Alma Mater Studiorum – Università di Bologna

DOTTORATO DI RICERCA IN

Biodiversità ed Evoluzione

Ciclo XXV

Analysis and development of ecologically based approaches to coastal defense

Presentata da: **Filippo Ferrario**

Coordinatore	Relatore
Prof.ssa Barbara Mantovani	**Prof.ssa Laura Airoldi**
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Esame finale anno 2013

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Abstract

Climate-change related impacts, notably coastal erosion, inundation and flooding from sea level rise and storms, will increase in the coming decades enhancing the risks for coastal populations. Further recourse to coastal armoring and other engineered defenses to address risk reduction will exacerbate threats to coastal ecosystems. Alternatively, protection services provided by healthy ecosystems is emerging as a key element in climate adaptation and disaster risk management. I examined two distinct approaches to coastal defense on the base of their ecological and ecosystem conservation values. First, I analyzed the role of coastal ecosystems in providing services for hazard risk reduction. The value in wave attenuation of coral reefs was quantitatively demonstrated using a meta-analysis approach. Results indicate that coral reefs can provide wave attenuation comparable to hard engineering artificial defenses and at lower costs. Conservation and restoration of existing coral reefs are cost-effective management options for disaster risk reduction. Second, I evaluated the possibility to enhance the ecological value of artificial coastal defense structures (CDS) as habitats for marine communities. I documented the suitability of CDS to support native, ecologically relevant, habitat-forming canopy algae exploring the feasibility of enhancing CDS ecological value by promoting the growth of desired species. Juveniles of *Cystoseira barbata* can be successfully transplanted at both natural and artificial habitats and not affected by lack of surrounding adult algal individuals nor by substratum orientation. Transplantation success was limited by biotic disturbance from macrograzers on CDS compared to natural habitats. Future work should explore the reasons behind the different ecological functioning of artificial and natural habitats unraveling the factors and mechanisms that cause it. The comprehension of the functioning of systems associated with artificial habitats is the key to allow environmental managers to identify proper mitigation options and to forecast the impact of alternative coastal development plans.

Contents

Attachment :

Perkol-Finkel, S., F. Ferrario, V. Nicotera, and L. Airoldi. 2012. Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures. Journal of Applied Ecology 49:1457-1466.

Chapter 1: General introduction

Climate change and coastal hazards risk

Climate change is already impacting the ability of marine and coastal ecosystems to provide food, income, protection, and cultural identity to millions of people. Even if efforts to reduce greenhouse gas emissions are successful, climate-change related impacts, notably coastal erosion, inundation and flooding from sea level rise and storms, will still increase in the coming decades (Zhang et al. 2004, Nicholls et al. 2007, Stouffer 2012). In particular, it is emerging that the frequency of storm events is increasing and, in parallel, the return period for extreme surges is decreasing (Grinsted et al. 2012, Lin et al. 2012), enhancing the risks for coastal populations.

Nearly two thirds of the world's population lives in coastal areas (Creel 2003) and of that 10 % inhabits low-lying zones (where the coast is less than 10 meters above the sea level), mostly in developing countries and small island states such as e.g. the Maldives, Caribbean (McGranahan et al. 2007). These countries are particularly vulnerable to disasters, because of low capabilities and resources to cope with natural disasters and likely pay a higher toll in human lives. Developed nations suffer greater economical damages, due to destruction of e.g. coastal assets and infrastructures. Indeed, in the United States the recent coastal disasters that occurred in important urban areas like New Orleans and New York and associated with hurricane and storms, namely hurricanes Katrina and Sandy, have revamped the discussion on long-term sustainability of development and coastal resilience (Tollefson 2013) thus becoming icons of the need for a coastal hazard risk reduction all over the world (UNISDR 2011).

Natural ecosystems in climate adaptation and disaster risk management

The international community currently considers climate adaptation (e.g. managed retreat and accommodation) as a primary response to best cope with coastal hazards (Smith et al. 2011, UNISDR 2011). Adaptation can be a way to reduce the impacts of climate related hazards “via behavioral changes, beginning with individual actions and ranging to collective coastal management policy, such as upgraded defenses and warning systems and land management approaches” (Nicholls 2011). Disaster Risk Management (DRM) on the other side, is a suite of actions that aim to achieve the policy objective to reducing risk (UNISDR 2011). Following the United Nations Global Assessment Report on Disaster Risk Reduction, both DRM and climate adaptation need to be integrated; and the protection of ecosystems is considered a key element (UNISDR 2011).

Scientists increasingly acknowledge that different coastal ecosystems around the globe deliver services valuable for the reduction of coastal hazards and risks related to flooding and/or erosion (Sheppard et al. 2005, Wells et al. 2006, Gedan et al. 2010, Shepard et al. 2011). For example, salt marshes represent a buffer zone, able to slow down and dampen waves and storm surges, to stabilize sediments and to modify the topography (Zedler and Kercher 2005, Gedan et al. 2010, Smith et al. 2010, Wamsley et al. 2010, Shepard et al. 2011, Barbier et al. 2013). Mangrove forests provide similar services in tropical regions (Wells et al. 2006, Gedan et al. 2010, Zhang et al. 2012). Beside coastal vegetation, biogenic reefs (e.g. oyster and coral reefs) offer shoreline protection services (Sheppard et al. 2005, Wells et al. 2006, Beck et al. 2011).

