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Review paper

The basket shell, *Corbula gibba* Olivi, 1792 (Bivalve Mollusks) as a species resistant to environmental disturbances: A review

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Structural changes in bottom communities in many coastal and offshore areas result from enhanced eutrophication and are characterized by the presence of species that are tolerant to a wide range of environmental disturbances. In soft bottom communities that are degraded or recovering from stress, Corbula gibba *appears to be a highly abundant, ecologically important species and, therefore, an interesting subject for investigation. The literature compiled in this review reveals that,* Corbula *is a short-lived species with high fecundity, enormous production of small eggs, and a prolonged spawning season. The fertilization of spawned eggs in open waters is followed by pelagic development of larvae, accompanied by dispersal sometimes far from the mother population. High larvae settlement frequently appears as a "recruitment boom" in a new community after a catastrophe, making* Corbula *a short-term dominant species until the perished invertebrate species repopulate. As a dominant suspension feeder with rapid juvenile and adult growth,* Corbula *becomes an important element in the food chain as a transferor of organic matter from plankton to benthos. In a relatively stable soft-bottom community, the size of the* Corbula *population is mainly limited by the activity of competitors and predators. Dense* Corbula *populations may occur in a community with low species diversity in constantly and occasionally eutrophic areas. Generally,* Corbula *is considered an indicator of environmental instability caused by pollution, low oxygen content, or increased turbidity.*

Key words: Bivalvia, *Corbula gibba*

INTRODUCTION

The basket shell, *Corbula gibba* (OLIVI, 1792), is a small marine bivalve frequently sampled from soft-bottom communities in European seas. Due to its ecological importance in marine ecosystems, information about *Corbula* appears in many publications. This review is an attempt to amalgamate this information.

REVIEW

Taxonomic position

GINANNI (1757) published the first short notice on the common basket shell under the name *Tellina gibba*, sampled about 14 nautical miles offshore from the Adige estuary in the northwest Adriatic Sea. The name *Corbula gibba* was established later by OLIVI (1792). The species is located taxonomically as follows, according to the Check List of European Marine Mollusca (CLEMAM, MNHN, Paris).

Phylum: Mollusca Linné, 1758

Class:	Bivalvia Linné, 1758
Subclass:	Heterodonta Neumayr, 1884
Order:	Myoida Stoliczka, 1870
Family:	Corbulidae Lamarck, 1818
Species:	*Corbula gibba* (Olivi, 1792: *Tellina*)
Synonyms:	*Tellina gibba* Olivi, 1792
	Mya inaequivalvis Montagu, 1803
	Corbula nucleus Lamarck, 1818
	Tellina olimpica Costa O.G. 1829
	Corbula ovata Forbes 1838
	Corbula nautica Brusina 1870
	Corbula curta Locard, 1886

Evolutionary history

The evolutionary history of the Corbulidae family began in the Tithonian stage of the Late Jurassic period (DÁVID, pers. comm.). Fossil *C. gibba* shells were found in Miocene sediments in marine Badenial marl facies in perturbed coastal areas of Croatia (KOCHANSKY, 1944; SREMAC, 1999), in molluscan clay and marine silty fine grained sandstone in the Late Oligocene in Hungary (DÁVID, 1999a), and in Middle Miocene Korytnica clays of Poland (ZŁOTNIK, 2001).

Geographic distribution

Today, this species is widely distributed in European seas (Table 1), from the Norwegian Sea southward to the Mediterranean and Black Seas (only near the Bosporus) (YONGE, 1946; TEBBLE, 1966; NORDSIECK, 1969; SKARLATO & STAROBOGATOV, 1972; FREDJ, 1974; POPPE & GOTO, 1993). *Corbula* populations are distributed from low intertidal zones to considerable depths (Table 2). Individuals can penetrate down to 250 m (POPPE & GOTO, 1993; SALAS, 1996) and even deeper to 2200 m (NORDSIECK, 1969; FREDJ, 1974), but usually are found at depths to approximately 36 m.

In the late 1980s, *Corbula* was introduced to Australia where, in Port Phillip Bay, it became abundant in benthic communities (WILSON et al., 1998; TALMAN & KEOUGH, 2001). In some areas of this bay, *Corbula* reaches densities up to 2600 indididuals m^{-2} in sandy-muddy sediments at depths of 7-22 m (see Introduction in TALMAN & KEOUGH, 2001), similar to normal *Corbula* habitats in Europe.

