and related phenomena such as massive marine snow events ("mucilagine") and the accepted correlation between anthropogenic eutrophication and mass mortalities, our results are valid for both types of oxygen-deficiency related mortality and recovery scenarios. Stachowitsch (1991) observed wide-ranging mortalities during anoxia in the Northern Adriatic Sea in 1983, with an affected area of 250 km². In the Gulf of Mexico, large hypoxic areas with a size of over 15,000 km² were documented in the years after 1993 (Conley et al., 2009). Clearly, recovery depends on the extent of the destruction. Although the experimental area was very small compared with those documented during past hypoxia events, no recovery was recorded. Importantly, settlement and growth of sessile organisms depends on the presence of adequate substrates. In the Northern Adriatic, these are typically gastropod and bivalve shells and in some cases echinoderm tests (Nebelsick et al.,1997). Although shells were recorded in the two experimental plots, they were apparently not large enough, sufficiently exposed, or available at larval settlement times for an epigrowth to develop. 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.

After benthic trawling the recovery time for slowly growing sponges could take 8 years (Kaiser et al., 2006); sponge recolonization in Alaska, without further disturbances, could take decades (Rooper et al., 2011). In the Northern Adriatic Sea, the ORM-community showed little recovery at the end of 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 fishery damage by dredging and trawling (Stachowitsch, 1995; Kollmann & Stachowitsch, 2001). 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 coverage of vagile fauna was measured inside the chamber at the start of the experiment, i.e. when the vagile fauna was trapped and unable to leave the plots. After anoxia, most of the sponges and ascidians were moribund or dead and provided a food source for the vagile fauna. The high coverage of vagile fauna in relation to the sessile fauna at the start of the September experiment reflects the seven trapped *Hexaplex trunculus*. The rapid decrease of sessile fauna within the first 6 days is attributed to its consumption by the vagile fauna. The subsequent decline in food items was correlated with a corresponding drop in the vagile fauna. Six days (August plot) and 13 days (September plot) after the artificial anoxia (open EAGU), the entire sessile fauna had been removed or consumed. The coverage of the plots by vagile fauna after 1 and 2 years consisted mainly of *Paguristes eremita*, *Hexaplex trunculus*, *Psammechinus microtuberculatus* and *Ophiothrix quinquemaculata*. Kollmann and Stachowitsch (2001) consider that lebensspuren are helpful parameters to quantify community status and activity of vagile fauna. Our lebensspuren observations in the September plot revealed a coverage of between 418 and 1360 cm² (Fig. 26). 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 keep larval recruits low: grazing on and manipulation of the empty shells that the multi-species clumps initially require to grow on (Zuschin et al., 1999) could also help explain the lack of recovery.

Successful new epigrowth could also be negatively affected by sedimentation and resuspension, which buries 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, pers. observ.). 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 further resuspend sediment. All these factors may help explain the great variation in the visible coverage by shells, in turn explaining the lack of larval-based recolonization in these 2 plots. Finally, another possible reason for the decrease of shells is that sea urchins such as *Psammechinus microtuberculatus* took pieces of shells to camouflage themselves, as observed by Steckbauer (2008).

The fact that the coverage by shells and coquina varied greatly shows that the sediment surface is a very active habitat. This is determined by small-scale factors (manipulation by vagile species, sea urchin use of shells, etc.) and large-scale factors. The presence and effect of such larger-scale factors (versus those restricted to experimental-plot-size) is supported by the parallel trends in shell and coquina coverage in the two experiments, e.g. overall increase in coquina with peaks at “10-days” as well as at year 1, followed by the decline at year 2 (Fig. 24). Resuspension of finer, overlying sediment (swirled up by vagile fauna, currents, ships, fishing gear) could be a further explanation for the increase of coquina. In both experiments the coverage of coquina increased considerably after 1 year (respectively 1 year + 10 days). This was the time between 7 August and 17 August, 2010.

We consider the results obtained from the small-scale plots experiments to be valid for larger spatial scales. The distinct sequence of arrivals (in both experiments initially 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 compared to our results: immediate immigration would be slower due to the larger areas affected and greater distances involved (Stachowitsch et al., 2011), but the sequence would presumably be the same as we 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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6 Abstract

The Northern Adriatic Sea is a shallow, semi-enclosed water body which shows most features known to promote low dissolved oxygen (DO) deficiencies. Meteorological and hydrological conditions (e.g. water column stratification, slow currents) along with anthropogenic eutrophication are key factors for the development of late-summer hypoxia (low oxygen conditions) and anoxia (no oxygen). This is often associated with marine snow events. The result is benthic mortalities and altered community and ecosystem structure and function over the long-term. The macroepibenthos (dominated by sponges, ascidians, brittle stars) is additionally stressed by benthic fisheries, which can impede and/or delay full recovery of the benthic communities here.

We deployed an underwater device (EAGU, Experimental Anoxia Generating Unit) to induce small-scale anoxia and subsequently document behavioral responses and mortality sequences to decreasing oxygen and increasing hydrogen sulphide (H_2S) concentrations. In the present study, two EAGU time-lapse camera deployments (total area 0.5 m²) were examined to determine short-term post-anoxia scavenging over a 3-day period (August: 71.5 h, September: 67.5 h). Longer-term recovery (2 years) in the same plots was examined with a photo-series. Predators and scavengers arrived in a distinct sequence. The first to arrive were demersal (*Gobius niger*, *Serranus hepatus*), benthopelagic (*Diplodus vulgaris*) and pelagic fishes (*Pagellus erythrinus*), followed by hermit crabs (*Paguristes eremita*) and gastropods (*Hexaplex trunculus*). This sequence of arrival is attributed to the relative speeds of the organisms and their densities. The scavengers, for example up to 33 *P. eremita* individuals at one time, were present 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 the artificial anoxia. The hermit crabs showed a clear day/night rhythm. 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 anthropogenic disturbances such as eutrophication and damaging commercial fishing practices.