In order to effectively integrate coastal ecosystems in risk reduction strategies, it is important to clearly demonstrate and quantify the actual value of their services in terms of their effect on physical parameters (e.g. sediment stabilization, accretion, wave attenuation). This knowledge can then be used by coastal managers and policy makers. The assessments have already been carried out for some ecosystems (e.g. salt marshes, mangroves and sea grasses), while others still need to be addressed (e.g. coral reefs, oyster reefs, kelp forests).

Coastal armoring and its ecological consequences

Coastal armoring is the hard engineering approach traditionally adopted in an attempt to protect coastal features (e.g. beaches), socio-economic assets (e.g. private properties and economical activities) and public infrastructures (e.g. harbors, roads and railways) from coastal flooding and erosion. The abundance of artificial structures such as breakwaters, seawalls, groynes, jetties and dykes is predicted to increase in parallel with growing coastal development and the predicted higher frequency and severity of storms and sea level rise due to climate change (Dugan et al. 2011).

Although the value of natural coastal ecosystems for coastal hazard risk reduction is emerging stirring new adaptation strategies in coastal planning and management (UNISDR 2011), existing man-made coastal defense structures are still widespread, severely altering the coastal seascapes. Moreover, coastal armoring may still represent the only viable option where original natural ecosystems have been irreparably lost or where no trade-offs can be accepted, in particular in more urbanized areas (Anthoff et al. 2010). For example, in the light of the recent devastation suffered by New York City due to hurricane Sandy, it has been proposed to build a barrier 8 km wide and 6 m high at the entrance to the harbor (Tollefson 2013). Along the Italian coast of the northern Adriatic Sea, severe erosion and land subsidence (both natural and human-induced) has lead to proliferation protection schemes, mainly groynes and offshore breakwaters (Bondesan et al. 1995). Nowadays over 60 % of Emilia Romagna shores are protected by 190 km of artificial structures forming an almost continuous line along a 300 km sandy littoral, which has lead to severe hardening of originally sedimentary environments and alterations to the coastal landscape (Bacchiocchi and Airoldi 2003, Airoldi et al. 2005, Bulleri and Airoldi 2005).

Once deployed in the marine realm, coastal artificial structures inevitably interact with and alter both environmental and biological features in the surrounding seascape in a complex way. For example hydrodynamics, sedimentation and grain size composition are affected at different spatial scales (Martins et al. 2009, Munari et al. 2011, Reed et al. 2012) with consequences for both infaunal assemblages and mobile fauna (Martin et al. 2005). Further, infrastructure and armouring introduce in prevailingly sedimentary environments new intertidal or subtidal hard substrata that was not previously available.

Marine artificial structures represent novel habitats that cannot be considered surrogates of natural hard bottom habitats (Bulleri and Chapman 2010, Feary et al. 2011). The biological communities that establish in artificial habitats are generally poorer than natural habitats, in terms of both species and genetic diversity and structural complexity (Bacchiocchi and Airoldi 2003, Chapman 2003, Perkol-Finkel et al. 2006, Fauvelot et al. 2009, Miller et al. 2009). Also they are frequently dominated by opportunistic and invasive species (Bacchiocchi and Airoldi 2003, Bulleri and Airoldi 2005, Dafforn et al. 2012, Marzinelli 2012). Depending on the spatial configuration of the artificial structures in the seascape, they can affect the meta-population connectivity by removing barriers between distinct regions (Dethier et al. 2003, Bulleri 2005, Zintzen and Massin 2010) and facilitate the spread of non indigenous species (Bulleri and Airoldi 2005, Vaselli et al. 2008). Moreover, artificial structures increase the fragmentation of natural habitats (Goodsell et al. 2007) potentially affecting the openness of their populations (Pinsky et al. 2012). Also, they alter the distribution of mobile fauna, for example by either attracting or increasing the production of fish species (Brickhill et al. 2005, Edelist and Spanier 2009, Simon et al. 2011, Wehkamp and Fischer 2013), resulting in a stronger predation pressure on prey species in the surrounding areas (Langlois et al. 2005, Einbinder et al. 2006, Galvan et al. 2008).

Because the creation of artificial habitats will likely increase as a result of burgeoning coastal populations, expansion of coastal cities, and greater threats from climate change, storm surges and sea level rise (Inger et al. 2009, Shepard et al. 2012), the need to fully understand and mitigate their ecological impacts is a pressing challenge (Dugan et al. 2011). Man-made coastal defense structures are ‘urban hardscapes’ and consequently should be managed to meet desired ecological and conservation goals (Lundholm and Richardson 2010) and preserve the functioning of native ecosystems.

