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LONG-TERM CHANGES IN THE BENTHOS OF THE NORTHERN ADRIATIC SEA

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ABSTRACT

The Northern Adriatic Sea, like many shallow coastal waters, is subject to a wide range of stresses and threats. These include oxygen deficiencies, marine snow events, and fishing pressure. A mass mortality event in 1983 led to the collapse of a wide-ranging benthic community. A long-term sampling series between 1984 and 1994 showed that the benthos has not recovered even after a decade. The investigated macroepibenthic community, which consists largely of filter and suspension feeders, plays an important role in stabilizing the entire ecosystem. Due to repeated disturbances the function of this community has been impaired. The reaction of the benthos to these disturbances shows that such communities serve not only to accurately interpret current conditions, but also serve as a memory of past events. More effort should be made to decipher the rich information that the benthos provides.

Keywords: benthos, macrofauna, North Adriatic Sea, Gulf of Trieste, disturbance, mortality, recolonization, anoxia, marine snow, long-term
Ključne besede: bentos, makrofavna, Severni Jadran, Tržaški zaliv, motnje, smrtnost, rekolonizacija, anoksija, morski sneg, dolgoročne spremembe

INTRODUCTION

The Northern Adriatic Sea can be classified as a sensitive ecosystem. As the northernmost part of the Mediterranean, it is subject to high annual fluctuations of physical parameters such as temperature and salinity. Its shallow depth (< 30 m), strong stratification, high riverine input, along with pressure from tourism and commercial fishing contribute to making it a classical example of an endangered marine ecosystem. In addition to the above features, the Northern Adriatic is also susceptible to other phenomena such as oxygen deficiencies and marine snow production, which have taken on dramatic proportions in recent years (Brambati, 1988; Stachowitsch *et al.*, 1990; Vollenweider & Rinaldi, 1995).

Despite the above sources of instability, the sublittoral soft bottoms of the Northern Adriatic are characterized by well-developed benthic communities. The benthic communities in this area have been studied for almost a century and have been summarized in regular intervals (Vatova, 1949; Pérès, 1967; Gamulin-Brida, 1974; Ott, 1991). These communities consist not only of a well-developed infauna, but also of a characteristic macroepifauna (Orel & Mennea, 1969). One of the most widespread epibenthic communities is the O-R-M community, named after three dominant genera, the brittle star *Ophiothrix*, the sponge *Reniera,* and the ascidian *Microcosmus* (Fedra *et al.*, 1976). This community consists largely of mobile and sessile filter or suspension feeders which are aggregated in the form of so-called multi-species clumps.

During the course of ecological investigations in the

1970s, this community was found to maintain a stable biomass and structure. The community plays an important role in stabilizing the entire ecosystem by removing suspended material from the water column and storing it in the form of benthic biomass (Ott & Fedra, 1977; Ott, 1981). However, a series of recent disturbances including oxygen deficiencies and massive marine snow development have overwhelmed this stabilizing function and led to the collapse of the benthos (Stachowitsch, 1984). These developments have been increasingly related to eutrophication (Rosenberg, 1985; UNESCO, 1988). While such perturbations may be visible in the pelagic system in the form of reduced transparency, discoloration of the water, surface layers of mucus, and other short-term clues, the impact on the benthos is much more long-lived. Long-term studies are necessary to accurately detect the impact of such disturbances on the benthos and to determine how various short-term perturbations influence the overall system.

MATERIAL AND METHODS

In 1974 and 1975 the benthic communities in the Gulf of Trieste / Northern Adriatic Sea were investigated by means of an underwater TV-camera sled consisting of a 1" Vidicon black and white videocamera, a Hasselblad 500-el camera and a series of lamps (for a detailed description of the system, see Machan & Fedra, 1975). Twelve profiles with a total length of 80 km and covering an area of about 200 km² were examined in order to define the borders of the O-R-M community (Fedra *et al.*, 1976). Additional profiles were also made in the Italian sector of the gulf to define adjoining communities (Fedra, 1978). This, coupled with a series of samples taken between 1973 and 1977 at a central position in the O-R-M community (station 1, Fig.1 in Stachowitsch, 1984) provided information on the undisturbed (premortality) condition of the benthic community.

In 1983 a mass mortality event was observed at twelve stations in the Gulf of Trieste from 12 - 26 September. One station (station 1) was revisited on six separate days in order to document the course of mass mortality. Photographs were taken with a NIKONOS II and NIKONOS IV-A camera equipped with a specially designed electronic flash and a NIKON SB-101 flash, respectively. ILFORD PAN F and KODACHROME 64 film was used. Samples for species identification were collected by hand.

The recolonization process after the 1983 mass mortality event was investigated by taking 4 to 10 1 m² macroepifaunal samples each year using SCUBA. All organisms or biogenic structures on or projecting from the sediment were collected by hand and placed into 1 mm² mesh bags. An effort was also made to collect the fauna lying immediately beneath the sediment surface. The samples were fixed in a 4% formaldehyde:seawater solution. The recolonization process described in this contribution is based on a single, randomly chosen 1m² sample for each year between 1984 and 1994. Wet weights of the macrofauna (> 1mm) were determined with a Sartorius H 120 electronic balance (+/- 0.001 g). Wet weight measurements include mollusc shells but omit serpulid tube weights.