7 Zusammenfassung

Bereits im Jahr 1990 lebte fast ein viertel (23 %) der Weltbevölkerung (ca. 1,2 Milliarden Menschen) in Küstengebieten (Nicholls & Small, 2002) und die Prognose ist, dass bis 2015 weltweit etwa 33 sogenannte „Megastädte“ mit jeweils mehr als 8 Millionen Einwohnern/Stadt in Küstennähe entstehen werden (UN/DESA, 2001). Die zunehmende Besiedlung dieser Gebiete durch den Menschen hat großen Einfluss auf die Verschmutzung der Küstengewässer und die Zerstörung wichtiger Seichtwassserlebensräume. Besonders das Mittelmeer mit seiner hohen Biodiversität gilt durch menschliche Aktivitäten als stark gefährdet (Danovaro & Pusceddu, 2007).

Die Nordadria weist mehrere Eigenschaften auf, die ein sensibles Ökosystem ausmachen (Stachowitsch, 1986, 1991; Ott, 1992): geringe Wassertiefe (im Durchschnitt 30 m), Feinsediment-Böden, hoher Süßwassereintrag (v.a. Po-Fluss, Italien), lange Residenzzeit des Wassers, hohe Primärproduktion sowie eine stabile Pyknokline während der Sommermonate.

Ein Großteil des Meeresbodens der Nordadria ist von epibenthischen Lebensgemeinschaften besiedelt, deren Organismen in Form von sogenannten „multi-species clumps“ aggregiert sind. Fedra et al. (1976) hat diese Lebensgemeinschaft die *Ophiothrix-Reniera-Microcosmus* (O-R-M) community genannt, da die Gesamtbiomasse vom Schlangenstern *Ophiothrix quinquemaculata,* dem Schwamm *Reniera* spp. und der Seescheide *Microcosmus* spp. dominiert wird. Durch ihre enorme Filterleistung können diese Gemeinschaften große Mengen an suspendiertem organischem Material in der Wassersäule abbauen (Ott and Fedra, 1977) und dienen daher als „natürliche Eutrophierungskontrolle“ (Officer et al., 1982). Eine Kombination von ungünstigen hydrologischen und meteorologischen Gegebenheiten (z.B. langanhaltende, stabile Stratifikation der Wassersäule durch ruhige Wetterbedingungen) kann im Spätsommer/Frühherbst am Meeresboden, Hypoxie (Sauerstoffarmut) oder Anoxie (kein Sauerstoff), hervorrufen (Malej & Malacic, 1995). Solche Störungen können die Gemeinschaftsstruktur massiv verändern (z.B. reduzierte Artendiversität bis hin zu Massensterben, (Stachowitsch, 1984, 1991) und die ursprüngliche ökosystemare Funktion schwächen (Wu, 2002; Helly & Levin, 2004;

Diaz and Rosenberg, 2008; Riedel et al., 2008; Breitenburg et al., 2009; Levin et al., 2009; Middelburg & Levin, 2009; Zhang et al., 2010).
Durch das Zusammenspiel von Wasserstratifizierung und dem einbringen enormer Mengen an Nährstoffen (Eutrophierung) durch große Flüsse in Küstenregionen, werden die Auswirkungen von Phytoplanktonblüten verstärkt, und können in weiterer Folge zu Hypoxien/Anoxien am Meeresboden führen (Nixon, 1995; Rabalais et al. 2010; Zhang et al. 2010). Diaz and Rosenberg (2008) beschrieben mehr als 400 durch Überdüngung entstandene „Todeszonen“, die eine Fläche von insgesamt mehr als 245.000 km² umfassen. Zudem führt kommerzieller Fischfang mit Bodenschleppnetzen zu negativen Veränderung seichter Meeresökosysteme (Jennings & Kaiser, 1998; Thrush & Dayton 2002; Thrush & Dayton 2010). Auch in der Nordadria sind negative Auswirkungen von geringen Sauerstoffkonzentrationen im Meer auf die O-R-M-Gemeinschaft dokumentiert (Kollmann & Stachowitsch, 2001, Fuchs and Stachowitsch, 1995). Oft wird die erste Phase der Wiederbesiedelung nach einer Störung von juvenilen Stadien, mobilen Arten und schnellen Kolonisten dominiert (Pearson & Rosenberg 1978; Dayton et al., 1995). Zwei Hauptmöglichkeiten der Wiederbesiedlung können unterschieden werden: durch Ansiedlung freischwimmender Larven (großflächig betroffenen Gebiete), sowie Migration mobiler Organismen (kleinflächige Gebiete) (Günther, 1992; Pearson & Rosenberg, 1978; Whitlatch et al., 1998). Damit auf Weichböden, wie sie in der Nordadria typisch sind, jedoch neue „multi-species clumps“ entstehen können, werden Hartstrukturen (z.B. Muschel- oder Seeigelschalen) als Aufwuchssubstrat benötigt. Durch Sedimentation und Bodenschleppnetze können Schalenstücke jedoch mit Sediment überlagert oder gewendet werden, und damit neu entstehende „multi-species clumps“ wieder zerstört (Stachowitsch and Fuchs, 1995).