Bioengineering consideration in the design of coastal defense and other marine infrastructures

Due to the projected expansion of artificial structures there is an increasing interest in identifying bioengineering options that mitigate the impacts and enhance the ecological value of marine infrastructures, without compromising their original function. Attempts have been made to reproduce as much as possible the structural complexity of natural rocky habitat by adding morphological features to seawalls and breakwaters such as tidal pools, crevices, rough or complex surfaces (Airoldi et al. 2005, Moschella et al. 2005, Chapman and Blockley 2009). The adoption of ecological criteria in artificial structures design effectively affected the abundance and diversity of epibiota colonizing these novel habitats (Airoldi et al. 2005, Moschella et al. 2005, Chapman and Blockley 2009). Additionally it has been highlighted that minimizing the impacts from the severe disturbances from maintenance is important to ensure colonization and succession of species (Moschella et al. 2005, Airoldi and Bulleri 2011). Moreover, encouraging results from recent experimental works are shedding light on the feasibility of managing benthic communities on artificial structures. Indeed, direct “gardening” of important native habitat-forming species would foster the colonization of ecologically valuable benthic fauna and flora on artificial structures (Falace et al. 2006, Susini et al. 2007, Perkol-Finkel et al. 2012), possibly providing important ecosystem services.

Thesis objectives and structure

I analyzed two distinct approaches to coastal defense on the base of their ecological and ecosystem conservation values. I first dealt with the valorization of natural coastal ecosystems as a key element in the coastal hazard risk reduction process, quantifying the wave attenuation service provided by coral reefs. I then studied the feasibility of elevating the ecological and biological value of coastal defense structures while minimizing their ecological footprint. This approach is built on the analysis of the different ecological performance of artificial habitats compared to natural reefs and of the underlying ecological processes. The thesis has been developed as a series of manuscripts for publication and thus each chapter represents a stand-alone manuscript, with possible cross-references.

Chapter 2: the value of several coastal habitats in wave attenuation has been explored by reviewing the scientific literature. For most habitats considered (kelp forests, oyster reefs and seagrasses) there was limited information, and I ultimately focused this chapter on coral reefs, due to their ecological relevance and to the availability of published data that allowed the use of a meta-analysis approach. The coral reefs relevance for disaster risk reduction has been discussed considering the global population receiving direct and indirect benefits and comparing coral reefs with hard engineering artificial defenses.

Chapter 3: the feasibility of using coastal defense structures as a scaffold for the conservation of threatened Mediterranean canopy forming algae of the genus *Cystoseira* has been evaluated in the light of their declared conservation priority. The study investigated whether juveniles of *Cystoseira barbata* can be successfully transplanted onto breakwaters and whether recruitment was affected by substratum material or complexity.

Chapter 4 and 5: the ecological performance of artificial structures as habitat for epibiota has been assessed and compared with that of natural rocky habitats at local to regional scales. Specifically the unequal success of native, ecologically relevant, habitat-forming canopy algae on coastal artificial structures compared to natural rocky reefs has been documented, and some relevant ecological processes (e.g. species interactions) underlying this different functioning of artificial structures have been identified and quantified by using field experiments.

Chapter 6: some ecologically based options in the design of artificial structures deal with developing tools/techniques for the enhancement/gardening/farming of desired species. This chapter focused on species of seaweeds of conservation value, such as the threatened canopy-forming fucoid algae belonging to the genus *Cystoseira*. The regeneration potential of the canopy-forming algae *Cystoseira barbata* was evaluated. Fragments of adult *Cystoseira* thalli were cultured *in vitro* to assess whether they developed new structures such as lateral branches. The study investigated how regeneration was affected by different environmental and procedural factors, to identify optimal conditions for growth

Statement of co-author contributions

Chapter 2-6 of the thesis have been prepared as a series of manuscripts for publication in peer reviewed journals. In all cases I contributed to the design and implementation of the research, data collection and analysis, interpretation and preparation of the manuscript in consultation with the supervisors and other contributors. I took first responsibility in writing chapters 2, 4, 5, and 6. The contributions of other authors are outlined below.

Chapter 2: Prof. Laura Airoldi, Dr. Michael W. Beck conceived the study, contributed conceptual knowledge to design the research, prepared the manuscript; Dr. Curt Storlazzi provided oceanographic expertise to interpret the results, prepared the manuscript; Prof. Fiorenza Micheli, provided statistical expertise to undertake meta-analysis, prepared the manuscript; Dr. Christine C. Shepard, provided spatial data analysis.

Chapter 3: Prof. Laura Airoldi, Dr. Shimrit Perkol-Finkel conceived the study, contributed conceptual knowledge to design the research, ran field work and data analysis, prepared the manuscript; V. Nicotera contributed to field work and data collection.

Chapter 4: Prof. Laura Airoldi, contributed conceptual knowledge to design the research, ran field work and prepared the manuscript; Dr. Shimrit Perkol-Finkel contributed conceptual knowledge to design the research; Dr. Ljiljana Ivesa, contributed conceptual knowledge to design the research and ran field work; Andrej Jaklin ran field work.

Chapter 5: Prof. Laura Airoldi, contributed conceptual knowledge to design the research, ran field work and prepared the manuscript. Dr. Beth Strain contributed conceptual knowledge to design the research and ran field work.