RESULTS

The O-R-M community:

The large-scale underwater TV-camera sled survey showed that the O-R-M community covered a large area of the Gulf of Trieste. Based on the observations of Czihak (1959) and Riedl (1961), who reported high densities of the brittle star *Ophiothrix quinquemaculata* off Rovinj, Croatia, this community is thought to extend far down into the Northern Adriatic. The evaluation of the videofilms showed that the designating genera *Ophiothrix, Reniera,* and *Microcosmus* were not only biomass dominants, but also visually characterized the community. These genera, along with a wide range of other sponges and ascidians, were clearly aggregated in the form of multi-species clumps (Fedra *et al.*, 1976), with the intervening sediment surface containing scattered deposit feeders and carnivores. These multi-species clumps intitially grow on a biogenic base or "nucleus" consisting of gastropod shells *(Murex brandaris, Trunculariopsis trunculus, Aporrhais pes-pelecani),* bivalve shells *(Arca noae, Chlamys spp.),* or sea urchin tests (*Schizaster canaliferus, Psammechinus microtuberculatus).* The aggregated biomass in the O-R-M community shows that fixo-sessile, hemi-sessile, and mobile species require such substrates. In the intact community, the former include sponges and ascidians and constitute the underlying structure of the multi-species clumps. Typical hemi-sessile species are *Cucumaria planci* and *Chlamys varia*, while the latter group includes the most visible mobile species, *O. quinquemaculata* (Fig. 1).

SCUBA-diver-samples taken before, during, and after the TV-sled profiles showed the O-R-M community to be characterized by a high macroepifauna biomass of 370 g wet weight/m², with maxima of more than 1000 g wet weight/m². The designating group, *Ophiothrix- Reniera-Microcosmus*, comprised 64% of the total biomass, with *O. quinquemaculata* alone contributing 28%. In contrast, the mean biomass outside the community borders (the "peripheral areas" of Fedra *et al.*, 1976) was evaluated at 166 g wet weight/m², with *O. quinquemaculata* contributing only 6% to the total biomass. The benthos outside the O-R-M community borders was characterized by a distinctly lower biomass, different species composition, smaller multi-species clumps, and a predominance of mobile deposit feeders (hermit crabs, holothurians, and sea urchins). For a more detailed description of other communities in the shallower parts of the Gulf of Trieste, see Fedra (1978).

Mass mortalities

A series of mass mortalities was observed in the course of our investigations on the benthos of the Northern Adriatic Sea over the past 20 years. The first mortality was documented in September 1974 during the TV-camera sled profile work. This area of decaying organisms was termed the "graveyard phenomenon" and affected the central region of the Gulf of Trieste (Positions 28 and 36, Fig. 1 in Fedra *et al.*, 1976). The exact boundaries of the affected area could not be determined at that time because they extended beyond the territorial waters of former Yugoslavia. However, the composition of the decaying organisms clearly showed that this area was occupied by the O-R-M community.

In 1983 a renewed mass mortality event was observed at the central station in the gulf (station 1 = position 39 in Fedra *et al.*, 1976). At this location, the entire course of ecosystem collapse, from behavioral modifications to the sequence of mortality was documented and described in detail by Stachowitsch (1984). The affected area was estimated to measure 250 km² and covered most of the bottom below 18 m in the gulf.

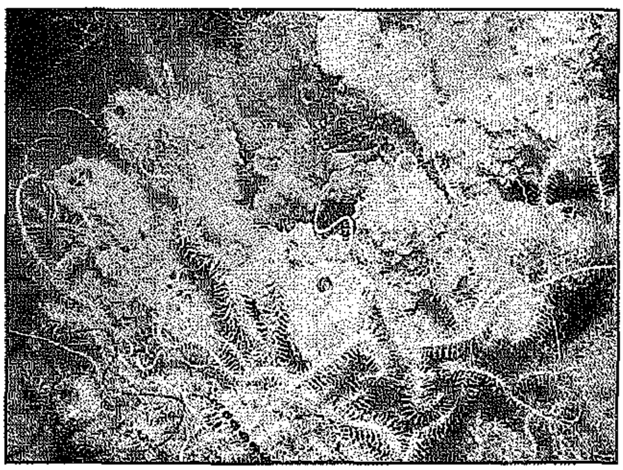

Fig. 1: Large, intact multi-species clump consisting of horny sponge, colonial ascidian and* Cucumaria planci *(top, middle), serpulid tubeworms and hydrozoans (top, right), and hermit crab in* Truncularlopsis trunculus *shell (center). Sponge serves as a substrate for a dense aggregation of the brittle star* Ophiothrix quinquemaculata. *Gulf of Trieste, 25 m.

Slika 1: Velika, v naravnih razmerah živeča večvrstna skupina, ki jo sestavljajo rožičasta spužva, kolonijski kozolnjak, brizgača* Cucumaria planci *(zgoraj, v sredini), serpulidni mnogoščetinci in trdoživnjaki (zgoraj, desno) ter rak samotar v hišici čokatega voleka* Truncu-lariopsis trunculus *(v sredini). Spužva deluje kot podlaga za čvrsto spojitev pegastega kačjerepa vrste* Ophiothrix quinquemaculata. *Tržaški zaliv, 25 m.

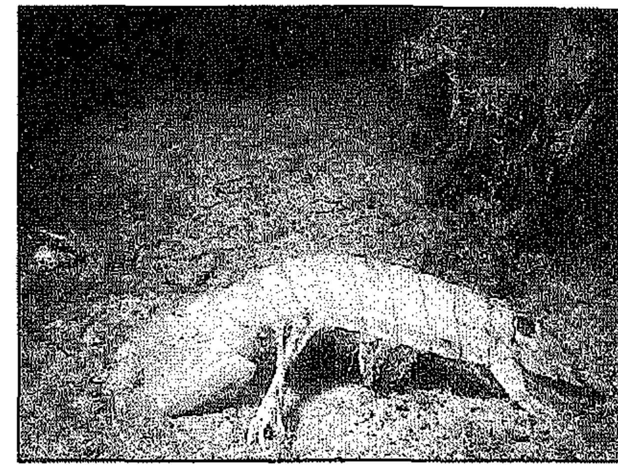

Fig. 2: Moribund* Squilla mantis *on sediment surface in Sept. 1983. In background, decaying, mucus-covered multi-species clump.

