

# Organism responses to habitat fragmentation in two shallow-water brackish environments: the Goro Lagoon (Adriatic Sea) and the Padrongiano Delta (Tyrrhenian Sea)

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*Habitat fragmentation from natural or human-mediated causes is a common phenomenon in terrestrial and aquatic environments. In this study, the effects of varying the size of habitat patches on the abundance of benthic invertebrates inhabiting date mussel (*Musculista senhousia*) patches was studied at two different transition environments, the Goro Lagoon (Adriatic Sea) and the Padrongiano Delta (Tyrrhenian Sea). Benthic fauna responded to habitat patchiness in a complex manner that varied according to habitat type, taxon and animal body size (small: 0.5–2.0 mm; large >2 mm). Small invertebrates were mostly polychaetes, nemertea, amphipods and isopods. Large invertebrates were mostly large polychaetes, bivalves, gastropods and crabs. Invertebrate population size and diversity seemed to be maximized in landscapes that include both small and large patches of mussel beds 'embedded' in a continuous matrix. *Musculista senhousia* patches served as a critical refuge and foraging habitat for many species. Patchy and continuous areas may promote the persistence of organisms with different life histories, especially in environments like those studied where mussel patches represent the only structural refuge available.*

**Keywords:** organism responses, habit fragmentation, shallow-water brackish environments, Goro Lagoon (Adriatic Sea), Padrongiano Delta (Tyrrhenian Sea)

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## INTRODUCTION

Habitat fragmentation is a recognized threat to biodiversity in marine ecosystems, and its consequences have been recently considered (Bell *et al.*, 2001). Patchy habitats are not necessarily poor quality habitats, rather the combination of patchy and contiguous habitats in a given area may be required to maximize diversity, particularly if certain taxa demonstrate an affinity for isolated habitat patches (Healey & Hovel, 2004). In nearshore marine ecosystems, complex benthic habitats such as sea grass and algal beds, oyster reefs and mussel beds, possess a suite of spatial and ecological characteristics that make them amenable to assess the effects of habitat patchiness on animal abundance (Eggleston *et al.*, 1999; Ragnarsson & Raffaelli, 1999; Bell *et al.*, 2001; Roberts & Poore, 2005). Mussel beds, for example, range in size from small intertidal patches of less than 1 m<sup>2</sup>, to continuous subtidal structures over hundreds of hectares. For soft-sediment, aquatic invertebrates, the spacing of mussel shell among unstructured flat bottoms is large (up to hundreds of

metres) compared to their body size (0.5–10 mm). Moreover, mussels themselves create a secondary space or habitat within which different (from the surrounding bare sediment matrix) animal assemblages can develop (Ragnarsson & Raffaelli, 1999). In such mosaics, it is of great importance how an organism perceives the habitat. Smaller organisms might have a different perception of a mosaic of habitat patches in respect to larger organisms (Kotliar & Wiens, 1990), thus, abundance of small invertebrates might change significantly to varying patch size more often than abundance of large invertebrates.

*Musculista senhousia* Benson in Cantor 1842, is a mytilid bivalve native from Asia which has recently spread throughout Mediterranean lagoons and estuaries (Hoenselaar & Hoenselaar, 1989; Mastrototaro *et al.*, 2003; Mistri, 2003). The species is defined as 'an ecosystem engineer' (Crooks, 2001), since individuals aggregate with byssal filaments in dense patches (over 10,000 ind m<sup>-2</sup>) in the upper layer of estuarine and lagoonal soft sediments. Mussels create novel three-dimensional episurface structures that can provide increased habitat heterogeneity on an otherwise soft bottom, including hard-surface areas and crevices, holes or cracks for the colonization of sessile and mobile species (Mistri *et al.*, 2004). Moreover, by removing a huge volume of suspended organic material from the water column, *M. senhousia* deposits that

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filtered material on the bottom as faeces and pseudofaeces and modifies the nutritional quality of sediments (Mistri *et al.*, 2003). Natural patches of *M. senhousia* vary in size, ranging from less than 0.50 m<sup>2</sup> to over 100 m<sup>2</sup> (Creese *et al.*, 1997).

In this study, the main effects of *M. senhousia* patch size and habitat diversity on benthic invertebrates were examined, considering taxa and body size. Specifically, two main questions were addressed: (1) does the abundance of fauna vary with the size of naturally occurring patches of the mussel *M. senhousia*?; and (2) do small and large invertebrates perceive habitat patchiness in the same way?

## MATERIALS AND METHODS

### Study sites

Sampling was conducted on the sub-tidal flats of two Mediterranean, microtidal waterbodies, the Goro Lagoon and the Padrongiano Delta (Figure 1), where *Musculista senhousia* has been present in high abundance for several years (Mistri *et al.*, 2004). The Goro Lagoon (44°50'10 N 12°17'40 E, Adriatic Sea) is located in the southernmost Po Delta area, and receives nutrient rich fresh water primarily from two deltaic branches of the Po river. Average depth is about 1.5 m, and the sediment is muddy sand. The Padrongiano Delta (40°55'09 N 09°32'31 E, Tyrrhenian Sea) is located in north-eastern Sardinia, and receives polluted waters from the Olbia harbour, the most important industrial and tourist port of Sardinia. Average depth is about 1.0 m, and the sediment is coarse sand.