Chapter 6: Prof. Laura Airoldi, contributed conceptual knowledge to design the research, prepared the manuscript; Andrea Magani, provided expertise to undertake in vitro propagation, ran laboratory work and prepared the manuscript. Mauro Masini, provided expertise to undertake in vitro propagation, laboratory space and consumables.

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Chapter 2: Coral reefs are effective for coastal hazard risk reduction

Under review: Filippo Ferrario, Michael W. Beck, Curt D. Storlazzi, Fiorenza Micheli, Christine C. Shepard, Laura Airoldi. Coral reefs are effective for coastal hazard risk reduction. *Proceedings of the National Academy of Science*.

Abstract

The world's coastal zones are undergoing rapid development while also experiencing an increase in storms and flooding. When these changes are accompanied by losses of coastal ecosystems such as reefs and marshes, there can be an exacerbation of exposure and vulnerability to these natural hazards, which puts hundreds of millions of people in coastal communities at heightened risk. Here, we apply a mix of spatial- and meta-analyses to examine the role of coral reefs in mitigating natural hazards by reducing wave height and wave energy. We demonstrate quantitatively that coral reefs provide substantial protection against natural hazards by reducing wave energy and wave height by an average of 97% and 85%, respectively. Reef crests dissipate the most wave energy overall (88%) with the adjacent reef flat dissipating on average approximately half of the remaining wave energy. Globally we show that 197 million people live in low coastal areas (below 10 meters elevation) and near reefs (within 50 kilometers). These are the at-risk communities who may receive direct and indirect benefits from reefs or bear coastal defense and other risk mitigation costs if reefs are degraded. Our results indicate that coral reefs can provide wave attenuation comparable to hard engineering artificial defenses such as breakwaters and at lower costs. Conservation and restoration of existing coral reefs are cost-effective management options for disaster risk reduction.

Keywords: coral reefs, ecosystem services, risk reduction, coastal defense, meta analysis

Introduction

Nearly 40% of the world’s population lives within 100 kilometers of the coast and that percent is increasing (Agardy and Alder 2005). The increase in coastal development combined with growing natural hazards from coastal storms, flooding, and rising sea level creates social, economic, and ecological risks of global significance. The UN global report on disaster risk reduction identified that the risks of economic loss associated with floods and tropical cyclones is increasing across the world (UNISDR 2011). The proportion of the world’s Gross Domestic Product (GDP) annually exposed to tropical cyclones increased from 3.6 % in the 1970s to 4.3 % in the first decade of the 2000s (UNISDR 2011). Moreover the impacts associated with inundation and flooding from sea-level rise and storms are expected to increase substantially. As a consequence, huge investments are being made in coastal hazard mitigation and increasingly in climate adaptation, and these investments are often for artificial defense structures such as seawalls and breakwaters. In recent climate negotiations, developed nations pledged US$100 billion per year by 2020 to support mitigation and adaptation in developing countries many of which are tropical and coastal. Funds are already starting to flow from these commitments at US$1 - $4 billion/year (Smith et al. 2011).

As an alternative to investing solely in artificial coastal defenses, there is a growing awareness that nature-based solutions can be a part of risk reduction approaches. A growing body of evidence suggests that natural solutions can be effective for risk reduction (Gedan et al. , Shepard et al. 2011, Zhang et al.). This evidence is clearest for mangroves and marshes, but it is surprisingly less well developed for coral reefs, and there is not a synthesis of the role of coral reefs in risk reduction (Zedler and Kercher 2005, Wells et al. 2006, Barbier et al. 2008, Koch et al. 2009, Gedan et al. , Smith et al. 2010, Barbier et al. 2011, Shepard et al. 2011, Zhang et al. 2012). Reefs should be especially attractive for hazard mitigation because they are widely known to provide numerous benefits including food security and livelihoods. Without a clear assessment of the effectiveness of coral reefs for hazard mitigation, the likelihood that reefs will be managed to reduce their degradation and sustain all the benefits they provide is greatly diminished. For example, there is growing evidence that where coral reefs have been damaged following extensive coral mining or land reclamation that investments increased in artificial defenses (Brown and Dunne 1988, Frihy et al. 1996, Knight et al. 1997).

Here we provide the first global synthesis and meta-analysis of the contributions of coral reefs to natural hazard mitigation. The specific objectives of this study were to: quantitatively assess the effects of reefs on wave attenuation; examine which parts of the reef have the greatest effects on wave attenuation; determine where and how many at-risk people might receive benefits from reefs; and provide a physical and economic comparison of the risk reduction value of reefs relative to built infrastructure.

Methods

To identify articles with sufficient quantitative data for assessing wave attenuation by coral reefs, we conducted a literature search using Web of Science (1900-2011, cutoff date 15 March 2011). We systematically searched the literature using a combination of the following keywords: “coral reef*” and “wave attenuation*”, “wave energy”, and “wave breaking”. We based the keyword selection on the results of a wider preliminary literature search. We used meta-analysis to combine the results of independent experiments and assess the magnitude and direction of the difference between pairs of treatment and control groups (Rosenberg et al. 2000). We identified studies examining wave attenuation at different sites aligned along a cross-reef transect from offshore (control) to onshore (treatment). We adopted a screening protocol based on two selection criteria to identify relevant articles (Shepard et al. 2011). We first evaluated abstracts to exclude languages other than English, publication of abstract only, and articles clearly not focused on wave attenuation. We further reviewed the full text of publications that passed the first screening and selected only publications reporting original data acquired from either lab experiments or field surveys. We considered modeling studies only in the presence of original data used for model validation.