Slika 2: Morska bogomoljka* Squilla mantis *na površju morskega dna septembra 1983. V ozadju s sluzom prekrita razpadajoča večvrstna skupina.

Both the infauna and epifauna were affected by the 1983 mortality event. All organisms showed modified behavior before death occurred. Among the infauna, the most common visible reaction was emergence from the sediment. At a later stage, most of these species were observed motionless, in a moribund state, on the sediment (Fig. 2), although some left short tracks on the surface (the heart urchin *Schizaster canaliferus*, the gastropod *Aporrhais pes-pelecani*) or were recorded swimming in the water column (*Squilla mantis*). Other reactions included evisceration (*Thyone fuscus*), aggregating on mounds (*Amphiura chiajei*), as well as gaping valves and extended syphons in bivalves. Furthermore there was a distinct sequence of emergence and death in the in-fauna, with burrowing crustaceans (*Upogebia tipica, Jaxea nocturna*) and echinoderms (*S. canaliferus*) emerging first, followed by polychaetes, sipunculans (*Golfingia elongata, Sipunculus nudus*), gastropods, and bivalves.

The initial behavioral modifications of most of the mobile epifauna involved aggregating on elevated sediment structures (mounds of burrowing crustaceans). Specific, characteristic behaviors of individual species included eviscerated holothurians (*Holothuria tubulosa*), the humped posture of the brittle star *Ophiura texturata*, overturning sea stars (*Astropecten sp.*) and, in the case of hermit crabs, the abandonment of the occupied shells by the crabs along with the detachment of symbiotic anemones (*Calliactis parasitica*).

A key development was the destruction of the characteristic structure of the O-R-M community. Specifi-

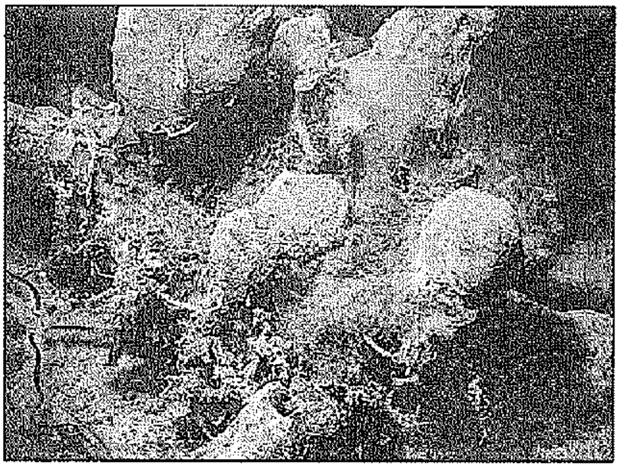

Fig. 3: Close-up of decaying multi-species clump in Sept.1983. Adult O.* quinquemaculata *have left the clump, while dead, juvenile brittle stars are still attached to decomposing sponge substrate (top, left). Associated fauna includes the bivalve* Chlamys varia *covered with decaying, encrusting sponge (center) and tubeworm (left).

Slika 3: Bližnji posnetek razpadajoče večvrstne skupine septembra 1983. Odrasli pegasti kačjerepi vrste* O. quinquemaculata *so že zapustili skupino, medtem ko so poginuli mladostni osebki še vedno pritrjeni k razpadajoči spužvi (zgoraj, levo). Združena favno sestavljata pokrovača vrste* Chlamys varia, *prekrita z razpadajočo spužvo (v sredini), in mnogoščetinec (levo).

cally, the multi-species clumps were very susceptible to the mortality phenomenon. Sponges, for example, which were a major component in many multi-species clumps, were among the first species to die and become discoloured (Fig. 3). This had an immediate effect on the other species in the clumps, especially those species that use sponges as a substrate or habitat. Thus, motile species such as the designating species *Ophiothrix quinquemaculata* left the multi-species clumps on which they were normally aggregated and lay overturned on the sediment. This mortality event was coupled with large amounts of marine snow in the water column. As relatively large structures projecting from the sediment, the sponges in multi-species clumps snagged this drifting mucus material. The decaying sponges and marine snow caused the small fauna (e.g., nestlers and sponge dwellers) to emerge. For example, a wide range of dead crustaceans such as *Pisidia longicornis, Pilumnus spinifer,* small shrimp, and amphipods were observed entangled in mucus-covered sponges.

After the onset of the oxygen deficiency-induced behavioral modifications, the collapse of the community proceeded very rapidly. Thus, the time interval between first unusual behavior and the onset of mortalities in the individual species was very rapid. Within 4 days over 90% of the macroepifaunal biomass was destroyed and most of the emerged infauna species began to die. Fourteen days later, at the end of the investigation period (26 Sept. 1983), only few living organisms were recorded and the sediment was covered with a dark layer of decaying organic material.

Recolonization

Compared with the rapidity of the collapse of the O-R-M community in 1983, recolonization is a long-term process. Our investigations over a period of more than 10 years show that the community still has not recovered from this initial disturbance. This conclusion is based on total macroepibenthic biomass and the percent contribution of the former designating species (Fig. 4).