Mit einem an der Universität Wien entwickelten Unterwassergerät (EAGU, Experimental Anoxia Generating Unit) welches mit einer Zeitrafferkamera sowie Messsensoren für Sauerstoff, Schwefelwasserstoff, Temperatur und pH ausgestattet ist, wurden die Reaktionen (z.B. Verhalten, Interaktion, Mortalität) benthischer Organismen hinsichtlich Hypoxie und Anoxie dokumentiert (Stachowitsch et al., 2007, Riedel et al., 2008a, Riedel et al., 2008b, Haselmair et al. 2010, Pretterebner et al. 2011). In dieser Studie wurde EAGU eingesetzt um die unmittelbaren Entwicklungen nach einer künstlich induzierten Sauerstoffarmut zu untersuchen. Auf zwei jeweils 0.25 m² großen Flächen wurde die Reihenfolge und die Arten der eintreffenden Räuber und Aasfresser beobachtet. Weiters wurde die langfristigere Wiederbesiedlung (bis zu 2 Jahren) benthischer Organismen auf denselben Flächen mittels einer Fotoserie dokumentiert.

Die Auswertung der Bilder zeigt eine bestimmte Reihenfolge der eintreffenden Arten. Die Fische (*Diplodus vulgaris*, *Gobius niger*, *Serranus hepatus*, *Pagellus erythrinus*) kamen als erstes an, gefolgt von den ersten Einsiedlerkrebsen (*Paguristes eremita*) und den Schnecken (*Hexaplex trunculus*). Diese Reihenfolge wird mit den Fortbewegungsgeschwindigkeiten der jeweiligen Arten sowie deren Dichte erklärt. Die Flächendeckung innerhalb der Untersuchungsquadrate durch sessile Organismen wurde vor dem Experiment berechnet (Experiment August: 1939 cm² und September: 631 cm²). Die toten Organismen wurden innerhalb von 7 Tagen (August-Experiment) und 13 Tagen (September-Experiment) nach der künstlichen Anoxie großteils konsumiert. Solange die toten Organismen vorhanden waren, war die Dichte der Aasfresser hoch. Bei *Paguristes eremita* konnte eine eindeutige Tag/Nacht-Rhythmus festgestellt werden. Dabei wurde beobachtet, dass während der Nachtstunden die Individuenzahl stark abnahm.

Auch zwei Jahre nach der künstlich hervorgerufenen Anoxie konnte keine makroskopisch sichtbare Wiederbesiedlung der Areale festgestellt werden.

Damit hebt diese Studie die hohe Empfindlichkeit von Lebensgemeinschaften auf Weichböden hervor und unterstreicht die dringliche Notwendigkeit einer Reduzierung anthropogener Störungen durch Eutrophierung und kommerziellen Fischfang mit Bodenschleppnetzen.

8 Acknowledgment

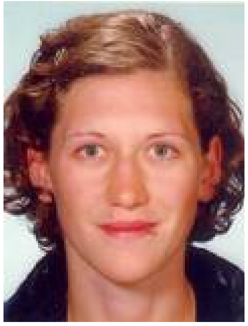
I would like to thank all who gave me the possibility to complete my diploma thesis. Special thanks to the whole EAGU-team. I am deeply grateful to my supervisor Doz. Dr. Michael Stachowitsch for his support across the board and for correcting the manuscript. Further, I would like to thank Dr. Bettina Riedel for her advice and encouragement, and Ao. Prof. Dr. Martin Zuschin for his help concerning statistical analyses. I also want to thank the Marine Biology Station in Piran, Slovenia, for the support during field work.

This thesis would not have been possible without my mum Heidi, my aunt Gabi and my boyfriend Punyo, who with their persistence always believed in me and got me moving in the right direction. Thank you also for financial support.

Thanks to Julia, Fabian and Denym for long walks through nature and to Kristin and Felix for creative support.

Finally, I would like to thank my brother Sam, my father Herbert and all my friends. I´m so happy to know you all.

9 Curriculum Vitae



Name: Marita Blasnig
Date of birth: 08.11.1983
Place of birth: St. Veit/Glan, Carintia
Citizenship: Austria
Residence: Missindorfstrasse 10/15, 1140 Vienna

E-mail: marita8@gmx.at

Education

2011 - 2012	Diploma thesis at the Department of Marine Biology, University of Vienna. Thesis: Short-term post-mortality predation and scavenging and longer-term recovery after anoxia in the Northern Adriatic Sea The thesis was part of the Austian Science Fund (FWF) project P21542-B17 - Low dissolved oxygen events in the Northern Adriatic: in situ experimental insight into benthic responses before, during and post-anoxia. Supervisor: Doz. Dr. M. Stachowitsch, Advisors: Dr. B. Riedel and Ao. Prof. Dr. M. Zuschin
since 2007	Studies in Zoology with special emphasis on marine biology at the University of Vienna, Austria.
2004 - 2007	Studies in Biology at the University of Vienna, Austria
2002 - 2004	Veterinary medicine, 1st section

Research activities and qualifications

2010	Marine ecology course, Station de Recherches Sous-Marines et Océanographiques, Calvi, Corsica – Natural habitat comparison and light optimum experiments with *Peyssonnelia squamaria*
2010	Coral reef course, Dahab, Egypt
2009	Marine biological field course in Rovinj, Croatia. Course title: “Fauna and Flora in the Mediterranean Sea”
2009	Morphology and preparation of regional birds
2009	Bio-acoustic internship with the catfish *Plecostomus* at the University of Vienna, Ao. Univ.-Prof. Dr. Friedrich Ladich
2009	Work experience – bird ringing at Auring, biological station Hohenau, Ringelsdorf
2008	Sea turtle project in Fethiye, Turkey, for 5 weeks, University of Vienna
2008	Biological Internship in the Tyrolean Alps (Zillertaler Alpen), University of Vienna

Secondary school and high school

University-entrance diploma: 5 June 2002

1998 - 2002	High school with special emphasis on Fine Arts, 1230 Vienna, Anton-Krieger Gasse 25
1994 - 1998	“Schulverband Mittelschule“, 1230 Vienna, Anton Krieger-Gasse 25