We identified 177 relevant articles on coral reefs and wave attenuation from the literature search and identified five additional references from article citations and previous preliminary article searches. After thorough review, we identified twenty articles with quantitative data on wave attenuation that matched our criteria for meta-analysis. After checking for independence, we extracted data from 18 publications for our analyses (Table S1, Dataset S1, Dataset S2, Dataset S3).

Wave attenuation measure

We assessed two response variables to measure the wave attenuation service of coral reefs: wave energy reduction and wave height reduction. Energy is lost during wave breaking (Young 1989, Hardy and Young 1996, Massel and Gourlay 2000, Lowe et al. 2005a) and as a consequence of friction (Lowe et al. 2005a, Lowe et al. 2007) due to interactions with the reef substrate. Wave energy reduction is defined as the loss in wave energy density that occurs as the waves interact with the reef during their propagation towards shore. Wave height reduction is the reduction in wave height that occurs when waves interact with the reef. An oceanic surface gravity wave begins to interact with the sea floor when the water depth is equal to half the wavelength ($d= \lambda/2$). Along an ideal cross-shore transect on a typical coral reef, water depth decreases rapidly on the fore reef up to the reef crest and it remains shallow on the reef flat (Fig. 1). Incident wave heights approaching the reef can increase locally due to wave energy convergence from refraction and/or shoaling (Gourlay 1996a, b), but then generally rapidly decrease at the reef crest due to depth-induced breaking. Wave heights are typically depth-limited on the relatively shallow reef flat (Hardy and Young 1996).

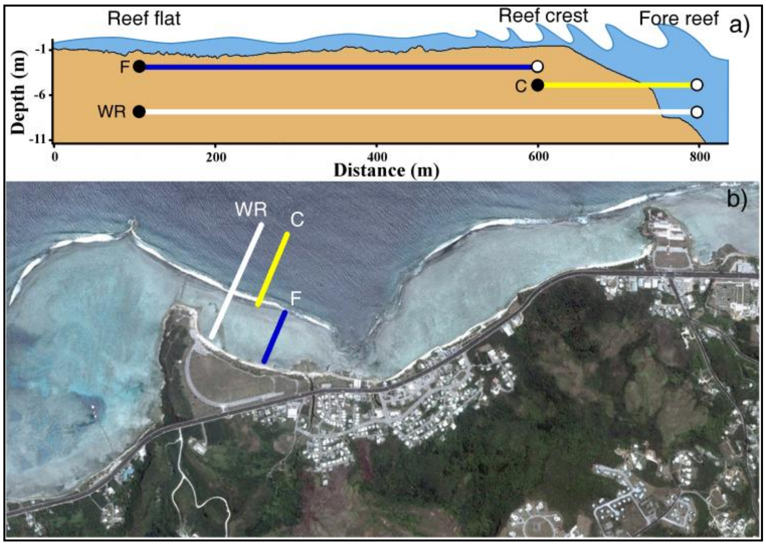

Figure 1 Example of coral reef zones and sample transects. Transects along which wave attenuation was estimated for the three zones are indicated: reef flat (F, blue line), reef crest (C, yellow line) and whole reef (WR, white line). Measurements of wave parameters were compared between an offshore control (open circle) and a landward treatment (solid circle) in each transect. a) Cross-section of the Camel Rock, Guam, fringing reef, from US Army Corps of Engineers SHOALS lidar data (Storlazzi et al. 2009). b) Aerial view of Asan Bay, Guam (© 2012 Google, Image © 2012 DigitalGlobe).

Wave energy reduction and wave height reduction are functionally related, and thus we presented both variables. Wave energy is the most critical factor governing coastal processes. However, wave height reduction is a more easily understood parameter and also used in many engineering applications.

The energy of a wave (energy density) is a function of its height as follows:

$$E = 1/8\,\rho\, g\, H^2 \qquad \text{Eq. 1}$$

where E is the energy density, ρ is water density, g is gravitational acceleration, and H is the significant wave height. In particular, the amount of energy delivered by a wave is expressed as the wave energy flux (P):

$$P = constant\ H^2\ T. \qquad \text{Eq. 2}$$

where T is the period of the wave. From eq. 2, it is evident that for a given wave height, the longer the wave period, the greater the wave energy delivered. We focused on wave energy density (hereafter just wave energy) and whenever possible we separated out components related to wave period.

Reefs and waves characteristics

The median width of reef flats analyzed was 145 m and ranged between 34 m and 3200 m. The majority of the reefs flats were 34 m to 300 m wide. For the studies included in our analysis, waves approaching reefs had an average height of 1.0 ± 0.2 m (mean ± standard error), while those propagating from the reef crest to the shoreline were on average 0.3 ± 0.1 m high (Fig. S1).