A key to the reestablishment of community structure is the growth of the formerly characteristic multi-species clumps. A prerequisite for this is the availability of biogenic structures on which the larvae of sessile and motile epifauna species can settle. Not all substrates are suitable for epigrowth, and many factors can render potentially suitable ones unsuitable. The most conspicuous structures on the sediment surface after the 1983 and 1988 mortality events were bivalve shells and sea urchin tests. New epigrowth on such structures is heavily influenced by sedimentation. Sedimenting particles can rapidly cover smaller substrates (Fig. 5) and the top surface of even larger substrates such as the shells of the scallop *Pecten jacobaeus* can be covered by settling particles. In such cases, the renewed growth of sessile organisms typically begins along the edges or from the underside.

The first species registered after the 1983 mass mortality event differed from the structurally dominant forms previously recorded in the intact O-R-M community. The initial settlers on dead bivalve shells or sea urchin tests were encrusting bryozoans (e.g., *Schizoporella sp., Schizomavella sp.)* and serpulid tubeworms such as *Pomatoceros triqueter* and *Serpula vermicularis.* The tubes of the serpulids eventually extended away from the substrates in an upright position, enlarging the "clumps" and giving them a more three-dimensional structure. These erect tubes favored the settlement of other epigrowth. Many juvenile bivalves (e.g., *Hiatella arctica),* as well as rapidly growing ascidians *(Ciona intestinalis)* and hydrozoans were found between the serpulid tubes. In later successional stages, slower-growing ascidians *(Microcosmus spp.)* successfully settled. This led to a corresponding increase in the species associated with the thick tunic of these more long-lived ascidians (e.g., the bivalve *Musculus subpictus).* These developing multi-species clumps consisted not only of epifauna, but also of many mobile and nestling species like polychaetes, crustaceans, sipunculans and nemertines. These stages of

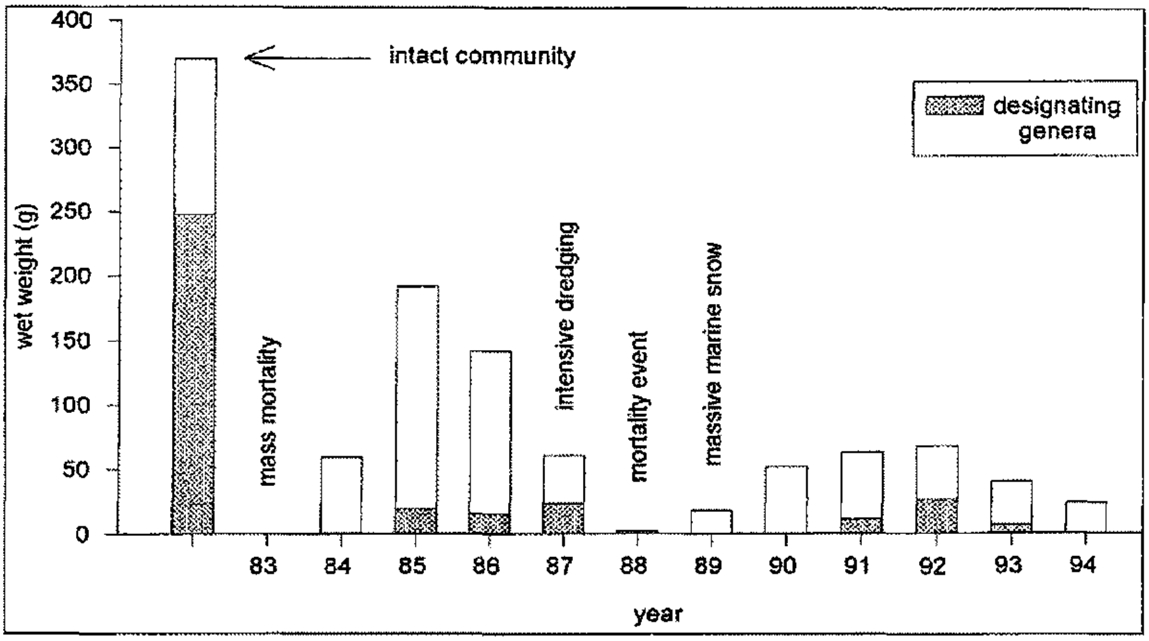

Fig. 4: Recolonization of benthic community between 1984 and 1994, based on 1 m²-sample taken in September of each year. Total macroepifaunal biomass and contribution of designating genera (stippled: *Ophiothrix, Reniera, Microcosmus*). ***The community has been subject to repeated disturbance and has not recovered even after 10 years.***
Slika 4: Rekolonizacija bentoške združbe med letoma 1984 in 1994 na osnovi vzorca (s površino 1 m²) v septembru vsakega leta. Skupna biomasa makroepifavne in prispevek posameznih rodov (pikčasto: *Ophiothrix, Reniera, Microcosmus*). ***Združba je bila izpostavljena nenehnemu vznemirjanju in si ni opomogla celo po desetih letih.***