Table 1. Selected literature on Corbula gibba *distribution in European seas*

Sea	References
Mediterranean	BONVICINI-PAGLIAI *et al*. (1985); BAKALEN & ROMANO (1988); THEODOROU (1994); SALAS (1996); ZENETOS (1996); BERNASCONI & STANLEY (1997); GIACOBBE & RINELLI (2002); ALBAYRAK *et al*. (2004)
Adriatic	VATOVA (1949); GAMULIN-BRIDA *et al*. (1968); SPECCHI & OREL (1968); ZAVODNIK (1971); HRS-BRENKO (1981, 1997, 2003); LEGAC & HRS-BRENKO (1982); STJEPČEVIĆ *et al*. (1982); SENEŠ (1988); OREL *et al*. (1989); CREMA *et al*. (1991); ALEFFI *et al*. (1992); VIO & DE MIN (1996); ZENETOS (1996); ADAMI *et al*. (1997); HRS-BRENKO *et al*. (1998); MOODLEY *et al*. (1998); ALEFFI & BETTOSO (2000); PEHARDA *et al*. (2002); SOLIS-WEISS *et al*. (2004)
Atlantic Coast	YONGE (1946); TEBBLE (1966); KITCHING *et al*. (1976); PEARSON & ELEFTHERIOU (1981); JENSEN (1988, 1990); SALAS (1996); PRUVET (2000); RUEDA *et al*. (2001)
Kattegat and Baltic	ROSENBERG (1972, 1973, 1974, 1977); ARNTZ (1981), WEIGELT & RUMOHR (1986); BADEN *et al*.(1990), WEIGELT (1990); JOSEFSON & JENSEN (1992); ROSENBERG *et al*. (1992)

Table 2. Selected literature on population densities, sampling depth, and sediment type for Corbula gibba *in various European localities*

Locality	*Density (ind/m^{-2})*	*Depth (m)*	*Sediment type*	*Reference*
Northern Adriatic				
Northern Adriatic	22400*	34-36	Loam	ŠIMUNOVIĆ *et al*. (1999)
Pula harbor	605**	8	...	HRS-BRENKO (1981)
Umag area (Istra)	470	16	...	HRS-BRENKO (1981)
ZI-012 (Istra)	1113**	23	Silty sand	HRS-BRENKO (present study)
Muggia Bay	2570	8-20	Mud	SOLIS-WEISS *et al*. (2004)
Northern Italian coast	4086***	12	Pelite	ALEFFI & BETTOSO (2000)
SJ-101 (Po River)	1217**	31	Clay	HRS-BRENKO (present study)
SJ-10 (Po River)	>1600	30	Silt	HRS-BRENKO (1981)
Ravena area	1001**	15	...	CREMA *et al*. (1991)
Ravena area	1800	18	Silty clay	MOODLEY *et al*. (1998)
Other European Seas				
Saltkällefjord (Sweden)	490	10	Sandy clay	ROSENBERG (1972)
Byfjord (Sweden)	4458	8	Silt	ROSENBERG (1977)
Oresund (Denmark)	1200 juv	18	Silty sand	MUUS (1973)
Limfjord (Denmark)	53000	3-8	Muddy clay	JENSEN (1990)
Limfjord (Denmark)	67000 juv	3-6	Clay	JENSEN (1988)
Dunkerque (France)	1090	...	Muddy sand	PRUVOT *et al*. (2000)
Off Cádiz (Spain)	166	26	Mud	SALAS (1996)
Elefsis Bay (Greece)	1396	20	...	THEODOROU (1994)

*individuals hour^{-1} by trawl ** mean individuals m^{-2} *** individuals 50 l^{-1}

Population density

The population density of *C. gibba* (number of individuals per area) varies in space and time. Literature shows that dense *Corbula* populations are well represented in unstable environments such as constantly polluted bays and harbors and in coastal and offshore areas exposed to seasonal or occasional environmental disturbances. The density in the northern Adriatic is in good agreement with data in the literature (Fig. 1).

Habitat

Corbula, an infaunal species with a sedentary mode of life, inhabits soft bottom sediments mixed with molluscan shell fragments. *Corbula* uses byssal thread to attach to gravel, pebbles, or shell fragments (YONGE, 1946; TEBBLE, 1966; YONGE & THOMPSON, 1976; JENNSEN, 1988; POPPE & GOTO, 1993). Due to interstitial spaces, such sediments create convenient sheltered niches for settlement of *Corbula* larvae and protection from predators. LEGAC & LEGAC (1989) found live individuals inside unbroken amphoras filled with silt and rough sand, collected at depths of 17-31 m. In areas with coarser and clean sandy sediments, *Corbula* populations are rare or absent (HRS-BRENKO, 1981; ŠIMUNOVIĆ *et al.,* 1999; ALEFFI & BETTOSO, 2000).