### Sampling of the matrix and natural patches of varying size

The effect of changes to the configuration of habitats is commonly examined by classifying the landscape as areas that support the organisms of interest (habitat patches)

and the remaining areas (the matrix) (Wiens, 1995). The relationship between the size of naturally occurring patches of *M. senhousia* and the abundance of fauna was examined by sampling mussel beds from each of two different patch size-classes. Patches were classified as small (SM, greatest patch dimension smaller than about 1.0 m<sup>2</sup>) and large (LG, greatest patch dimension larger than about 10.0 m<sup>2</sup>). Four small and four large patches were sampled in March, July and October 2003. Each patch was separated by at least 100 m from neighbouring habitat patches. Invertebrates from the matrix habitat (MX, bare sediments) among the patches of *M. senhousia* were also sampled (four randomly-chosen plots at each sampling date). Fauna was collected with a Van Veen grab. The contents of the grab were washed on a 0.5 mm sieve. The material retained on the sieve was preserved in 8% buffered formalin, and stained with Rose Bengal to facilitate sorting and identification. Invertebrates were identified at the species level, then measured by length and divided into 2 classes of body size: small (0.5–2.0 mm) and large (>2.0 mm).

### Statistical analysis

The interactive effect of habitat type (SM, LG and MX) on large and small invertebrates (after the exclusion of *M. senhousia*) was analysed using six response variables: (1) total number of large species; (2) total number of small species; (3) total number of large crustaceans; (4) total number of small crustaceans; (5) abundance of large individuals; and (6) abundance of small individuals. Small invertebrates were mostly polychaetes, nemertea, amphipods and isopods. Large invertebrates were mostly large polychaetes, bivalves, gastropods and crabs. Each response variable was analysed with a separate two-way ANOVA with habitat type (SM, LG and MX) and time (March, July and October) as factors. Heteroscedastic variances were corrected with log-transformation. Differences between means were revealed with a lower-level ANOVA, or a Tukey's comparison test.

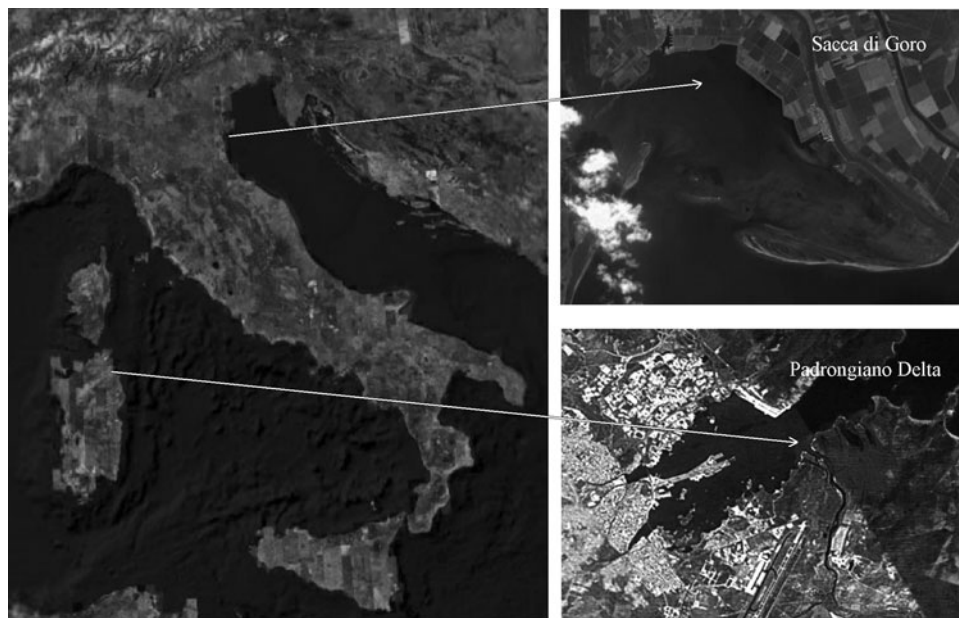


Fig. 1. Study sites: Goro Lagoon (northern Adriatic Sea) and Padrongiano Delta (north-eastern Tyrrhenian Sea).

## RESULTS

A total of 33 invertebrate taxa were found in the Goro Lagoon, and 115 in the Padrongiano Delta. Analysis of similarities (Clarke & Warwick, 1994;  $R = 1.0$ ) confirmed sharp differences in invertebrate assemblages between the two study sites, reflecting biogeographical differences. In Appendix A, the taxonomic list of the fauna collected at the two study sites is reported.

Abundance of *Musculista senhousia* within beds greatly varied with time (Figure 2). Single specimens or small clumps (abundance  $< 20$  ind clump<sup>-1</sup>) of the mussel were also found in the matrix, far from the beds, at Goro (March) and Padrongiano (October). At both sites, mussel abundance was significantly higher at LG (one-way ANOVA, all  $P < 0.001$ ) in March and July, while in October it was similar at LG and SM (one-way ANOVA,  $P = \text{NS}$ ), suggesting a differential mussel mortality within large patches.