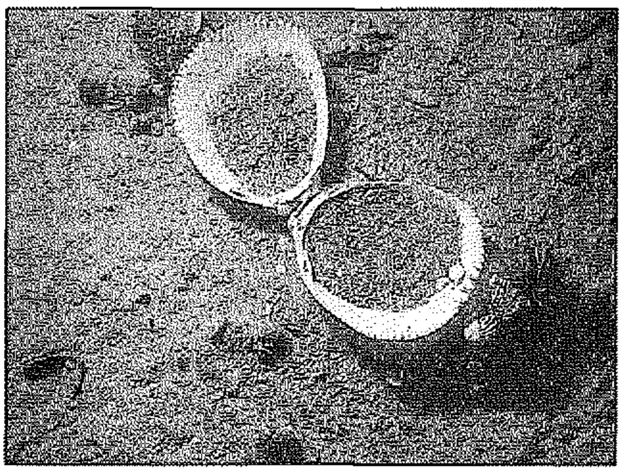

Fig. 5: Layer of sediment partially covering fresh *Laevicardium oblongum* ***shell. The sea urchin*** *Psammechinus microtuberculatus* ***grazing on right valve. New epigrowth typically begins on underside or edges of such fresh substrates.***
Slika 5: Plast usedlin delno prekriva še svežo lupino srčanke vrste *Laevicardum oblongum*. ***Mali morski ježek*** *Psammechinus microtuberculatus* ***na paši. Nova obrast se značilno začenja na spodnji strani ali robovih še svežih podlag te vrste.***

community recolonization clearly represent a succession. A detailed distinction and description of the individual stages of succession is the focus of ongoing research.

Renewed disturbances

The normal succession process was hampered several times in the course of the decade. The first disturbance of the recolonization of the O-R-M community is related to the scallop *Pecten jacobaeus* which, along with the pen shell *Pinna sp.*, established themselves in greater numbers on the sediment surface. Both species may represent distinct stages in the recolonization of the bottom. *Pinna*, for example, was rarely recorded in the samples of the premortality community. By 1987, the scallop population reached a size large enough to support commercial fishing operations. The subsequent use of bottom trawls scarred the sediment and even crushed the scallops themselves (Fig. 6). More important with regard to the reestablishment of the O-R-M community, these operations overturned or broke apart many of the newly established multi-species clumps. We consider this activity to have played a role in the biomass decrease to 61 g wet weight/m² in 1987 (Fig. 4). One of the most visible effects of bottom trawling was on the *Pinna* population. The opening of younger *Pinna* lies

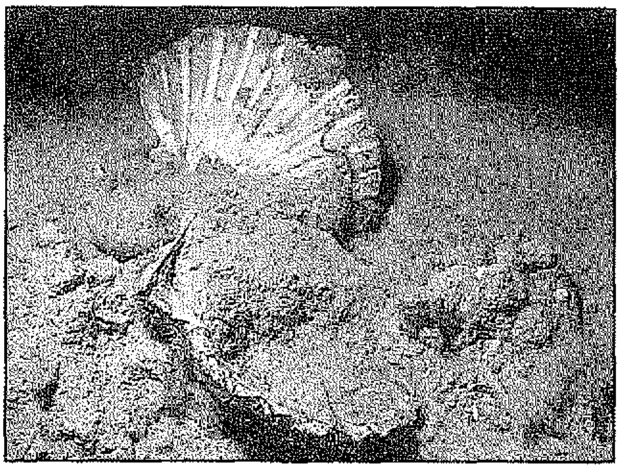

Fig. 6:** Pecten jacobaeus* ***shell broken apart and dislodged by bottom trawling gear. Initial growth of serpulids on top valve, arms of *Ophiothrix quinquemaculata* ***projecting from underside of lower valve. Two anemones*** *(Calliactis parasitica)* ***between the valves are probably associated with a hermit crab.***
Slika 6: Lupina velike pokrovače *Pecten jacobaeus,* ***ki jo je iz dna iztrgala in razbila globinska vlečna mreža. Začetna rast serpulidnih mnogoščetincev na gornji lupini, kraki kačjerepa vrste*** *Ophiothrix qiuquemaculata* ***štrlijo s spodnje strani spodnje lupine. Dve stražni vetrnici med*** *(Calliactis parasitica)* ***lupinama sta najbrž v združbi z rakom samotarjem.***

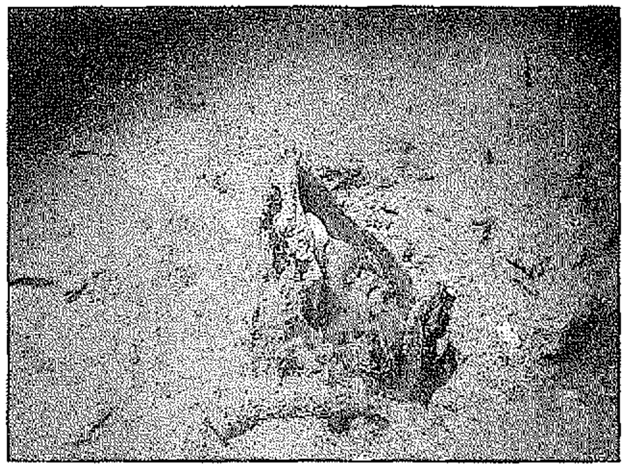

Fig. 7: Freshly killed *Pinna sp.* ***with decaying soft parts still within the shell. Top part of valves sheared off by bottom trawl (Sept. 1987).***
Slika 7: Pred kratkim uničen leščur *Pinna sp.,* ***z razpadajočimi mehkimi deli še vedno v lupini. Gornji del lupine je očitno odrezala globinska vlečna mreža (sept. 1987).***

flush with the sediment surface and the bivalves are inconspicuous. Later, the valves project above the sediment, with the outer surfaces serving as a further substrate for epigrowth. The fishing gear broke off the projecting part of the shells, killing the bivalves (Fig. 7). These empty shells subsequently served as a substrate for a dense epigrowth consisting largely of serpulid tubeworms (both on the inner and outer valve surfaces). The effect of ongoing, regular trawling activity was clearly evident: the gear continued to shear off the ends of the valves and often snagged on the tubeworms extending from the apertures. The force is sufficient to pull the deeply buried bivalves from the sediment (Fig. 8).