Data extraction

For each variable, we extracted the mean, error of the mean (standard deviation or standard error), and sample size. If the error of the mean or the sample size was not clearly reported and a minimum of 3 replicate values were available, we pooled data to calculate a new mean value, its associated error, and sample size. In one case, where authors reported mean, sample size, and the range, we estimated standard deviations using the methodology described by Hozo and others (Hozo et al. 2005).

For several papers, we had to extract data from time series plots of wave height to calculate the relevant statistics. Where the data were depicted on the plot with a symbol and referred to a specific time point we collected all of the data in the series. Otherwise, if only the wave height trend was shown and no specific symbols were drawn, we sampled the time series with an effort proportional to the series length. We extracted 5 random points for series from 0 to 14 days, increasing 5 units every other 14 days (e.g., n=5 for 14 days, n=10 for 28 days). We sampled the same time points along the time series for both control and treatment groups. Using equation 1, we transformed wave height data extracted for wave height reduction into energy data to increase the sample size of related wave energy reduction studies.

We estimated the influence of reefs on waves across three reef zones: Crest, Flat, and Whole Reef (Fig. 1). The effect of the reef crest was estimated by extracting data from along transects offshore (control) and inshore (treatment) the reef crest. The effect of the reef flat was assessed by comparing waves measured at points along transects just inshore of the reef crest or on the outer reef flat (control) to the inner reef flat adjacent to the shoreline (treatment). The effect of the whole reef was estimated along transects from the fore reef (control) to the inner reef flat adjacent to the shoreline (treatment). When reported, we extracted the specific distance between wave sensors.

When possible we extracted data about specific wave periods and wave frequency (1/period) bands, and sorted studies by the frequency band of the waves. This information is useful because the amount of energy hitting the shore or breakwaters varies by wave frequency (eq. 2). We considered three T or wave frequency categories: wind or sea waves (T = 3-8 s), swell (T = 8-20 s), and infragravity waves (T >20 s). Wind and swell waves are both gravity waves generated by wind friction on the sea surface (Holthuijsen 2007). Infragravity waves are primarily generated by nonlinear-wave interactions along coastlines (Herbers et al. 1995, Bromirski et al. 2010). When no information on T was available for a given study, we assigned it to a fourth category, “unknown band”. We also recorded information about reef morphology and the geographical region of each study.

Meta-analysis

We defined each transect in the different reef zones as an “experiment”. Depending on the number and the position of sensors deployed on the reefs, we could identify more than one experiment for some of the published studies considered. For each independent experiment, we calculated the effect size as the log-response ratio (*ln R*) and a weighting factor, calculated as the reciprocal of the variance (Hedges et al. 1999, Borenstein et al. 2009). The effect size was calculated by taking the natural logarithm of the ratio (R) between the mean of treatment (L, onshore) and the mean of control (S, offshore):

$$\text{Log Response Ratio} = \ln (L/S). \qquad \text{Eq. 3}$$

For each analysis, the overall effect size was calculated by summing the products (effect size multiplied by weight) and dividing by the sum of the weights (Borenstein et al. 2009).

The log-response ratio expresses the size of the treatment effect as a proportion of the control (Borenstein et al. 2009), which enables a clear assessment of the magnitude of the effects of reefs on wave attenuation. In addition, we used *ln R* because it was easily converted to a percent decrease of wave energy or height, which is more intuitive than the effect size itself. Statistical significance of the analyses is maintained after conversion, and we therefore reported the results as both percentage wave energy reduction and wave height reduction while showing actual effect sizes as supporting information for completeness. We calculated this index from the weighted log response ratio (*ln R*) using the following equation:

$$\% \text{ Decrease} = 100 - (e^{lnR} \times 100). \qquad \text{Eq. 4}$$

To ensure independence between the experiments in cases where the studies were conducted on the same reef, at different locations or times, we defined two transects as independent if they differed for at least one of the sensors by which they were delimited and if they could not be interpreted as one subset of the other (Fig. 1).

We used a random-effects model for the meta-analyses as most sets of experiments were heterogeneous as determined by calculating, Q_T (the total heterogeneity), and testing it against a χ^2 distribution with n-1 degrees of freedom (Rosenberg et al. 2000). For each response variable, we considered the summary effect size to be statistically significant ($p<0.05$) if its 95% confidence interval did not overlap zero. All the analyses were also run using the Hedge's *g*-effect size, a common effect size in meta-analysis, to check the robustness of the results. Hedge' *g* is based on the difference between treatment and control divided by their pooled standard deviation. Results of the Hedge's *g* analyses are provided in the supplemental materials (Fig. S2). All analyses were done using R 2.11.1.

WER and WHR as function of incoming wave energy and reef flat width.

To describe the relationship between wave energy reduction and the incoming wave energy, we plotted the percentage energy reduction for each individual experiment (calculated by replacing e^{lnR} with the ratio R in eq.4, only when energy data were reported as Jm^{-2}) as a function of wave energy value at the relative control. Adopting the same procedure, we analyzed both wave energy reduction and wave height reduction as a function of the reef flat width for each experiment where this was known. In both cases we fitted asymptotic regression models to the data and constrained the asymptote to be less than or equal to 100% reduction of wave energy and height and, we forced the regression model to start from the axis origin when studying the relationship between wave energy reduction and the incident wave energy.