Having a short siphon, *Corbula* burrows vertically and embeds itself into the upper 0-5 cm of the sediment (YONGE, 1946; ROSENBERG 1974; YONGE & THOMPSON, 1976; MOODLEY *et*

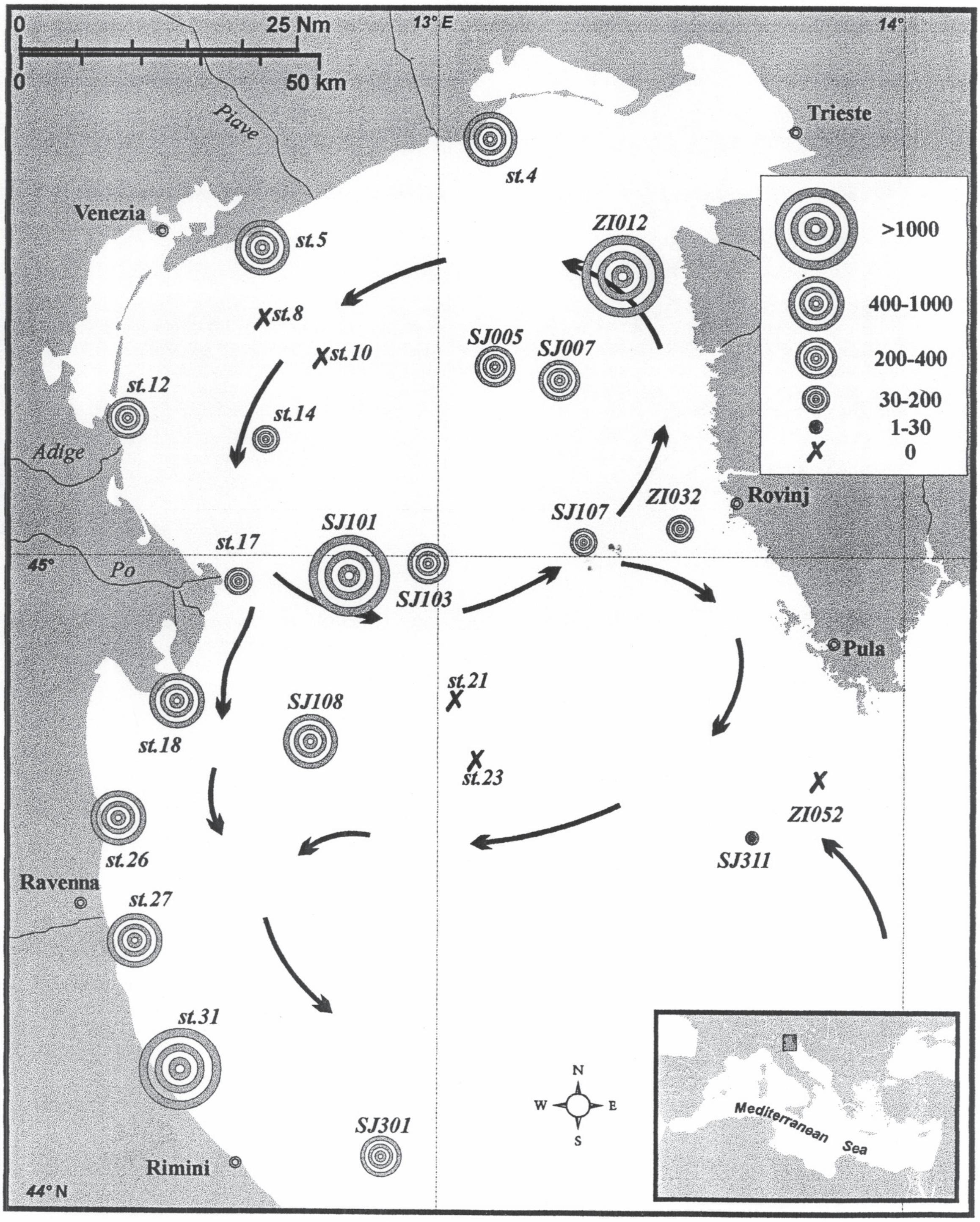

Fig. 1. Population density (individuals m^{-2}*) of* Corbula gibba *in the northern Adriatic Sea and seasonal surface sea currents (marked by arrows; ZORE-ARMANDA & VUČAK, 1984).* Corbula *data for stations (st.) 4, 5, 8, 10, 12, 14, 17, 18, 21, 23, 26, 27, and 31 were obtained by van VEEN grab (original data shown in individuals 0.5* m^{-2} *are converted to individuals* m^{-2}*; ALEFFI & BETTOSO, 2000) and for stations (SJ) 005, 007, 101, 103, 107, 108, 301, 311 and (ZI) 012, 032, 052 by van VEEN grab (HRS-BRENKO, 2003, and unpublished data)*

al., 1998). The burrowing process is slow and described in detail by YONGE (1946). *Corbula* seldom emerge from the sediment unless disturbed (YONGE, 1946). PISAROVIĆ *et al.* (2000) recorded irregular *Corbula* movements in small finger bowls on the sediment surface prior to burrowing. The burrowing furrows are 3-5 mm in height and width. Individuals bury themselves one-third, two-thirds, or entirely. The authors observed that individuals may change position after embedding; they move and bury themselves at night or in darkness during the day.