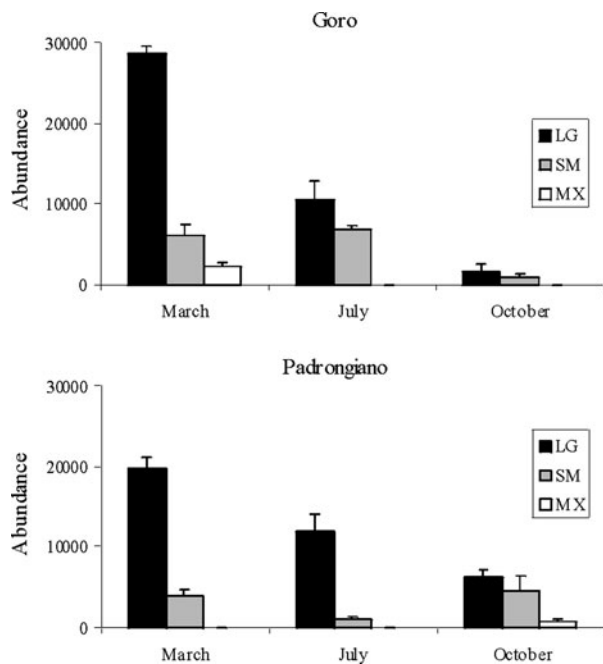
In the Goro Lagoon, a two-way ANOVA (factors: habitat heterogeneity and time; Table 1) revealed differences in the number of large species in response to both habitat type ( $P < 0.05$ ) and time ( $P < 0.001$ ). No differences were found on the number of small species due to habitat heterogeneity, while significant seasonal variations (one-way ANOVA;  $P < 0.001$ ; all pairwise comparisons:  $P < 0.01$ ) were detected. Large crustaceans (Table 2) responded to both habitat heterogeneity ( $P < 0.001$ ) and time ( $P < 0.001$ ). The interaction term was significant ( $P < 0.001$ ), revealing complex dynamics. Post-hoc tests showed significant higher numbers of large crustaceans at MX. Small crustaceans responded only to time (one-way ANOVA;  $P < 0.001$ ; all pairwise comparisons:  $P < 0.01$ ). Habitat heterogeneity had an effect upon the abundance of large invertebrates ( $P < 0.001$ ), as well as time ( $P < 0.001$ ); there were also significant interactions among the main effects (Table 3). Upon the abundance of small invertebrates, only the main factor time had an effect ( $P < 0.001$ ). Independently from the organism size,

**Table 1.** Goro: two-way ANOVA on the number of large species. Factors: habitat heterogeneity (HH) and time (T). Significant Tukey pairwise tests are also shown.

Factor	F	P	Tukey pairwise test	P
HH	3.52	0.04	MX > LG	0.03
T	11.26	0.001	Mar > Oct	0.02
			Mar > Jul	0.001
HH × T	5.49	0.002	MX Mar > LG Mar	0.002
			MX Mar > MX Jul	0.001

opportunistic species (*sensu* Borja *et al.*, 2000) represented 52.6% and 53.2% of the total density at LG and SM, respectively, while they accounted for only 21.5% of the total number of organisms at MX. Sensitive species were abundant at MX, representing 42.3%, 12.5% and 17.6% of total abundance of organisms at MX, LG and SM, respectively.

In the Padrongiano Delta, both factors habitat type and time had an effect on the number of large species (Table 4) and large crustaceans (Table 5), with significant interactions among the main effects. The number of large species and crustaceans were always significantly higher at SM and LG with respect to MX. Time had an effect on the number of small species (one-way ANOVA;  $P < 0.001$ ; all pairwise comparisons:  $P < 0.001$ ), and the number of small crustaceans (one-way ANOVA;  $P < 0.001$ ; all pairwise comparisons:  $P < 0.01$ ). A higher abundance of large invertebrates occurred in SM samples (one-way ANOVA;  $P < 0.001$ ), while a higher abundance of small invertebrates occurred in MX samples (one-way ANOVA;  $P < 0.01$ ), in March. Opportunistic species at LG accounted for 40.6% of all collected organisms; at SM and XM they represented 51.9% and 53.5% of total density, respectively. Differences among the types of habitat were more evident for sensitive species, which represented 32.6%, 34.3% and 52.2% at MX, SM and LG, respectively.



**Fig. 2.** Abundance (individuals m<sup>-2</sup>) of *Musculista senhousia* at the study sites (bars are SE).

## DISCUSSION

This study provides evidence that the response of an organism to the spatial arrangement of habitats is dependent upon the joint effects of habitat type and body size. At the two study sites, benthic invertebrates responded to habitat heterogeneity in a complex manner that varied according to species, animal body size, and type of environment. Moreover, *Musculista senhousia* was likely playing a double role: (1) as secondary substratum, enhancing the environmental structural complexity; and (2) as densely aggregated, living organisms, thus giving rise to a number of possible interactions with other

**Table 2.** Goro: two-way ANOVA on the number of large crustaceans. Factors: habitat heterogeneity (HH) and time (T). Significant Tukey pairwise tests are also shown.