A renewed, small-scale mortality was recorded at the long-term station in September 1988. Based on divertaken notes, underwater photography, and samples taken at adjoining stations, the area of this mortality was estimated to be 4 km². The seafloor was characterized by "black spots" indicating the position of small multispecies clumps and decaying organisms (Fig. 9). The bottom was also littered with fresh sea urchin tests *(Psammechinus microtuberculatus, S. canaliferus)* and numerous fresh bivalve shells *(Laevicardium oblongum, Cardium sp.).* The biomass in the September sample was reduced to 2 g wet weight/m² and consisted of 3 *Epizoanthus arenaceus* polyps, 1 sipunculan and 10 polychaetes. This small-scale event, which occurred within the area affected in 1983, most likely did not impede the overall recolonization process in the North Adriatic, but did directly affect our long-term sampling station in the Gulf of Trieste.

In 1988, 1989, and 1991, marine snow ("mare sporco") events were registered in the Adriatic. The 1989 event had a major impact on the entire Northern Adriatic Sea. Marine snow settled on the bottom in the form of macroflocs, stringers, and clouds (Stachowitsch *et al.,* 1990) as early as June 14. The amount of sinking material was sufficient to cover multi-species clumps (Fig. 7 in Stachowitsch *et al.,* 1990) and to interrupt the suspension-feeding posture of entangled *O. quinquemaculata,* for example. Interestingly, no severe anoxia or widespread mortality occurred at the sampling station itself. It should be noted, however, that the benthos in 1989 was already highly reduced (18 g wet weight/m²) due to the mortality of the previous year. At the same time, the wide-ranging creamy and gelatinous surface layers (Stachowitsch *et al.,* 1990) that covered large parts of the Northern Adriatic in summer 1989 apparently settled to the bottom further to the south, where they were associated with extensive mass mortalities over an area of 3000 to 4000 km² in winter 1989/90 (Fig. 13 in Ott, 1991).

Between 1990 and 1994 no major disturbances other than the ongoing bottom trawling operations were recorded. Nonetheless, the recolonization process did not lead to the re-establishment of the O-R-M community.

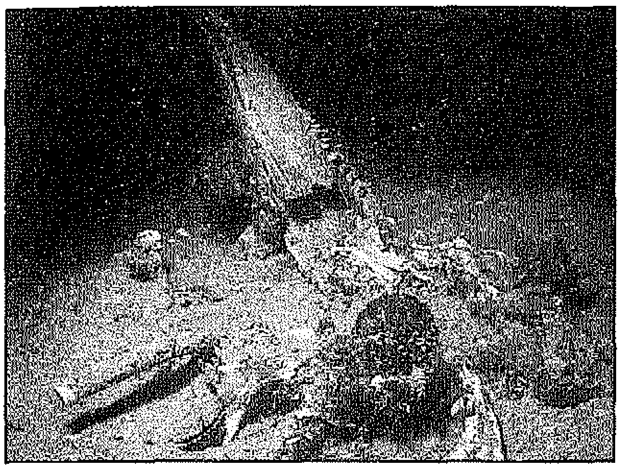

Fig. 8: *Pinna sp.* ***dislodged from the sediment by benthic trawl fishing equipment snags on projecting part of shell along with its epigrowth. Crushed serpulid tubeworms and*** *Chlamys varia* ***lying on the sediment surface. Note presence of predators*** *Truncularìopsis trunculus* ***and*** *Psammechinus microtuberculatus,* ***right) feeding on detached epigrowth. Note also*** *C. varia* ***attached to freshly exposed part of*** *Pinna sp.*
Slika 8: Leščur *Pinna sp.,* ***ki ga je iz podlage za štrleči del skupaj z obrastjo izvlekla globinska vlečna mreža. Na površju morskega dna ležijo uničeni serpulidni mnogoščetinci in mala pokrovača*** *Chlamys varia.* ***Z ločeno obrastjo se hranita plenilca - čokati volek*** *Truncularìopsis trunculus* ***in mali morski ježek*** *Psammechinus microtuberculatus* ***(desno). K sveže odtrganemu delu leščurja je pričvrščena mala pokrovača.***

Specifically, neither the biomass nor the designating species reached former levels (Fig. 4). The overall low biomass reflects the smaller size of multi-species clumps vs. pre-mortality values.The maximum biomass of individual clumps measured between 1990 and 1994, for example, was 9.5 g, with average values below 1g. Multi-species clumps can reach large dimensions. Wurzian (1977) classified these aggregations into weight classes of 0 to 80 g, 80 to 240g, 240 to 560g, and > 560g. No multi-species-clump of the larger weight classes were found in the ten years following the 1983 mortality. In fact, no 1 m² sample even approached the weight of a single, former medium- to large-sized clump.