Reefs and At-Risk Populations

To estimate the number of people by country that might receive risk reduction benefits from coral reefs, we examined the number of people that were both in (a) low-lying areas (below 10 m elevation) and (b) near a reef (within 50 km). For detailed methods, please see Text S1 and Fig. S3.

Risk reduction benefits include the direct reduction of exposure (e.g., wave energy reduction) and we considered these effects first in developing appropriate spatial proxy measures for where people might accrue benefits. Importantly risk reduction benefits also include effects on reducing vulnerability through the provision of livelihood opportunities (e.g., coastal jobs at ports, hotels or markets) or food security.

We included those areas that might be frequently flooded, e.g., elevations of 1-2 m or just a few km from reefs. However the benefits even from exposure reduction extend well beyond these areas. For example, the number of people who might benefit from avoided replacement costs for coastal defense extends well beyond those living in frequently flooded areas; indeed the populations bearing these coastal defense and replacement costs can include whole provinces or whole island nations – for example, the entire USA bears some of the costs of hurricanes. Typical examinations of global coastal populations (i.e., populations influenced by or influencing coastal ecosystems) consider areas 50 km from the coastline or all areas below 10m elevation no matter how far inland (e.g., (McGranahan et al. 2007)). By intersecting these considerations and by examining areas 50 km inland from reefs not coastlines, we focused on the subset of coastal populations who may receive direct and indirect risk reduction benefits from reefs. The sources of the data were: World Resources Institute, *Reefs at Risk Revisited*, 2011, National Geophysical Data Center (NGDC) for Global Digital Elevation Model (ETOPO2), Global Rural-Urban Mapping Project (GRUMP): Urban Extents Data Collection, Alpha Version, Center for International Earth Science Information Network (CIESIN), Columbia University, and VLIZ (2011) Maritime Boundaries Geodatabase, version 6.1, Flanders Marine Institute.

Results

Wave attenuation

In our meta-analysis review, we identified 182 studies on coral reefs and wave attenuation. We could extract data from 18 independent publications that covered reefs from the Caribbean, Maldives, Australia, China, Japan, Guam and Hawaii to quantitatively estimate the effectiveness of coral reefs in wave attenuation in terms of both wave energy reduction and wave height reduction. We examined wave attenuation across 3 reef zones: the reef crest, reef flat, and the whole reef (Fig. 1). Only a few studies examined wave attenuation across all three zones (Table S1) so the whole reef effects we report are not simply additive of the reef flat and reef crest effects.

Reefs significantly reduced wave energy across all three zones (Fig. 2a; log-response ratios are shown in Fig. S4a). Reef crests dissipated on average 88% (95% confidence interval: 77-93%) of the incoming wave energy (Fig. 2a). After breaking on the reef crest, waves propagating to shore lost a further 55% (49-60%) of their remaining energy on the reef flat. In addition, the whole reef accounted for a total wave energy reduction of 97% (86-99%, Fig. 2a).

For the studies where wave frequency could be extracted, we examined the effects of reefs in reducing different types of swell and wind waves (i.e., different wave frequency (period^{-1}) bands). Reefs reduced wave energy across all zones and frequency bands but not always significantly. Reef crests significantly dissipated 79% (58-89%) of the incoming swell wave energy and the whole reef significantly reduced both wind and swell wave energy (Fig. S5). Reef flats reduced wind and swell wave energy, but we could not detect significant effects when these frequency bands were separated (Fig. S5). The change in wave energy across the reef flat, particularly for the studies where bands could be separated, was much lower than across the reef crest or whole reef, which makes detection of individual band effects more difficult.

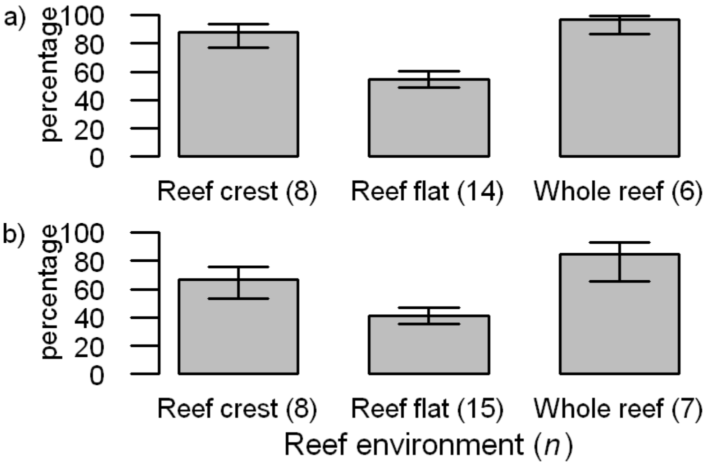

Figure 2 Coral reef and wave attenuation meta-analysis results in the three reef zones. Values are the average percentage of a) wave energy reduction, and b) wave height reduction. Error bars represent 95% confidence interval. (n) is the number of independent experiments.