Factor	F	P	Tukey pairwise test	P
HH	8.83	0.001	MX > LG	0.001
			MX > SM	0.02
T	25.86	0.001	Mar > Oct	0.001
			Mar > Jul	0.001
HH × T	15.76	0.001	MX Mar > LG Mar	0.001
			MX Mar > SM Mar	0.001

**Table 3.** Goro: two-way ANOVA on the abundance of large organisms. Factors: habitat heterogeneity (HH) and time (T). Significant Tukey pairwise tests are also shown.

Factor	F	P	Tukey pairwise test	P
HH	30.79	0.001	LG > MX	0.001
			SM > MX	0.001
T	79.19	0.001	Mar > Jul	0.001
			Mar > Oct	0.001
			Jul > Oct	0.001
			SM Mar > LG Mar	0.007
HH × T	13.12	0.001	SM Mar > MX Mar	0.001
			SM Mar > SM Oct	0.001
			SM Mar > SM Jul	0.001
			SM Jul > SM Oct	0.001
			SM Jul > MX Jul	0.001
			LG Mar > LG Oct	0.001
			LG Jul > LG Oct	0.007
			LG Jul > MX Jul	0.001
			MX Mar > MX Jul	0.001
			MX Mar > MX Oct	0.001

invertebrates. Mussel patches had a likely gross structural effect, but at extremely high mussel density (e.g. Goro, LG and March), the effect seemed to be opposite. The architectural complexity of mussel beds results from the number, shape, and size–frequency of mussels (Eggleston *et al.*, 1998; Ragnarsson & Raffaelli, 1999; Commito & Rusignuolo, 2000). Final conclusions on the role of scale-dependent biotic processes underlying interactions between animal body size, patch size, and habitat type on invertebrate abundance remains to be determined experimentally.

Although the mechanisms underlying invertebrate abundance patterns described in this study remain unknown, the results suggest that certain groups of invertebrates may be more sensitive to habitat fragmentation. In general, large invertebrates were more sensitive to habitat patchiness. At both sites, small species did not show any response to a supposed edge effect, notwithstanding small patches should give a higher surface area to intercept for small species, due to the high perimeter–area ratio. Conversely, large organisms responded to habitat fragmentation and patch size, showing higher abundance alternatively at LG and SM, depending on time. It should be noticed that large species were mostly predators (crabs and snails: *Brachynotus sexdentatus*, *Nassarius corniculus*, *Haminoea navicula* and *Hexaplex trunculus*) that at LG probably found higher numbers of prey. Small prey organisms, as well as small predators (e.g. *Schistomeringos rudolphii*) probably avoided frequent encounters with large

**Table 4.** Padrongiano: two-way ANOVA on the number of large species. Factors: habitat heterogeneity (HH) and time (T). Significant Tukey pairwise tests are also shown.

Factor	F	P	Tukey pairwise test	P
HH	7.31	0.003	LG > MX	0.016
			SM > MX	0.004
T	10.94	0.001	Mar > Jul	0.001
			Oct > Jul	0.007
			SM Mar > SM Jul	0.027
HH × T	2.75	0.049	SM Oct > SM Jul	0.003
			SM Oct > MX Oct	0.018

**Table 5.** Padrongiano: two-way ANOVA on the number of large crustaceans. Factors: habitat heterogeneity (HH) and time (T). Significant Tukey pairwise tests are also shown.

Factor	F	P	Tukey pairwise test	P
HH	6.35	0.005	LG > MX	0.022
			SM > MX	0.008
T	4.56	0.02	Oct > Jul	0.023
HH × T	3.54	0.019	SM Oct > SM Jul	0.045
			SM Oct > MX Oct	0.045

predators refuging at SM and MX. It is noteworthy that in March, in the Goro Lagoon, large crustaceans responded to habitat heterogeneity preferring MX. It must be stressed, however, that the majority of such large crustaceans were not predators, but tube-builder *Ampelisca*, which probably suffered hard competition for space within mussel beds. *Ampelisca* is a brooder, able to rapidly build-up large populations in spring. The tubes increase the spatial heterogeneity of the habitat at MX, and other species are able to coexist with the amphipod, subsequently explaining the elevated number of invertebrate species found in the matrix at March. Conversely, large predatory crabs, such as *Rhithropanopeus harrisi* and *Carcinus aestuarii*, preferred, as at Padrongiano, the LG habitat. Differences in predation pressure between fragmented and contiguous habitats may shape the responses of communities to habitat configuration (Hovel & Lipcius, 2002; Laurel *et al.*, 2003). If predation pressure is enhanced at patch edges, small patches with a greater proportion of patch edge to interior habitat offer lower protection from predation than do large patches (Hovel & Lipcius, 2002). Alternatively, predators may aggregate within and concentrate foraging efforts upon larger patches (Laurel *et al.*, 2003). In this study, the effects of predation on the entire community can only be speculated, but the finding that large predators respond preferentially to large mussel patches seems evident. It should also be noted that crabs and snails are voracious consumers of Asian date mussels (Mistri, 2004a, b).