Although the percent contribution of the former designating group of species increased (for example from 0 to 39% between 1984 and 1987), the composition within the group remained atypical. While *Microcosmus* began to reestablish itself, the sponge *Reniera* was virtually absent (present for example in the 1993 sample: 6.8 g) and only isolated specimens of *Ophiothrix quinquemaculata* (mostly juveniles) were collected in the samples. Not one adult *O. quinquemaculata,*

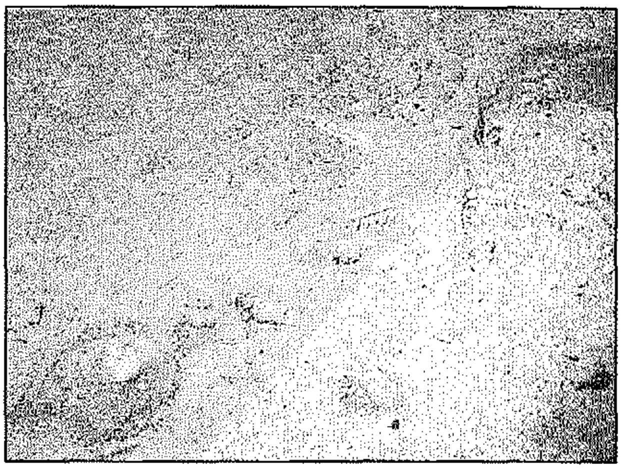

Fig. 9: ***The sea star*** *Astropecten aurantiacus* ***surrounded by several "black-spots" representing decaying organisms in Sept. 1988. Fresh test of the sea urchin*** *Psammechinus microtuberculatus* ***(top, middle) and emerged gastropods*** *(Aporrhais pes-pelecani,* ***center).***
Slika 9: Oranžno morsko zvezdo *Astropecten aurantiacus* ***obkrožajo številni razpadajoči organizmi v obliki črnih pik (sept. 1988). Sveže testiranje malega morskega ježka*** *Psammechinus microtuberculatus* ***(zgoraj, v sredini) in pojavljajočih se polžev pelikanovih stopalc*** *(Apporrhais pes-pelecani,* ***v sredini).***

which was formerly present in numbers of up to 500 individuals/m², was found in the samples evaluated between 1991 and 1994.

DISCUSSION

Due to the narrower range of fluctuations of physical parameters in marine versus terrestrial ecosystems, large-scale natural disturbances in the marine environment are relatively uncommon and poorly documented. This is particularly true in sublittoral soft bottoms. When disturbances do occur, they tend to be most overtly manifested in the pelagic subsystem (e.g., discoloration due to plankton blooms). In cases where disturbances in the pelagic subsystem are coupled with or trigger perturbations in the benthic subsystem, the discrepancy between the duration of the phenomena in the two realms can be very large: the transient nature of pelagic disturbances stands in contrast with the long-term disturbances in benthic communities, especially in the case of a well-developed macrofauna. This makes benthic communities ideally suited to detect the actual effect of perturbations on the overall ecosystem.

In the investigated O-R-M community, for example, the perturbations that triggered mass mortality, i.e., marine snow events and anoxias in the water column, were short-term events on the scale of days, weeks, and months. The recolonization process (notwithstanding the renewed disturbances), on the other hand, clearly involves periods of years or even decades (Fig. 4). This period is on the longer end of the range reported for other sublittoral bottoms. Total recovery in the New York Bight after anoxia was expected to take several years due to the extensive area affected (Steimle & Radosh, 1979). Recolonization in the Bornholm Basin in the Baltic after a 1968 mortality led, even after several years, to a community showing very little resemblance to the original *Macoma baltica* community (Leppäkoski, 1971). Repeated disturbances complicate the process, leading to steady impoverishment (German Bight; Rachor, 1980) or the annual reestablishment of transitory successional stages (Chesapeake Bay; Officer *et al.*, 1984).

Compared with the communities mentioned above, which are dominated by infauna species, recovery in the O-R-M community is no doubt compounded by the complex structure and associations of the macroepibenthic invertebrates (e.g., multi-species clumps). Fully developed multi-species clumps are perennial structures. A wide range of physical and biological conditions are necessary for mature aggregations to develop. Clearly, this proceeds via a number of successional stages. Different types of multi-species clumps (e.g., sponge- versus ascidian-dominated) can arise depending on larval settlement factors, space competition, predation, etc. Their final appearance can further be modified by ecological interactions. For example, the distribution of *O. quinquemaculata* can be interrupted or modified when the sponges are occupied by the crab *Pilumnus* spinifer; in this case, crab number and clump size determine the small-scale distribution pattern of the brittle star (Wurzian, 1977).

A second path of multi-species-clump formation, involving hermit-crab occupied gastropod shells, is also known. Virtually all gastropod shells go through the hermit crab population. Because they are transported over long distances by the crabs (Stachowitsch, 1979), these structures are sediment-and predator-free, maintained in a stable orientation, and elevated above the bottom. These shells are therefore optimal substrates with manifold advantages for the epifauna. They serve as a substrate for a diverse community consisting of more than 120 species and a wide range of functional groups and are essentially mobile multi-species clumps (Fig. 10). When these shells are eventually deposited by the crab - after they have been modified by a complex interplay of "constructive" epibionts and "destructive" endolithic forms - the complex community of "symbionts" can survive to form typical multi-species clumps (Stachowitsch, 1980).

Fully developed multi-species clumps in the intact community are important functional units. 87.5% of the biomass consists of filter- and suspension-feeding organi-

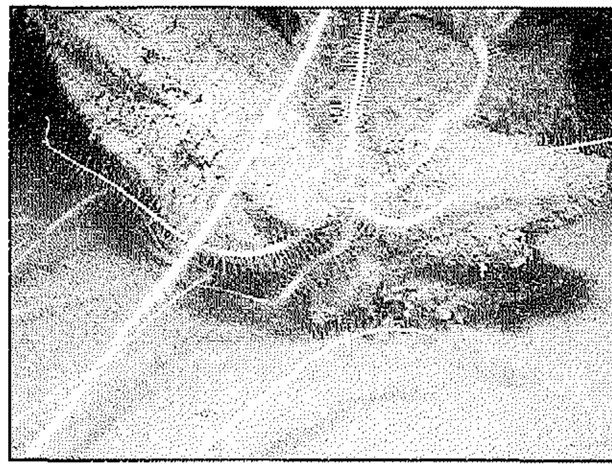

Fig. 10: "Mobile multi-species clump" consisting of large epigrowth carried by the hermit crab** Paguristes eremita **(eyes and antenna of crab visible, bottom center). Epigrowth consists of two ascidians** (Microcosmus vulgaris) **and the bivalve** Arca noae, **the latter bearing several small ascidians** (Distomus variolosus). **Ascidians serve as substrate for brittle stars.