Spawning season

Corbula produces a large number of small eggs (60 μm diameter), fertilized in open waters (JØRGENSEN, 1946; THORSON, 1950). Information on the *Corbula* spawning season is scarce. GRAEFFE (1903) found many ripe individuals in the Trieste harbor in September while YONGE (1946) registered spawning in early October at the Isle of Cumbrae. BONVICINI-PAGLIAI & SERPAGLI (1988) discovered that June-September is the spawning season, based on complex micro growth patterns with marked growth breaks in thin sections of the shell.

BOON *et al.* (1998) reviewed the relationship between invertebrate reproduction and spring phytoplankton bloom. Polyunsaturated fatty acids, derived from phytoplankton in sedimentary and near-bottom particles, are essential compounds for reproduction and growth of many benthic species (BOON & DUINEVELD, 1996). Reproductive potential, growth, and abundance in the bivalve *Abra alba* increased in eutrophic environments, resulting in three spawning seasons per year instead of two as in oligotrophic conditions (DAUVIN & GENTIL, 1989). After an extraordinarily high phytoplankton bloom in the northern Adriatic Sea in 1989 (DEGOBBIS *et al.*, 2000), *Corbula* probably increased its fecundity and prolonged spawning and settlement seasons throughout almost all of the following year (HRS-BRENKO *et al*., 1994; HRS-BRENKO, 2003), suggesting that *Corbula* may behave similarly to *Abra.*

Larvae development and dispersion

Corbula has a long pelagic larval stage. The length of larvae development in bivalves is usually 2-4 weeks depending on the temperature and available food. In poor food conditions and at low temperatures, larval development is prolonged and often accompanied by high losses due to predation (THORSON, 1950). Until now, few studies focused on larvae development in *Corbula*. Larvae were found in plankton between March and June in the Rovinj harbor and the Limski Kanal in northern Adriatic (ODHNER, 1914). *Corbula* larvae were observed in Danish waters (MUUS, 1973) in October (JØRGENSEN, 1946; SCHRAM, 1962), July-August, October-November, and January-February, with a maximum in July (FOSSHAGEN, 1965). The finding of larvae in plankton in so many months clearly indicates a prolonged reproductive and larvae development season.

A long larvae development period promotes spatial distribution by sea currents, sometimes to considerable distances from parent populations (THORSON, 1950; GIANGRANDE *et al.,* 1994). In such a manner, planktonic larvae constantly expand existing populations in stable and damaged communities and colonize new zones, extending their distribution area.

In a large and relatively enclosed area such as the northern Adriatic Sea, larval distribution (except for diurnal migration between bottom and surface levels) depends on complex water circulation. In the spring, there is an imaginary east-west line between the Po River delta and Rovinj, north of which a cyclonic circulation system transports low salinity waters with silt from the vicinity of the Po River eastwards. This transversal current is accompanied by a southward current from the Po along the Italian coast (ZORE-ARMANDA & VUČAK, 1984; KRAJCAR, 2003). Both currents create ideal bottom conditions for the establishment of dense *Corbula* populations. The cyclonic water circulation encircles a zone north of the Po River-Rovinj line that is often eutrophic with stagnant water and soft bottoms highly populated by *Corbula*. This zone is assumed to be the main source of *Corbula* larvae dispersion throughout the entire northern Adriatic, which is also true for other invertebrates with long pelagic larvae development periods. SPECCHI & OREL (1968) found that the renewal of *Corbula* populations in Muggia Bay depends on immigration of larvae from offshore zones.

Similarly, owing to the local current regime, *Corbula* populations are dense in the inner zones of closed bays, canals, fjords, and harbors characterized by unstable environmental conditions and polluted freshwater inflows. In such cases, the majority of *Corbula* individuals must come from local sources, especially when *Corbula* populations are negligible in neighboring zones (ROSENBERG, 1972, 1973; HRS-BRENKO, 1981; PRUVOT *et al.,* 2000).

Recruitment

Recruitment is the process of larvae settlement and survival to 1 mm (JENSEN, 1988; DAME 1996). In species with long larvae development, such as *Corbula*, the length of the settlement season and its intensity significantly vary between years, depending on food supply, larval dispersion, predation, availability of appropriate bottoms, and environmental conditions (THORSON, 1950; GIANGRANDE *et al.,* 1994).

In high latitudes, MUUS (1973) recorded *Corbula* spat from mid-August to early January, ROSENBERG (1977) observed heavy and successful larvae settlement from September to November, and JENSEN (1988) reported on August and September. In the northern Adriatic, after the 1989 oxygen crisis, the settlement season of *Corbula* extended throughout the entire year of 1990 with a peak in summer at offshore and coastal stations (HRS-BRENKO *et al.,* 1994; HRS-BRENKO, 2003). ALEFFI *et al.* (1993) postulated that prolonged settlement seasons of *Corbula* results from high autumn temperatures and low competition for space after oxygen depletion.