It is often assumed that reductions in habitat patch size will result in reductions in the species richness and abundance associated with those habitats (Hill & Curran, 2003). This study showed that reductions of mussel patch size were associated with minor effects on the invertebrates inhabiting mussel beds. These results are consistent with other marine studies which have found few predictable impacts of variation in patch size on the abundance of invertebrates (Bell *et al.*, 2001). The prediction of decreased abundance in small patches versus large patches has been shown for species of infaunal bivalves (Irlandi, 1997) and for crustaceans (Eggleston *et al.*, 1998), while other studies showed greater abundance of invertebrates in smaller patches (Eggleston *et al.*, 1999). Thus, results from the present study add to the gathering evidence that simple patterns have not yet been identified as to the effect of patch size on organism abundance in aquatic ecosystems. Moreover, individual mobility and habitat/organism interactions are known to play a fundamental role in determining communities and maintaining populations on habitat patches in heterogeneous landscapes (Thrush *et al.*, 1996). As this study shows, there are many variables that may influence the community pattern in small and large patches, and prevent to individualize a univocal pattern for small species and another for large species. Information on

body size, feeding mode, and mobility can be used to predict small-scale spatial arrangement of aquatic benthic invertebrates (Hewitt *et al.*, 1996), but evidences from this and other studies (e.g. Fahrig, 2003) suggest that varying patch size has inconsistent impacts upon fauna. This study also shows that basic life history information is essential in predicting how organisms respond to habitat heterogeneity in lagoons and estuaries; where sediment transport is common, passive faunal advection may be substantially elevated and may even remove the patch size dependence of immigration.

Invertebrate population size and biodiversity, yet, may be maximized in landscapes that include both small and large patches of mussel beds 'embedded' in a continuous matrix. *Musculista senhousia* beds serve as a critical refuge and foraging habitat for many species, and patchy and continuous areas may promote the persistence of organisms with different life histories. Information on the interdependence of shallow aquatic habitats such as sea grass and mussel bed habitats, as well as their relative importance as refuge or settlement sites, is critical for understanding population dynamics of ecologically important species. This information can be particularly important in areas, like Goro Lagoon and Padrongiano Delta, lacking sea grass, where mussel beds may represent the only structural refuge available.

Ecosystem engineers add habitat heterogeneity to the otherwise homogeneous, bare sediments and provide space and refuge for many organisms (Bianchi & Morri, 1996; Schwindt *et al.*, 2001). Increasing of macrobenthic species richness or abundance of predators is also observed in structurally complex habitats, such as oyster and polychaete reefs, when compared with the surrounding areas (Bianchi & Morri, 1996; Rodney & Paynter, 2006; Dubois *et al.*, 2006; Rabaut *et al.*, 2007). Rodney & Paynter (2006) observed increased density and species richness of benthic macrofauna in *Crassostrea virginica* reefs. Their results indicated also a more complex trophic structure within the reefs, with high densities of omnivores and suspension feeders. Since macrofauna included many important crab and fish prey species, oyster reefs resulted in increased grazing rates (water filtration) and subsequent transfer of energy from the plankton community to the benthos, and increased transfer of energy to the higher trophic levels of the reef community. Another ecosystem-engineer established in many Mediterranean and Atlantic lagoons is the Australian polychaete *Ficomatus enigmaticus* (Bianchi & Morri, 1996; Fornós *et al.*, 1997; Bianchi & Morri, 2001; Occhipinti Ambrogi, 2000; Schwindt *et al.*, 2001). Schwindt *et al.* (2001) studying the effect of the reef-building *F. enigmaticus* on the benthic community of the Mar Chiquita lagoon (southern Atlantic coast) found that reefs strongly affected the infaunal community structure by offering refuge to omnivorous crabs, altering the interactions between preexistent species and also by changing the characteristics of the sediment. Although other studies have shown that species richness and diversity of the associated fauna increased with age and size of mussel patches (Tsuchiya & Nishihira, 1985, 1986), Borthagaray & Carranza (2007) found no correlations between bed traits (i.e. shell length and shell biomass) and species richness. Collins & Glenn (1991) suggested that the patterns in abundance and occurrence of different functional groups did not respond in the same way to the engineering effect and that dispersal capabilities and body size might affect the way in which the organisms interact with their environments. These observations raise concerns regarding the effect of invasive bio-engineers

on existing native communities, by providing refuge to crabs and also by changing the physical factors of the invaded environments. Also influences on the habitat itself, either directly or indirectly, could in a longer perspective drastically decrease the biodiversity (Wallentinus & Nyberg, 2007).

The European Water Framework Directive (WFD) 2000/60/EC (EC, 2000) requires Member States to assess the ecological quality status (EcoQS) of coastal and transitional waters. The biological quality elements to be used are phytoplankton, aquatic flora (sea grass and seaweeds), benthic invertebrates and fish. Introduced ecosystem engineers may produce contrasting effects. The large filtering capacity of introduced mussels have resulted in positive environmental effects by clearing water masses (Wallentinus & Nyberg, 2007). Moreover, the creation of dense mussel mats has negative effects on native eelgrass (Reusch & Williams, 1998). In the present investigation, a large amount of opportunistic organisms (*sensu* Borja *et al.*, 2000) has been found within mussel patches, in the Sacca di Goro. Opportunistic species were more dependent upon the response of secondary structure to patch size (such as amount of organic matter, hydrodynamic reduction and low oxygen content), rather than to patch size itself. This finding suggests a deterioration of the ecological quality caused by mussel invasion and dependent on the scale of habitat patchiness. It remains unclear, how biodiversity and habitat changes due to non-indigenous ecosystem engineers should be interpreted in a context of WFD. Therefore, preparation of a framework for assessment of the role of such non-indigenous species ecosystem engineers in a local biodiversity should attain more efforts in the near future when implementing WFD.