Preschool and primary school

1989 - 1994	“Schulkollektiv“ Vienna

Professional experience

1998 - 2010	Support service at “Sargfabrik“ 1140 Vienna, Goldschlagstraße 169
2003 - 2004	Veterinarian assistant, Dr. Maria Scheller, 1140 Vienna, Linzerstrasse 131
since 2003	Doctor’s assistant at the ordination of the gynaecologist Dr. Gabriele Knappitsch 1090 Vienna, Heiligenstädterstraße 12/23
2007 - 2009	Child care at “Kinderparties at“
since 2010	Selling and services in an organic grocery store Tongues, 1060 Vienna, Theobaldgasse 16

Personal skills

Languages:

German – mother tongue

English – reading, writing and verbal skills: good

Spanisch – school knowledge

Computer skills:

Microsoft Office applications, SigmaPlot, Image processing (Adobe Photoshop, Adobe Illustrator, Coral Draw), Past, Internet

Additional qualification:

Scuba diving (AOWD), underwater fieldwork and photography

Driving licence

First aid course

10 Appendix

10.1 Time series analyses

Hermit crabs August 2009

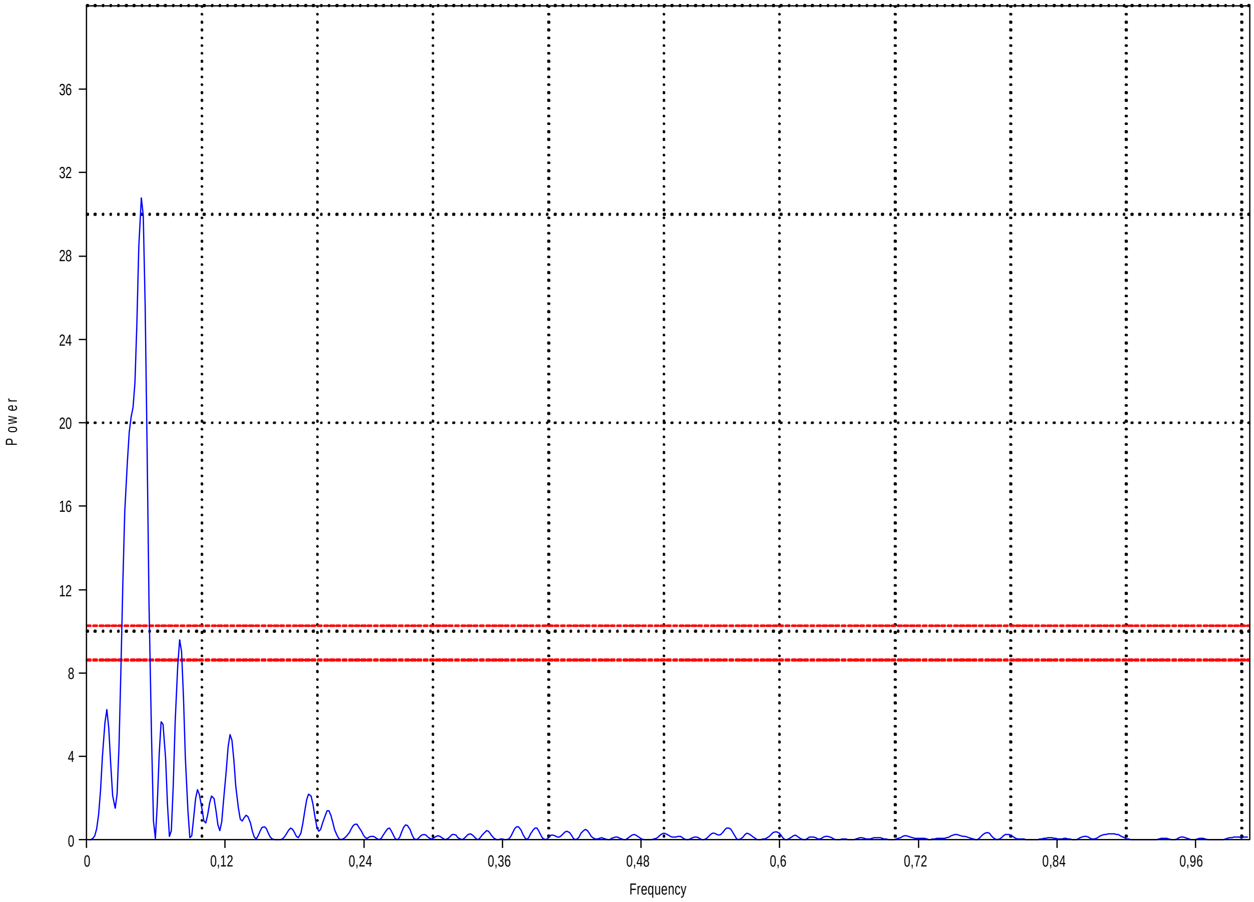


Figure 27: Time series analysis of the residence time of *Paguristes eremita* in the August 2009 plot, calculated with Past. Peaks above the red lines are highly significant (p=0.01), peaks between the red lines significant (p=0.05), and peaks below the red line not significant.

Table 5: Time series analysis of the residence time of *Paguristes eremita* in the August 2009 plot, calculated with Past. Yellow highlighting indicates highly significant (p=0.01) peaks, orange highlighting significant (p=0.05) peaks and green not significant peaks.