Many studies have shown that *Corbula* settlements boom in favorable environmental conditions following the cessation of a particular stress agent. *Corbula* booms were observed after dredging canals (SPECCHI & OREL, 1968; BONVICINI PAGLIAI *et al*., 1985), in the aftermath of oxygen crises and in oxygen deficient areas (ROSENBERG, 1977; OREL *et al.,* 1989; BADEN *et al.,* 1990; ALEFFI *et al.,* 1992, 1993; HRS-BRENKO *et al.,* 1992b, 1994), and after cessation of industrial waste water discharges (ROSENBERG, 1972, 1973). In such circumstances, *Corbula* tends to aggregate thanks to the low species diversity in the bottom community (ROSENBERG, 1977).

The boom phenomenon characterizes *Corbula* as an opportunistic bivalve that, together with some invertebrates, immediately colonizes destroyed communities. In general, abundant *Corbula* juveniles indicate areas where an environmental disaster recently happened and damaged communities are in the early recovery phase. BONVICINI-PAGLIAI & SERPAGLI (1988) called *Corbula* an environmental stress species and a “time recorder” that indicates the beginning of macrofaunal succession after a catastrophe.

Growth and life span

JØRGENSEN (1946) and MUUS (1973) recorded the length of *Corbula* in the prodissoconch stage (0.24-0.25 mm), at metamorphosis (0.25-0.33 mm), and after settlement (0.30-0.60 mm). Settled bivalves smaller than 2 mm are meiofauna, staying in this assemblage for about one month (THORSON, 1966).

The distribution of mean shell lengths of *Corbula* in Limfjord, Denmark (JENSEN, 1990) and length frequencies in the northern Adriatic (HRS-BRENKO, 2003) show that *Corbula* grow rapidly in spring and early summer. According to JENSEN (1990), *Corbula* growth ceases at temperatures below 13°C (October-May) while HRS-BRENKO (2003) observed the same phenomenon in winter. The increase in length during spring corresponds to the increased abundance of resuspended organic matter near the bottom and the bottom-living diatoms and bacteria that *Corbula* siphons from the bottom surface (YONGE, 1946; JENSEN, 1990). As an active suspension feeder, *Corbula* is an important transferor of organic matter to the benthos. This was evident during the early recovery period in 1990 when *Corbula* dominated the bottom community (HRS-BRENKO, 2003).

Table. 3. Mean length at about one year and maximum length in second year of Corbula gibba

Locality	Mean length (mm)	Maximum length (mm)	Author
Isle of Man	8	12.0	JONES (1956) see: MUUS (1973)
Limfjord	6-7	10.8	JENSEN (1988, 1990)
Northern Adriatic	7-10	13.5	ALEFFI & BETTOSO (2000)
Northern Adriatic	6-8	14.7	HRS-BRENKO (2003)

Corbula reaches its maximum length at 16 mm (NORDSIECK, 1969). In the northern Adriatic, the longest *Corbula* specimen measured 14.7 mm (HRS-BRENKO, 2003). The scarce data on mean and maximum lengths of *Corbula* show similar growth patterns in various study areas during a two-year period (Table 3). *Corbula*, like other small benthic species, has a short life span of about two years with natural mortality beginning at 10 mm in the second year (ROSENBERG, 1977; JENSEN, 1990; ALEFFI *et al.*, 1993; HRS-BRENKO, 2003).

Survival: abiotic stress agents

Corbula, an inhabitant of unstable environments, tolerates anthropogenic and natural disturbances. In bays, fjords, and harbors with excessive organic matter (domestic and industrial wastes, oil, etc.), *Corbula* can develop dense populations because of the low species diversity in the community (GRAEFFE, 1903; ROSENBERG, 1972, 1973, 1977; HRS-BRENKO, 1981; BAKALEM & ROMANO, 1988; JENSEN, 1990; THEODOROU, 1994; ADAMI *et al*., 1997; BORJA *et al*., 2000; PRUVOT *et al*., 2000; SOLIS-WEISS *et al*., 2004). For this reason, *Corbula* is a bioindicator of pollution of sea bottom communities (FAO/UNEP, 1986) and belongs to the ecological group of r-selected species (GRAY, 1979; GIANGRANDE et al., 1994).

In addition to its pollution tolerance, *Corbula* is an oxygen resistant species (ROSENBERG, 1977; DIAZ & ROSENBERG, 1995). It survives well for certain periods in low oxygen conditions but may diminish in prolonged hypoxia (BADEN *et al.,* 1990). This high oxygen resistance was confirmed in laboratory experiments in which adult *Corbula* survived several days in the anaerobic conditions of starfish stomachs (CHRISTENSEN, 1970).