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## REFERENCES

- Bell S.S., Brooks R.A., Robbins B.D., Fonseca M.S. and Hall M.O. (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* 100, 115–123.
- Bianchi C.N. and Morri C. (1996) Ficopomatus 'reefs' in the Po River Delta (Northern Adriatic): their constructional dynamics, biology, and influences on the brackish-water biota. *Pubblicazione della Stazione Zoologica di Napoli I: Marine Ecology* 17, 51–66.
- Bianchi C.N. and Morri C. (2001) The Battle is not to the Strong: Serpulid Reefs in the Lagoon of Orbetello (Tuscany, Italy). *Estuarine, Coastal and Shelf Science* 53, 215–220.
- Borja A., Franco J. and Pérez V. (2000) A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin* 40, 1100–1114.
- Borthagaray A.I. and Carranza A. (2007) Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. *Acta Oceanologica* 31, 243–250.
- Clarke K.R. and Warwick R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth: Plymouth Marine Laboratory, 144 pp.

- Collins S.L. and Glenn S.M. (1991) Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology* 72, 654–664.
- Commito J.A. and Rusignuolo B.R. (2000) Structural complexity in mussel beds: the fractal geometry of surface topography. *Journal of Experimental Marine Biology and Ecology* 255, 133–152.
- Creese R., Hooker S., Deluca S. and Wharton Y. (1997) Ecology and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31, 225–236.
- Crooks J.A. (2001) Assessing invader roles within changing ecosystems: historical and experimental perspectives on an exotic mussel in an urbanized lagoon. *Biological Invasions* 3, 23–36.
- Dubois S., Commito J.A., Olivier F. and Retière C. (2006) Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. *Estuarine, Coastal and Shelf Science* 68, 635–646.
- Eggleston D.B., Elis W.E., Etherington L.L., Dahlgren C.P. and Posey M.H. (1999) Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology* 236, 107–132.
- Eggleston D.B., Etherington L.L. and Elis W.E. (1998) Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 223, 111–132.
- EC (2000) European Commission Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework of Community action in the field of water policy. *Official Journal of the European Communities*, L327/1–72, Brussels.
- Fahrig L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecological and Evolutionary Systematics* 34, 487–515.
- Fornós J.J., Forteza V. and Martínez Taberner A. (1997) Modern polychaete reefs in Western Mediterranean lagoons: *Ficopomatus enigmaticus* (Fauvel) in the Albufera of Menorca, Balearic Islands. *Palaeogeography, Palaeoclimatology and Palaeoecology* 128, 175–186.
- Healey D. and Hovel K.A. (2004) Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA. *Journal of Experimental Marine Biology and Ecology* 313, 155–174.
- Hewitt J.E., Thrush S.F., Cummings V.J. and Pridmore R.D. (1996) Matching patterns with processes: predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. *Marine Ecology Progress Series* 135, 57–67.
- Hill J.L. and Curran P.J. (2003) Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *Journal of Biogeography* 30, 1391–1403.
- Hoenselaar H.J. and Hoenselaar J. (1989) *Musculista senhousia* (Benson in Cantor, 1842) in the Western Mediterranean (Bivalvia; Mytilidae). *Basteria* 53, 73–76.
- Hovel K.A. and Lipcius R.N. (2002) Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *Journal of Experimental Marine Biology and Ecology* 271, 75–98.
- Irlandi E.A. (1997) Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78, 511–518.
- Kotliar N.B. and Wiens J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59, 253–260.
- Laurel B.J., Gregory R.S. and Brown J.A. (2003) Predator distribution and habitat patch area determine predation rates on age of juvenile cod *Gadus* spp. *Marine Ecology Progress Series* 251, 245–254.
- Mastrototaro E., Matarrese A. and D’Onghia G. (2003) Occurrence of *Musculista senhousia* (Mollusca: Bivalvia) in the Taranto seas (eastern-central Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom* 83, 1279–1280.
- Mistri M. (2003) The non-indigenous mussel *Musculista senhousia* in an Adriatic lagoon: effects on benthic community over a ten year period. *Journal of the Marine Biological Association of the United Kingdom* 83, 1277–1278.
- Mistri M. (2004a) Predatory behavior and preference of a successful invader, the mud crab *Dyspanopeus sayi* (Panopeidae), on its bivalve prey. *Journal of Experimental Marine Biology and Ecology* 312, 385–398.
- Mistri M. (2004b) Effects of hypoxia on predator–prey interactions between juvenile *Carcinus aestuarii* and *Musculista senhousia*. *Marine Ecology Progress Series* 275, 211–217.
- Mistri M., Modugno S. and Rossi R. (2003) Sediment organic matter and its nutritional quality: a short-term experiment with two exotic bivalve species. *Chemistry and Ecology* 19, 225–231.
- Mistri M., Rossi R. and Fano E.A. (2004) The spread of an alien bivalve (*Musculista senhousia*) in the Sacca di Goro lagoon (Adriatic Sea, Italy). *Journal of Molluscan Studies* 70, 257–261.
- Occhipinti Ambrogi A. (2000) Biotic invasions in a Mediterranean lagoon. *Biological Invasions* 2, 165–176.
- Rabaut M., Guilini K., Van Hoey G., Vincx M. and Degraer S. (2007) A bio-engineered soft-bottom environment: the impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuarine, Coastal and Shelf Science* 75, 525–536.
- Ragnarsson S.A. and Raffaelli D. (1999) Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. *Journal of Experimental Marine Biology and Ecology* 241, 31–43.
- Reusch T.B.H. and Williams S.L. (1998) Variable response of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. *Oecologia* 113, 428–441.
- Roberts D.A. and Poore A.G.B. (2005) Habitat configuration affects colonization of epifauna in a marine algal bed. *Biological Conservation* 127, 18–26.
- Rodney W.S. and Paynter K.T. (2006) Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology* 335, 39–51.
- Schwindt E., Bortolus A. and Iribarne O. (2001) Invasion of a reefbuilder polychaete: direct and indirect impacts on the native benthic community structure. *Biological Invasions* 3, 137–149.
- Thrush S.F., Whitlatch R.B., Pridmore R.D., Hewitt J.E., Cummings V.J. and Wilkinson M.R. (1996) Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. *Ecology* 77, 2472–2487.
- Tsuchiya M. and Nishihira M. (1985) Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of island size on community structure. *Marine Ecology Progress Series* 25, 71–81.
- Tsuchiya M. and Nishihira M. (1986) Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Marine Ecology Progress Series* 31, 171–178.
- Wallentinus I. and Nyberg C.D. (2007) Introduced marine organisms as habitat modifiers. *Marine Pollution Bulletin* 55, 323–332.
- and
- Wiens J.A. (1995) Landscape mosaics and ecological theory. In Hansson L., Fahrig L. and Merriam G. (eds.) *Mosaic landscapes and ecological processes*. London: Chapman & Hall, pp. 1–26.