Frequency	Multitaper	Period
0.0017483	0.00070034	571.984213
0.0034965	0.011582	286.000286
0.0052448	0.061866	190.66504
0.006993	0.20951	143.000143
0.0087413	0.55026	114.39946
0.01049	1.2177	95.3288847
0.012238	2.3635	81.7126982
0.013986	4.0064	71.5000715
0.015734	5.6441	63.556629
0.017483	6.237	57.1984213
0.019231	5.3306	51.999376
0.020979	3.6402	47.6667143
0.022727	2.144	44.000528
0.024476	1.5145	40.8563491
0.026224	2.2031	38.1330079
0.027972	4.491	35.7500358
0.02972	8.1833	33.6473755
0.031469	12.311	31.7773046
0.033217	15.733	30.1050667
0.034965	18.078	28.6000286
0.036713	19.544	27.238308
0.038462	20.288	25.999688
0.04021	20.734	24.8694355
0.041958	21.946	23.8333572
0.043706	24.756	22.8801538
0.045455	28.429	21.99978
0.047203	30.782	21.1850942
0.048951	29.94	20.4285919
0.050699	25.601	19.7242549
0.052448	18.842	19.066504
0.054196	11.355	18.4515462
0.055944	4.8829	17.8750179
0.057692	0.90246	17.3334258
0.059441	0.085839	16.8234047
0.061189	1.7353	16.3428067
0.062937	4.1392	15.8889048
0.064685	5.6767	15.4595347
0.066434	5.5579	15.0525333
0.068182	3.9257	14.6666276
0.06993	1.6868	14.3000143
0.071678	0.16794	13.9512821
0.073427	0.44153	13.6189685
0.075175	2.5913	13.3022946
0.076923	5.6598	13.000013
0.078671	8.3332	12.7111642
0.08042	9.6041	12.4347177
0.082168	9.0431	12.1701879
0.083916	6.869	11.9166786
0.085664	3.9277	11.6735151

0.087413	1.3882	11.439946
0.089161	0.1119	11.215666
0.090909	0.18574	11.000011
0.092657	1.0509	10.7924927
0.094406	1.9686	10.5925471
0.096154	2.3933	10.3999834
0.097902	2.1562	10.2142959
0.09965	1.5001	10.0351229
0.1014	0.91811	9.86193294
0.10315	0.80838	9.69461949
0.1049	1.1977	9.53288847
0.10664	1.7714	9.37734434
0.10839	2.119	9.22594335
0.11014	1.9827	9.07935355
0.11189	1.4043	8.93734918
0.11364	0.73406	8.79971841
0.11538	0.4535	8.66701335
0.11713	0.87465	8.53752241
0.11888	1.9455	8.41184388
0.12063	3.3055	8.28981182

Hermit crabs September 2009

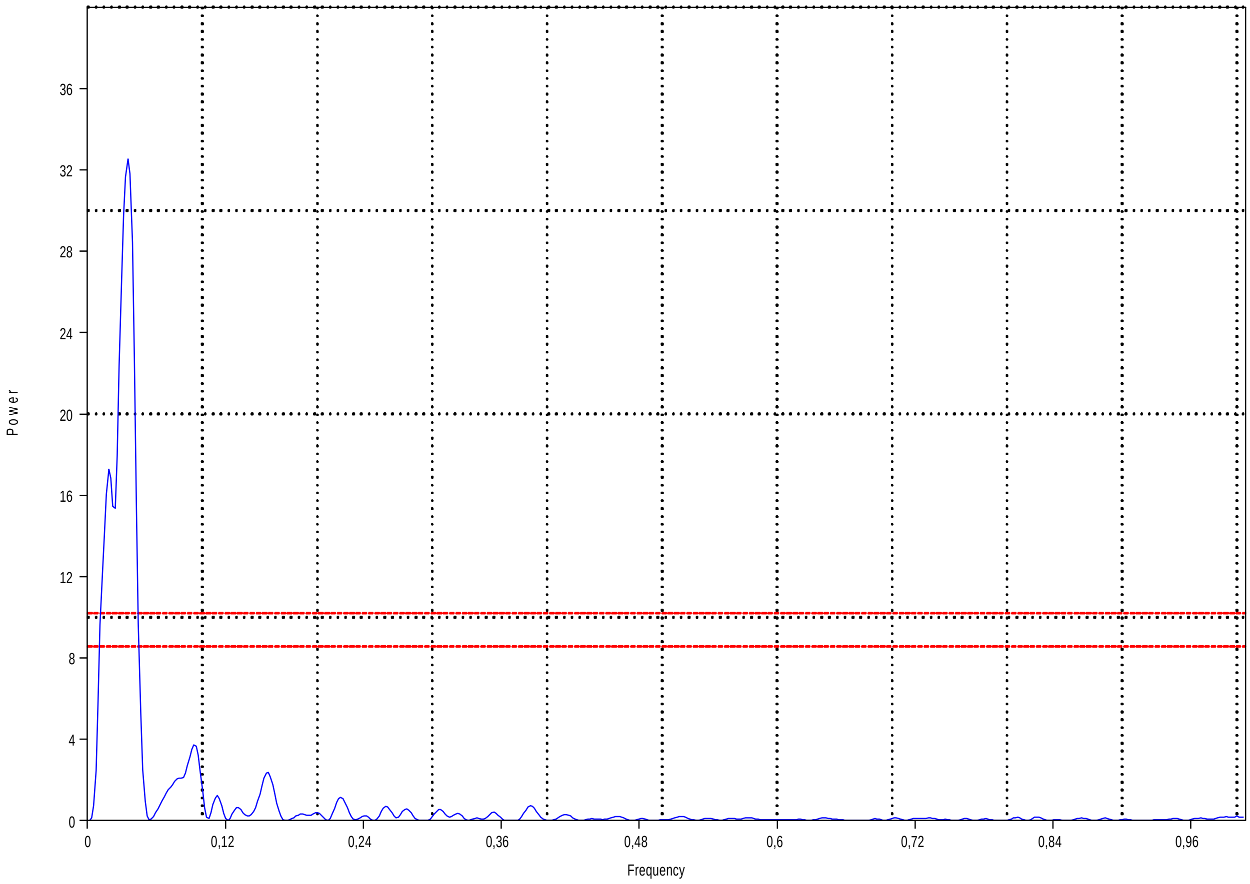


Figure 28: Time series analysis of the residence time of *Paguristes eremita* in the September 2009 plot, calculated with Past. Peaks above the red lines are highly significant (p=0.01), peaks between the red lines significant (p=0.05), and peaks below the red line not significant.