In a comprehensive review on the effects of hypoxia on benthic fauna, only *Corbula* survived mass mortality events (DIAZ & ROSENBERG, 1995). This was true in a sea loch, Lough Ine; (KITCHING *et al.,* 1976) and in the innermost part of a fjord in the Shetland Isles (PEARSON & ELEFTHERIOU, 1981). *Corbula* survived together with a few other species in Kiel Bay (ARNTZ, 1981; WEIGELT & RUMOHR, 1986; WEIGELT, 1990) and the Kattegat area (BADEN *et al*., 1990; JOSEFSON & JENSEN, 1992; ROSENBERG *et al.,* 1992). *Corbula* dominated in hypoxic water layers that covered anoxic layers in the Byfjord Estuary (ROSENBERG, 1977) while only *Corbula* was recorded in polluted Elefsis Bay in the Mediterranean in summer during strong thermal stratification accompanied by anoxic conditions (THEODOROU, 1994). *Corbula* survived frequent oxygen disasters in a sensitive northern Adriatic ecosystem (ALEFFI *et al.,* 1992; HRS-BRENKO *et al.,* 1992a, 1992b, 1994). Numerous live *Corbula* individuals were found among bottom deposited bivalve shells in the Malo Jezero salt lake (southern Adriatic) that is unpolluted but occasionally stressed with sulfide (PEHARDA *et al.,* 2002).

Corbula is resistant to high turbidity thanks to its ctenidia that efficiently separate organic from inorganic particles in resuspended bottom material (KIØRBOE & MØHLENBERG, 1981). Further, the asymmetric construction of the *Corbula* shell provides for better outflow of large amounts of pseudofeces (YONGE, 1946; YONGE & THOMPSON, 1976). Such features enable *Corbula* to form dense populations and survive in soft bottoms in closed bays with high sedimentation and reduced hydrodynamism (SOLIS-WEISS *et al.,*

2004) as well as in silted transversal currents in the northern Adriatic (HRS-BRENKO, 2003).

Most bivalve species protect themselves from temporary environmental stress by tightly closing their valves. *Corbula* does this well thanks to its special valve construction that allows hermetic shell closure (YONGE, 1946; YONGE & THOMPSON, 1976; BONVICINI-PAGLIAI & SERPAGLI, 1988). Shells formed in such a way keep the valves fast even after death. Many *Corbula* individuals sampled in the Adriatic with closed shells were either empty or filled with mud. This finding calls for careful inspection of whether *Corbula* individuals were alive at the time of sampling.

In addition to closing shells, bivalves have a protective mechanism that switches them to anaerobic metabolism by increasing the lactate concentration in the tissues (PISAROVIĆ *et a*l., 2000; ŽERJAV MEIXNER, 2000). Later, when normoxic conditions return, *Corbula* increases oxygen consumption for a short period of time to cover its "oxygen debt" during which accumulated anaerobic metabolic products are eliminated.

Survival: biotic stress agents

Predation and competition are important biotic causes of losses of bivalve larvae, juveniles, and adults. During planktonic life, *Corbula* larvae can be preyed upon by ctenophores, jellyfish, copepods, invertebrate larvae, and pelagic fish. Mature larvae swimming near the bottom or crawling on the sediment are eliminated by suspension feeders. Surface and subsurface carnivores, deposit feeders, and omnivores prey on *Corbula* juveniles and adults. Finally, intra and interspecies competition for food and space significantly regulates species abundance in a bottom community (THORSON, 1950, 1966; MUUS, 1973; MILEIKOVSKY, 1974; CROWE *et al.,* 1987; JENSEN, 1988; KELLEY, 1988; MORTON, 1991; AMBROSE, 1993; ANDRÉ *et al.,* 1993; SEED, 1993; GIANGRANDE *et al.,* 1994; ÓLAFSON *et al*., 1994; DAME, 1996; HRS-BRENKO, 1998; MOODLEY et al., 1998, ZŁOTNIK, 2001). All these aspects create a complex interaction of biotic factors that plays an important role in structuring benthic communities.

In spite of scarce evidence relating to meiofaunal and macrofaunal exterminators of *Corbula*, it is possible to speculate about its fate in the environment by considering the bivalve-predator and bivalve-competitor interactions mentioned above. Larger meiofaunal species may be active predators on recently settled *Corbula* larvae. If so, the reduced abundance of meiofaunal species (TRAVIZI, 2000) after the oxygen disaster in the Adriatic may have partly contributed to the simultaneous increase of the *Corbula* population during the ensuing six-month recovery period (HRS-BRENKO *et al.,* 1994).