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## APPENDIX A.

Phylum	Family	Taxa	Padrongiano Delta (Tyrrhenian Sea)	Sacca di Goro (Adriatic Sea)		
CNIDARIA	Aiptasiidae	<i>Aiptasia</i> sp.	*	*		
PLATHELMINTHES		Acoela	*			
		Polycladida	*	*		
NEMERTEA	Lineidae	<i>Lineus ruber</i>	*			
	Valenciniidae	<i>Valencinia longirostris</i>	*	*		
	Emplectonematidae	<i>Emplectonema gracile</i>	*			
	Prosorhochmidae	<i>Prosorhochmus claparedii</i>	*			
	Tetrastemmidae	<i>Tetrastemma</i> sp.	*			
	Malacobdellidae	<i>Malacobdella grossa</i>	*			
MOLLUSCA		Caudophoveata	*	*		
	Trochidae	<i>Gibbula</i> sp.	*			
	Naticidae	<i>Neverita josephina</i>	*			
	Ranellidae	<i>Cymatium parthenopeum</i>	*			
	Muricidae		<i>Hexaplex trunculus</i>	*		
			<i>Ocenebra erinaceus</i>	*		
			<i>Pisania striata</i>	*		
	Buccinidae		<i>Nassarius corniculus</i>	*		
			<i>Cyclope neritea</i>	*		
	Turridae	<i>Raphitoma</i> sp.	*			
	Ringiculidae	<i>Haminoea navicula</i>	*			
	Mytilidae		<i>Mytilus galloprovincialis</i>	*	*	
			<i>Musculista senhousia</i>	*	*	
	Ostreidae	<i>Crassostrea gigas</i>	*	*		
	Cardiidae	<i>Cerastoderma glaucum</i>	*	*		
	Mactridae		<i>Mactra stultorum</i>	*	*	
			<i>Dosinia exoleta</i>	*		
	Veneridae		<i>Tapes decussatus</i>	*		
			<i>Ruditapes philippinarum</i>	*	*	
			<i>Paphia aurea</i>	*		
		ANNELLIDA (Polychaeta)	Orbiinidae	<i>Nainereis laevigata</i>	*	
				<i>Phylo foetida</i>	*	
		Spionidae		Spionidae sp.	*	
			<i>Aonides paucibranchiata</i>	*		
			<i>Microspio mecznikovianus</i>	*		
			<i>Polydora ciliata</i>	*	*	
			<i>Prionospio cirrifera</i>	*	*	
			<i>Scolelepis</i> sp.	*		
			<i>Scolelepis foliosa</i>	*		
			<i>Spio decoratus</i>	*	*	
	<i>Spio filicornis</i>		*			
	<i>Spiophanes bombyx</i>		*			
	<i>Streblospio shrubsolii</i>		*	*		
Paraonidae	<i>Aricidea cerrutii</i>		*			
Cirratulidae	<i>Cirriformia tentaculata</i>		*			
Capitellidae		<i>Capitella capitata</i> cfr	*	*		
		<i>Capitomastus minimus</i>	*	*		
	<i>Heteromastus filiformis</i>	*				
	<i>Notomastus</i> sp.	*				
	<i>Notomastus latericeus</i>	*				
Opheliidae		<i>Armandia cirrhosa</i>	*			
		<i>Polyopthalmus pictus</i>	*			
Phyllodocidae		<i>Eteone</i> sp.	*			
		<i>Eumida sanguinea</i>	*			
		<i>Phyllodoce mucosa</i>	*	*		
Glyceridae	<i>Glycera tridactyla</i>	*				
Goniadidae	<i>Goniada maculata</i>	*				
Hesionidae	<i>Kefersteinia cirrata</i>	*				