Table 6: Time series analysis of the residence time of *Paguristes eremita* in the September 2009 plot, calculated with Past. Yellow highlighting indicates highly significant (p=0.01) peaks, orange highlighting significant (p=0.05) peaks and green not significant peaks.

Frequency	Multitaper	Period
0.0018519	0.0074903	539.98596
0.0037037	0.12894	270.00027
0.0055556	0.72304	179.99856
0.0074074	2.4796	135.000135
0.0092593	5.8515	107.999525
0.011111	9.6299	90.0009
0.012963	12.218	77.1426367
0.014815	14.101	67.4991563
0.016667	16.044	59.9988
0.018519	17.293	53.998596
0.02037	16.83	49.0918017
0.022222	15.467	45.00045
0.024074	15.372	41.5385893
0.025926	17.949	38.5713184
0.027778	22.37	35.999712
0.02963	26.665	33.7495781
0.031481	29.746	31.7651917
0.033333	31.659	30.0003
0.035185	32.547	28.4212022
0.037037	31.798	27.000027
0.038889	28.466	25.7142122
0.040741	22.594	24.5452983
0.042593	15.721	23.4780363
0.044444	9.6648	22.500225
0.046296	5.2749	21.6001382
0.048148	2.4993	20.7692947
0.05	0.95376	20
0.051852	0.2415	19.2856592
0.053704	0.033074	18.6205869
0.055556	0.077628	17.999856
0.057407	0.21555	17.4194785
0.059259	0.3805	16.8750738
0.061111	0.56264	16.3636661
0.062963	0.76015	15.8823436
0.064815	0.96374	15.4285273
0.066667	1.1665	14.999925
0.068519	1.3608	14.594492
0.07037	1.5284	14.2106011
0.072222	1.6615	13.8461964
0.074074	1.7858	13.5000135
0.075926	1.9264	13.1707189
0.077778	2.05	12.8571061
0.07963	2.0949	12.5580811
0.081481	2.0765	12.2727998
0.083333	2.1166	12.000048
0.085185	2.3284	11.739156
0.087037	2.7019	11.4893666
0.088889	3.13	11.2499859

0.090741	3.5029	11.0203767
0.092593	3.7216	10.7999525
0.094444	3.6631	10.5882851
0.096296	3.2229	10.3846473
0.098148	2.4271	10.1886946
0.1	1.4768	10
0.10185	0.65397	9.81836033
0.1037	0.17554	9.64320154
0.10556	0.11345	9.47328534
0.10741	0.3866	9.3101201
0.10926	0.79899	9.15248032
0.11111	1.1289	9.00009
0.11296	1.2296	8.85269122
0.11481	1.0755	8.71004268
0.11667	0.74296	8.57118368
0.11852	0.36681	8.43739453
0.12037	0.091442	8.30771787
0.12222	0.010712	8.18196694
0.12407	0.11936	8.05996615
0.12593	0.32759	7.94091956
0.12778	0.52714	7.82595085