At the macrofaunal level, in a stable bottom community, suspension feeders may accidentally inhale *Corbula* larvae during intensive filtration, decimating them prior to settlement. The ophiuroid *Amphiura filliformis*, a suspension feeder, may ingest larvae and newly settled juveniles of many invertebrates (CROWE *et al.*, 1987). The question is whether the period spent within the body of a suspension feeder is fatal for *Corbula* larvae. In the absence of numerous suspension feeders, *Corbula* may benefit from the low competition for space between survived invertebrates and among settling *Corbula* larvae. As with the bivalve suspension feeder, *Cerastoderma edule* (ANDRÉ *et al.,* 1993), *Corbula* may eliminate its own settling larvae and thus limit settlement intensity in areas where adults are abundant (JENSEN, 1988, 1990). It seems that such an adult-juvenile interaction occurred after the 1989 oxygen crisis in the northern Adriatic where the dominant adult population of 800 m^{-2} may have postponed the larvae settlement peak to the summer; meanwhile, at another station, the adult density of only 153m^{-2} allowed high recruitment already in February. In this case, of course, other suspension feeders were also limiting settlement factors.

Competition for food and space can limit the *Corbula* population. For example, the bottom-dwelling *C. gibba* competes for food and space with another suspension feeding species, the off-bottom amphipod *Amphelisca* sp. (MOODLEY *et al.*, 1998). When present in dense populations, *Amphelisca* consume detritus before it reaches the *Corbula* at the bottom, limiting the *Corbula* population. After widely occupying its new environment in Australia, *Corbula* significantly affected the juvenile size and growth of the native scallop *Pecten fumatus*, as both species are suspension feeders (TALMAN & KEOUGH, 2001). Another example of food competition was observed during the heavy *Corbula* settlement in February 1990, which was followed by mortality up to 45% in the 2.5 mm length class in March. Shells of sampled individuals were closed, empty, tiny, transparent, but undamaged. Without doubt, they were not eaten by predators but apparently died due to food limitation in the new densely populated community. ÓLAFSON *et al.* (1994) proposed that food limitation is a more important cause of mortality in newly settled invertebrates than in adults. JENSEN (1988) attributed the high mortality of *Corbula* juveniles (up to 31% in the first month after settling) to epibenthic predation while JENSEN (1990) attributed adult mortality to weakness after spawning.

Carnivorous gastropods, mobile crustaceans, starfishes, fishes, and birds are among the destructive bivalve predators. Predator-prey studies have mostly focused on commercial bivalves from shallow coastal and estuarine areas (MORTON, 1991; SEED, 1993; ÓLAFSON *et al.,* 1994; DAME, 1996). Little data related to predators of *Corbula* have been published.

Starfishes are voracious *Corbula* predators and frequently contain *Corbula* individuals in their stomachs (CHERBONNIER, 1966; SPECCHI & OREL, 1968; CHRISTENSEN, 1970; MILEIKOVSKY, 1974; JENSEN, 1988; POPPE & GOTO, 1993). In laboratory experiments, *Astropecten irregularis* excreted live *Corbula* adults several days after they were swallowed, which was not the case with juveniles of 2-3 mm (CHRISTENSEN, 1970). *Asterias rubens* and *Ophiotrix texturata* are also possible predators of juvenile *Corbula* immediately after settlement (JENSEN, 1988).

Since the Paleozoic era, carnivorous gastropods from the Muricidae and Naticidae families, predominantly *Natica* sp. and *Euspira* (*Polynices*) sp., have attacked infaunal suspension feeding mollusks including *Corbula* by drilling holes in their shells (JEFFREYS, 1865, in YONGE, 1946; KOCHANSKY, 1944; KELLEY, 1988; MORTON, 1991; DÁVID, 1999a, b; SREMAC, 1999; ZŁOTNIK, 2001). The drilling process is described in ZIEGELMEIER (1954), YONGE & THOMPSON (1976), and others (see ZŁOTNIK, 2001). Large naticids prefer to attack the right valve of *Corbula* in the central-ventral region, while small naticids drill more or less equally into both valves (ZŁOTNIK, 2001). DÁVID (1999b) found more boreholes in the right valve and rounded boreholes were more common than sickle perforations. Round boreholes were made by *Natica* sp. (YONGE & THOMPSON, 1976; DÁVID, 1999a; PISAROVIĆ *et al.,* 2000; ZŁOTNIK, 2001). Although *Corbula* dominate over other invertebrate species in fossils and recent bottom samples, only 8% (PISAROVIĆ *et al.,* 2000) to 17-20% (ZŁOTNIK, 2001) were attacked by boring gastropods. All sizes of *Corbula* were attacked, but completely perforated boreholes were relatively rare. On the shell of a 2.7 mm Adriatic *Corbula*, only one of three boreholes was completely perforated. Owing to variation in shell thickness and a dense inner calcareous shell layer, *Corbula* is better protected against gastropod acid secretion than other bivalve species (YONGE, 1946; BONVICINI-PAGLIAI & SERPAGLI 1988; KELLEY, 1988; DÁVID, 1999b; ZŁOTNIK, 2001).