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Table  
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Phylum	Family	Taxa	Padrongiano Delta (Tyrrhenian Sea)	Sacca di Goro (Adriatic Sea)
		<i>Microphthalmus</i> sp.	*	
	Syllidae	<i>Syllides edentulus</i>	*	
		<i>Syllides</i> sp. 2	*	
		<i>Exogone naidina</i>	*	
		<i>Grubeosyllis tenuicirrata</i>	*	
		<i>Sphaerosyllis</i> sp.	*	
		<i>Syllis gracilis</i>	*	
		<i>Syllis krohnii</i>	*	
	Nereididae	<i>Neanthes caudata</i>	*	
		<i>Neanthes succinea</i>		*
		<i>Perinereis cultrifera</i>	*	
	Nephtyidae	<i>Nephtys hombergi</i>	*	
	Polynoidae	<i>Harmothoe</i> sp.	*	
	Onuphidae	<i>Onuphis falesia</i>	*	
	Eunicidae	<i>Eunice vittata</i>	*	
	Lumbrinereidae	<i>Lumbrinereis latreilli</i>	*	
	Dorvilleidae	<i>Schistomeringos rudolphii</i>	*	
	Terebellidae	<i>Amphitritides gracilis</i>	*	
		<i>Axionice maculata</i>	*	
		<i>Eupolymnia</i> sp.	*	
		<i>Lanice conchylega</i>	*	
		<i>Pista cristata</i>	*	
		<i>Terebella lapidaria</i>	*	
		<i>Parathelepus collaris</i>	*	
		<i>Polycirrus</i> sp.	*	
	Sabellidae	Sabellidae sp.	*	
	Serpulidae	<i>Ficopomatus enigmaticus</i>		*
		<i>Filograna implexa</i>	*	
		<i>Hydroides dianthus</i>	*	*
		<i>Hydroides elegans</i>	*	
		<i>Serpula concharum</i>	*	
		<i>Serpula vermicularis</i>	*	
	Polygordiidae	<i>Polygordius appendiculatus</i>	*	
		<i>Polygordius neapolitanus</i>	*	
(Oligochaeta)	Tubificidae	<i>Tubificoides vestibulatus</i>		*
		<i>Peloscoclex</i> sp.	*	
		Tubificidae sp. 2	*	
CRUSTACEA	Nannastacidae	<i>Iphinoe serrata</i>	*	
	Leptognathiidae	<i>Leptognathia</i> sp.	*	
	Idoteidae	<i>Idotea baltica</i>		*
		<i>Idotea granulosa</i>	*	
	Anthuridae	<i>Cyathura carinata</i>	*	
	Cirolanidae	<i>Eurydice</i> sp.	*	
	Sphaeromatidae	<i>Sphaeroma serratum</i>	*	
		<i>Cymodoce truncata</i>	*	
		<i>Paracerceis sculpta</i>	*	
		<i>Paracerceis spinulosa</i>	*	
	Ampeliscidae	<i>Ampelisca diadema</i>	*	*
	Amphilochidae	<i>Amphilochus manudens</i>	*	
	Ampithoidae	<i>Ampithoe</i> sp.	*	
	Aoridae	Aoridae sp.	*	
		<i>Aora gracilis</i>	*	
		<i>Microdeutopus gryllotalpa</i>		*
		<i>Microdeutopus obtusatus</i>	*	
		<i>Microdeutopus stationis</i>	*	
	Corophiidae	<i>Corophium insidiosum</i>	*	*
		<i>Corophium orientale</i>		*
	Dexaminidae	<i>Dexamine spinosa</i>	*	
	Gammaridae	<i>Gammarus aequicauda</i>	*	*
		<i>Gammarus insensibilis</i>	*	*
	Melitidae	<i>Elasmopus rapax</i>	*	
		<i>Maera grossimana</i>	*	
		<i>Melita palmata</i>		*

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Table  
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Phylum	Family	Taxa	Padrongiano Delta (Tyrrenhian Sea)	Sacca di Goro (Adriatic Sea)
	Caprellidae	<i>Caprella</i> sp.	*	
	Crangonidae	<i>Crangon crangon</i>		*
	Portunidae	<i>Carcinus aestuarii</i>	*	*
	Panopeidae	<i>Rhithropanopeus harrissii</i>		*
	Grapsidae	<i>Brachyotus sexdentatus</i>	*	
INSECTA	Chironomidae	<i>Chironomus salinarius</i>	*	*
ECHINODERMATA	Amphiuridae	<i>Amphipholis squamata</i>	*	
	Ophiothricidae	<i>Ophiothrix gracilis</i>	*	
CHORDATA		Asciacea	*	