Gastropods August 2009

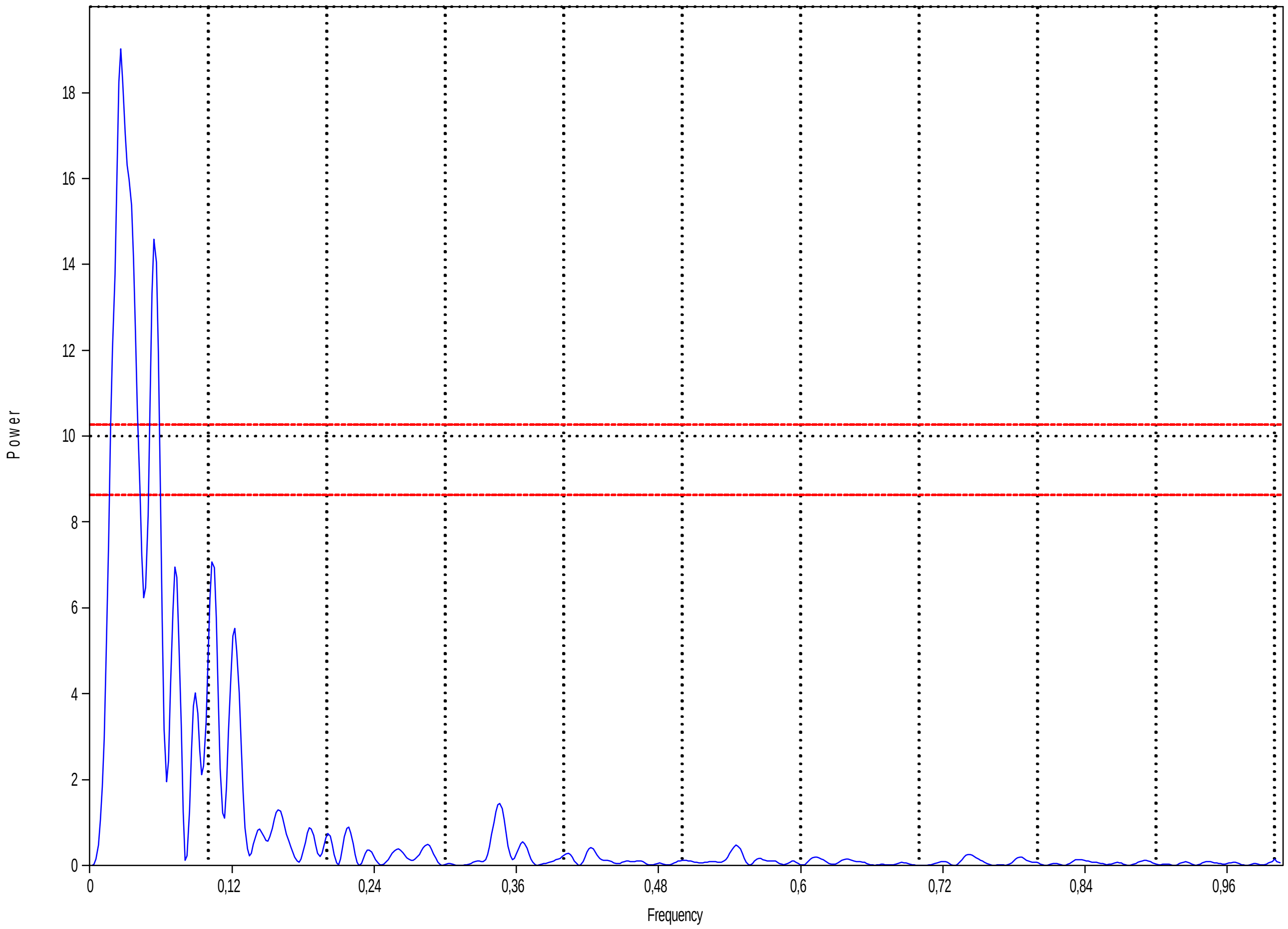


Figure 29: Time series analysis of the residence time of *Hexaplex trunculus* in the August 2009 plot, calculated with Past. Peaks above the red lines are highly significant (p=0.01), peaks between the red lines significant (p=0.05), and peaks below the red line not significant.

Table 7: Time series analysis of the residence time of *Hexaplex trunculus* in the August 2009 plot, calculated with Past. Yellow highlighting indicates highly significant (p=0.01) peaks, orange highlighting significant (p=0.05) peaks and green not significant peaks.

Frequency	Multitaper	Period
0.0017483	0.0017524	571.984213
0.0034965	0.028953	286.000286
0.0052448	0.15188	190.66504
0.006993	0.47963	143.000143
0.0087413	1.0637	114.39946
0.01049	1.8297	95.3288847
0.012238	2.9413	81.7126982
0.013986	4.8628	71.5000715
0.015734	7.5825	63.556629
0.017483	10.195	57.1984213
0.019231	12.043	51.999376
0.020979	13.769	47.6667143
0.022727	16.063	44.000528
0.024476	18.249	40.8563491
0.026224	19.024	38.1330079
0.027972	18.257	35.7500358
0.02972	17.04	33.6473755
0.031469	16.311	31.7773046
0.033217	15.981	30.1050667
0.034965	15.374	28.6000286
0.036713	14.138	27.238308
0.038462	12.453	25.999688
0.04021	10.631	24.8694355
0.041958	8.8267	23.8333572
0.043706	7.2112	22.8801538
0.045455	6.2377	21.99978
0.047203	6.4771	21.1850942
0.048951	8.1494	20.4285919
0.050699	10.795	19.7242549
0.052448	13.328	19.066504
0.054196	14.589	18.4515462
0.055944	14.055	17.8750179
0.057692	11.966	17.3334258
0.059441	8.9575	16.8234047
0.061189	5.7589	16.3428067
0.062937	3.1631	15.8889048
0.064685	1.9444	15.4595347
0.066434	2.4349	15.0525333
0.068182	4.1279	14.6666276
0.06993	5.9449	14.3000143
0.071678	6.9432	13.9512821
0.073427	6.7099	13.6189685
0.075175	5.326	13.3022946
0.076923	3.2533	13.000013
0.078671	1.2551	12.7111642
0.08042	0.12439	12.4347177
0.082168	0.22222	12.1701879
0.083916	1.2782	11.9166786
0.085664	2.6541	11.6735151

0.087413	3.7085	11.439946
0.089161	4.0185	11.215666
0.090909	3.5383	11.000011
0.092657	2.6783	10.7924927
0.094406	2.1088	10.5925471
0.096154	2.3184	10.3999834
0.097902	3.3278	10.2142959
0.09965	4.7902	10.0351229
0.1014	6.2128	9.86193294
0.10315	7.0704	9.69461949
0.1049	6.9399	9.53288847
0.10664	5.7564	9.37734434
0.10839	3.9565	9.22594335
0.11014	2.2546	9.07935355
0.11189	1.2267	8.93734918
0.11364	1.1049	8.79971841
0.11538	1.824	8.66701335
0.11713	3.0896	8.53752241
0.11888	4.4268	8.41184388
0.12063	5.3356	8.28981182