The crustaceans *Carcinus means* and *Crangon crangon* may also prey on *Corbula* (JENSEN, 1988) by smashing or chipping their shells. Fish from the Sparidae family and flat fishes from the Heterosomata order (KOVAČIĆ, pers. comm.) may swallow whole *Corbula* individuals. Many of these predators disappear from bottom communities when the oxygen level begins to drop. In such cases, the fish species either die or escape to normoxic areas, increasing fish catches there (STEFANON & BOLDRIN, 1982; DYER *et al*., 1983; ŠIMUNOVIĆ *et al*., 1999). In the interim, until predator fish species repopulate the damaged bottom communities either by returning as adults or by new recruitment, opportunistic species such as *Corbula* may proliferate.

CONCLUSIONS

Corbula gibba (Olivi, 1792) is a widespread European bivalve with an evolutionary history dating back to the Paleozoic era. Dense *Corbula* populations are established in soft bottom communities with low species diversity and in constantly or occasionally unbalanced environments. The populations are distributed from low intertidal zones to considerable depths, but optimally down to approximately 36 m. In deeper coarser and clean sandy sediments, *Corbula* populations are rare or absent.

As an infaunal sedentary species, *Corbula* inhabits soft sediments mixed with gravel and molluscan shell fragments that are necessary for byssal thread attachment. Having a short siphon, *Corbula* burrows vertically near the sediment surface and emerges when disturbed. *Corbula* displays a light/dark reaction and burrows in dark conditions.

The scarce literature indicates *Corbula* has a prolonged reproductive season during which it produces many small eggs that are fertilized in open water. The pelagic larvae development period extends throughout the year. *Corbula* take advantage of favorable sea currents and human activities to expand existing populations, increase populations in damaged communities, and colonize new areas. The potential of *Corbula* recruitment is evident in damaged, degraded, and newly occupied areas where “recruitment booms” may occur in summer and autumn. As such, *Corbula* functions as an indicator of the recovery of the bottom community.

As a suspension feeder, *Corbula* uses mainly decomposed and resuspended organic matter to increase its fecundity and juvenile and adult growth rates. Thus, *Corbula* is an important participant in the flow of energy to the benthos, particularly when it is dominant in the community.

Corbula tolerates a wide range of abiotic environmental disturbances. For this reason *Corbula* is a bioindicator of pollution, turbidity, and low oxygen content in benthic communities. Biotic factors, such as competition and predation, are the main factors that limit the expansion of *Corbula* populations in a stable community. In stressed environments, *Corbula* dominates until its most sensitive competitor and predator recovers it own population. Voracious macrofaunal predators are starfishes, demersal fishes, and crabs, while carnivorous gastropods attack *Corbula* only occasionally, thanks to its hard shell and dense inner calcareous shell layer that is resistant to the acidic secretions of gastropods.

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Školjkaš korbula, *Corbula gibba* (Olivi, 1792) (Bivalve Mollusks), otporna vrsta na poremećaje u okolišu. Pregledan rad

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SAŽETAK

Školjkaš korbula, Corbula gibba (Olivi, 1792), je rasprostranjena vrsta u evropskim morima i često je obilna u nestabilnim i eutrofiziranim sredinama. Zapažena kao ekološki važna vrsta u obnovi pridnenih zajednica u sjevernom Jadranu, nakon učestalih ugibanja vrsta makrobentosa uzrokovanih nestašicama kisika, korbula se smatrala zanimljivom vrstom za istraživanja populacijskih karakteristika. Pregled do sada objavljenih radova o korbuli ukazuje da je to mala kratko živuća vrsta visokog reprodukcijskog potencijala s obilnom proizvodnjom malih spolnih stanica tijekom produžene sezone mriješćenja. Oplodnja jajnih stanica i razvoj ličinki u planktonskoj zajednici omogućuje njeno širenje u nova područja, kao i u područja osiromašena vrstama nakon katastrofalnih ugibanja. Slobodni prostori, nastali nakon ugibanja brojnih vrsta u pridnenoj zajednici, omogućuju korbuli intenzivno naseljavanje novacima, u prvoj fazi obnove makrobentosa. Tada kao dominirajuća «suspension feeding» vrsta korbula postaje važnim prenosnikom proizvedene organske tvari iz fitoplanktona u bentos. U kasnijem periodu obnove pridnenih zajednica znatno se smanjuje veličina populacije korbule. Čini se da tome pridonosi kratak životni vijek korbule kao i obnova predatorskih vrsta. Sažeto rečeno korbula se zbog svoje otpornosti prema učestalim promjenama sredine smatra indikatorom nestabilnosti, najčešće uzrokovanim sniženjem slanoće morske vode, te pojačanim turbiditetom i zagađivačima, u okolišu snižene bioraznolikosti.

Ključne riječi: Bivalvia, *Corbula gibba*