Slika 10: "Gibljiva" večvrstna skupina, sestoječa iz velike obrasti, ki jo nosi rak samotar** Paguristes eremita **(lepo vidne so njegove oči in tipalnice, spodaj v sredini). Obrast sestoji iz dveh kozolnjakov** (Microcosmus vulgaris) **in noetove barčice** Arca noae, **na kateri je več majhnih kozolnjakov vrste** Distomus variolosus. **Kozolnjaki dajejo podlago kačjerepom.

sms. In such shallow environments, the benthos is not merely a receiving compartment. Rather, complex feedback processes, with the benthos controlling the pelagos, are in effect (Figs 11, 12 in Ott, 1991). Ott & Fedra (1977) estimated that the suspension feeders in the Gulf of Trieste can remove all the suspended material in the water column every 20 days. This is on the same order of magnitude as calculated for the Oosterschelde (Herman & Scholten, 1990), Swedish waters (Loo & Rosenberg, 1989), the USA (Cloern, 1982), and France (Hily, 1991). Such communities have therefore been termed a "natural eutrophication control" (Officer *et al.*, 1982). They play a key role in the stability of the entire ecosystem, and their loss makes the system more sensitive to perturbations. The current status of the O-R-M community, with its low biomass, atypical species composition, and altered structure, makes it unlikely that it fulfills its premortality regulatory capacity.

This stabilizing function is hampered by the abovementioned marine snow and oxygen deficiency events. This is compounded by the continuous threat to community structure due to bottom trawling. Such fishing operations are known to have a negative impact on benthic communities (de Groot, 1984; Langton &

Robinson, 1990). This activity is particularly destructive in the Gulf of Trieste, where fishermen can use landmarks to very efficiently space their trawls. The effect is clearly visible on the bottom due to furrow-like markings, destroyed fauna (Figs 6, 7), as well as the repeated demolition of underwater experiments. It is also responsible for unnatural features such as uprooted *Pinna* shells. Only such fishing gear, which snags on the serpulid tubeworms extending from the bivalve's aperture, is capable of extracting these deeply buried bivalves from the sediment (Fig. 8).

Clearly, detailed knowledge of benthic communities, preferably including direct observations, can provide valuable information on the status of the overall system. Three criteria or levels can be called upon to deliver such information: 1) behavior, 2) mortalities, and 3) recolonization.

1.) On the first level, behavioral criteria provide information on an ongoing disturbance. The time scale involves hours, days or weeks. Here, the severity and duration of oxygen deficiency can be gauged by the spectrum of species exhibiting unusual behavior and by the type of behavior exhibited by these species.

2.) On the second level the course of mortalities or the more immediate post-disturbance community composition of surviving species serve as a criteria to gauge anoxias. The time scale is weeks, months, or up to a year or more. The post-mortality absence of only sensitive species or age classes would indicate less severe oxygen depletions, while mortalities of more resistant forms would indicate more severe conditions.

3.) On a third, more long-term level, recolonization processes can provide information on earlier, perhaps undocumented oxygen crisis. The time scale here may involve years, and as in the case of the Northern Adriatic, even decades. A prerequisite for optimal reconstructions is knowledge of former community composition, of opportunistic species, and of successional and possible climax stages. Ideally, knowledge of these processes would allow the time of ecosystem collapses to be pinpointed with accuracy even years after the event. Thus, benthic communities can serve as the memory of recent disturbances (Stachowitsch, 1992). Ultimately, benthic communities also provide information on a fourth level, i.e., the paleontological/ geological record as well.

Many shallow-water marine ecosystems have common physical features and are subject to a similar range of threats and stresses; the reactions of macrobenthos also show parallel features worldwide (Pearson & Rosenberg, 1978; Stachowitsch & Avčin, 1988). This is important in recognizing and gauging such threats and suggesting solutions. The events in the Northern Adriatic Sea are therefore of high predictive value for endangered coastal waters worldwide. More effort should be made to decipher and utilize the information that benthic communities provide.

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POVZETEK

Severni del Jadranskega morja je tako kot mnoge plitve obrežne vode izpostavljen številnim obremenitvam in nevarnostim, med katere sodijo pomanjkanje kisika, morski sneg in ribištvo. Zaradi množičnega umiranja organizmov leta 1983 v tem delu Jadrana je propadla bentoška združba z močno razširjenim arealom.

Dolgoročno zbiranje vzorčnih primerkov med letoma 1984 in 1994 je pokazalo, da si tamkajšnji bentos ni opomogel celo v obdobju desetih let. Raziskovana makroepibentoška združba, sestoječa predvsem iz organizmov, ki se hranijo s filtratom, igra pomembno vlogo v stabilizaciji celotnega ekosistema. Nenehne obremenitve v severnem Jadranu so močno oslabile delovanje te združbe. Reakcije bentosa na motnje kažejo, da takšne združbe niso le natančen kazalec obstoječih razmer, marveč tudi nekakšno skladišče informacij o preteklih dogajanjih. Avtorja menita, da bi se bilo zatorej treba bolj potruditi pri razvozlavanju informacij, ki nam jih daje severnojadranski bentos.

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