Gastropods September 2009

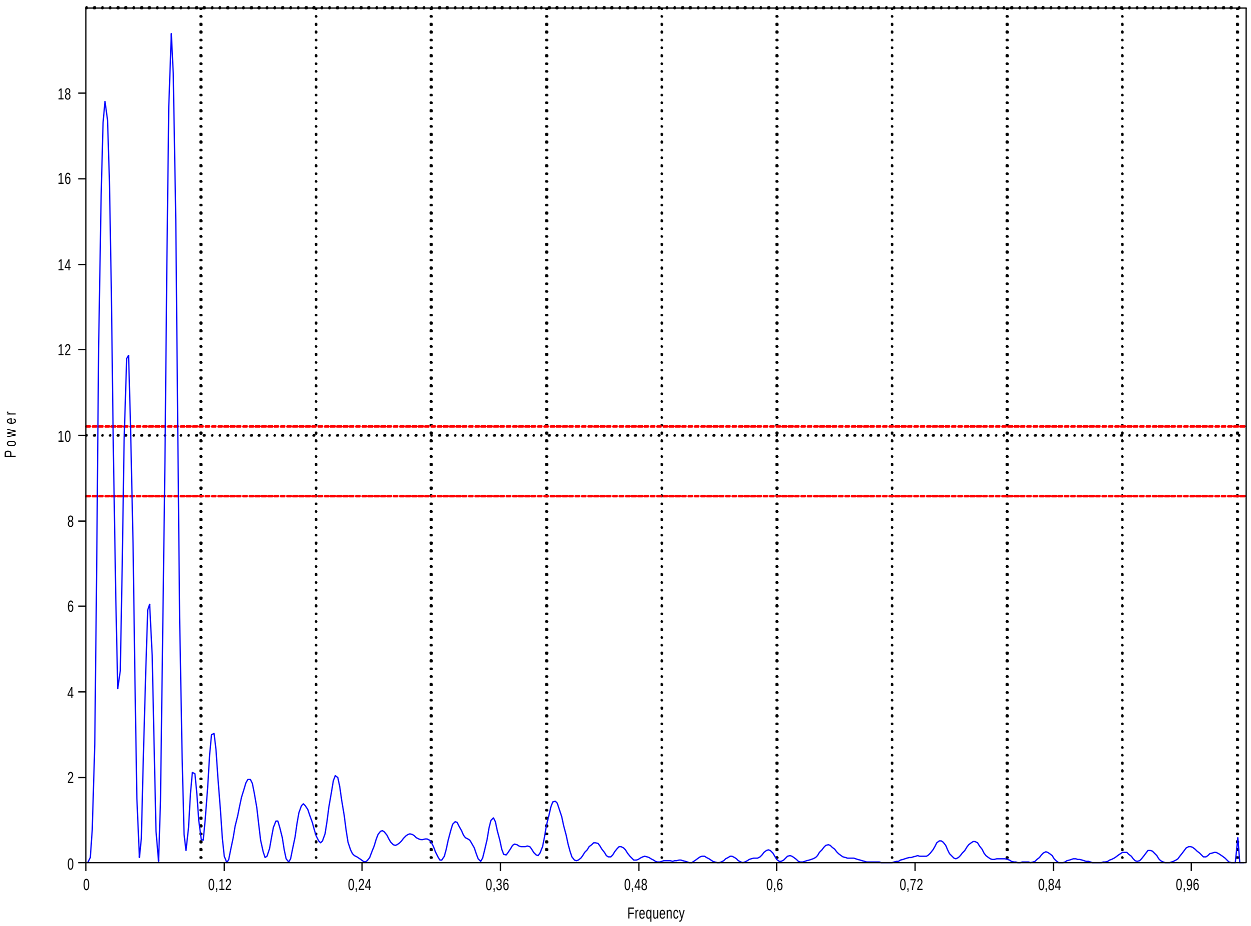


Figure 30: Time series analysis of the residence time of *Hexaplex trunculus* in the September 2009 plot, calculated with Past. Peaks above the red lines are highly significant (p=0.01), peaks between the red lines significant (p=0.05), and peaks below the red line not significant.

Table 8: Time series analysis of the residence time of *Hexaplex trunculus* in the September 2009 plot, calculated with Past. Yellow highlighting indicates highly significant (p=0.01) peaks, orange highlighting significant (p=0.05) peaks and green not significant peaks.

Frequency	Multitaper	Period
0.0018519	0.007536	539.98596
0.0037037	0.13251	270.00027
0.0055556	0.76987	179.99856
0.0074074	2.7723	135.000135
0.0092593	6.932	107.999525
0.011111	12.041	90.0009
0.012963	15.631	77.1426367
0.014815	17.315	67.4991563
0.016667	17.812	59.9988
0.018519	17.381	53.998596
0.02037	15.935	49.0918017
0.022222	13.357	45.00045
0.024074	9.775	41.5385893
0.025926	6.1495	38.5713184
0.027778	4.0805	35.999712
0.02963	4.4906	33.7495781
0.031481	6.9302	31.7651917
0.033333	9.9022	30.0003
0.035185	11.798	28.4212022
0.037037	11.872	27.000027
0.038889	10.255	25.7142122
0.040741	7.4716	24.5452983
0.042593	4.2556	23.4780363
0.044444	1.5094	22.500225
0.046296	0.13466	21.6001382
0.048148	0.58149	20.7692947
0.05	2.407	20
0.051852	4.5222	19.2856592
0.053704	5.9157	18.6205869
0.055556	6.0463	17.999856
0.057407	4.8544	17.4194785
0.059259	2.7661	16.8750738
0.061111	0.74462	16.3636661
0.062963	0.032985	15.8823436
0.064815	1.4393	15.4285273
0.066667	4.8296	14.999925
0.068519	9.3678	14.594492
0.07037	14.006	14.2106011
0.072222	17.689	13.8461964
0.074074	19.402	13.5000135
0.075926	18.465	13.1707189
0.077778	15.05	12.8571061
0.07963	10.315	12.5580811
0.081481	5.7581	12.2727998
0.083333	2.426	12.000048
0.085185	0.66712	11.739156
0.087037	0.30033	11.4893666
0.088889	0.82766	11.2499859

0.090741	1.6172	11.0203767
0.092593	2.1229	10.7999525
0.094444	2.0949	10.5882851
0.096296	1.6221	10.3846473
0.098148	0.9953	10.1886946
0.1	0.54721	10
0.10185	0.52767	9.81836033
0.1037	0.99379	9.64320154
0.10556	1.7676	9.47328534
0.10741	2.5287	9.3101201
0.10926	2.9932	9.15248032
0.11111	3.0309	9.00009
0.11296	2.6596	8.85269122
0.11481	1.9988	8.71004268
0.11667	1.2378	8.57118368
0.11852	0.57803	8.43739453
0.12037	0.15621	8.30771787
0.12222	0.0057945	8.18196694
0.12407	0.081561	8.05996615
0.12593	0.30425	7.94091956
0.12778	0.58786	7.82595085