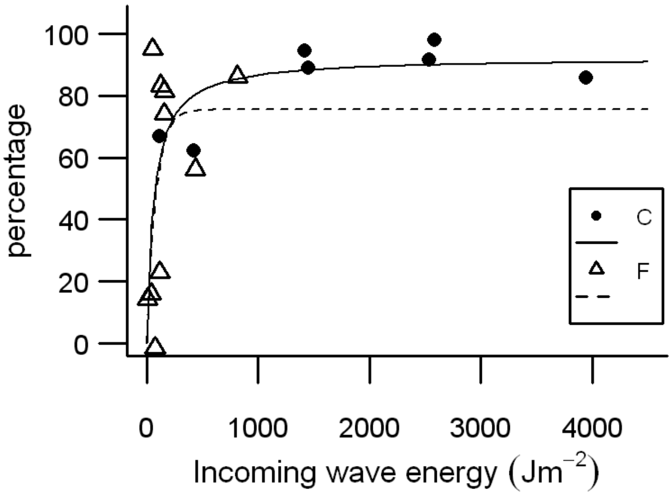

Figure 3 Wave energy reduction as a function of incident wave energy across reef crests (solid circle, solid line, N= 7) and reef flats (open triangle, dashed line, N=10). The points are percent energy reduction for each experiment with regression trend lines.

We examined if the effects of reefs on wave energy were affected by incoming wave energy. As wave energy increased, both reef crests and reef flats had even greater (non-linear) effects on wave energy reduction with asymptotes of 92% and 76% respectively (Fig. 3). There was a positive relationship between incoming wave energy and wave energy reduction across the whole reef, but it was not significant. There was a substantial gap between the highest incoming wave energy assessed across the whole reef and all other values, which may have influenced the ability to detect a pattern (Fig. S6).

Reefs significantly reduced wave height across all three zones (Fig. 2b; Fig. S4b). The reef crest reduced wave height by 66% (53-76%). The reef flat reduced wave height by 41% (36-47%, Fig. 2b). Together the whole reef reduced wave height by 85% (65-93%, Fig. 2b).

Wider reef flats had significantly greater effects on wave energy and height reduction, but most of the wave attenuation happened quickly. Reef flats dissipated up to 94% of the incident waves (Fig. 4), with 50% of the reduction occurring on the outer 133 m of the reef flat. Similarly, wave height reduction was 67% (Fig. 4), half of which occurred on the outer 127 m of the reef flat.

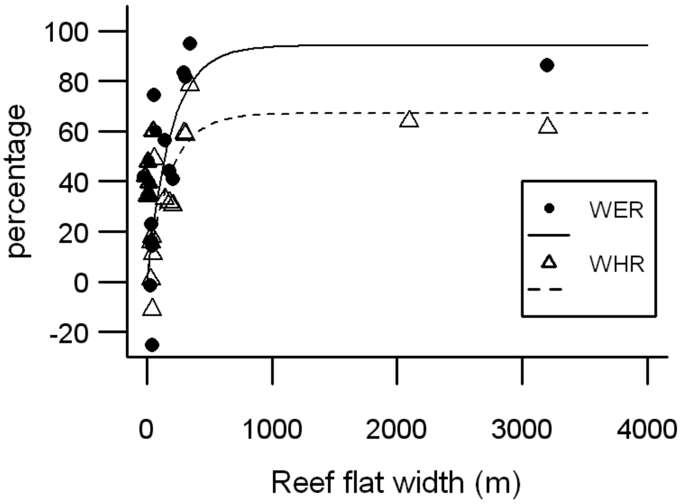

Figure 4 The effects of reef flat width on wave energy reduction (WER, solid circle, solid line, N= 13) and wave height reduction (WHR, open triangle, dashed line, N=14). Each point is the percent wave attenuation for each experiment with trend lines.

Comparisons of wave attenuation between natural and artificial structures

In terms of structure height and placement, low-crested detached breakwaters are the most comparable and common artificial structures to coral reefs (F.Burcharth and Hughes 2011). Coral reefs attenuate waves as much as and more than low-crested detached breakwaters. The wave attenuation efficiency of low-crested detached breakwaters is typically measured by the transmission coefficient K_t, which is the ratio of the transmitted to the incident significant wave height (H_t/H_i). K_t depends on design parameters such as crest freeboard, crest width, and structure permeability (van der Meer et al. 2005), as well as local wave height and period. The wave attenuation effectiveness of low-crested detached breakwaters is sometimes purposefully reduced due to social and economic considerations such as concerns about poor water quality in stagnant waters behind these structures (Burcharth et al. 2007). K_t values of low-crested detached breakwaters typically range from 0.3-0.7, which represents a wave height reduction of 30-70% (Armono and Hall 2003, Calabrese et al. 2008, Zanuttigh et al. 2010, F.Burcharth and Hughes 2011, Irtem et al. 2011), a similar range to the average wave height reduction of 66% (53-76%) shown here for coral reefs.

Reefs and At-Risk Populations

There are 197 million people who live in at-risk coastal areas (below 10 m elevation) and within 50 km of coral reefs (Fig. 5). The countries with the greatest number of at-risk people who may receive risk reduction benefits from reefs are Indonesia and India (>35 M people each); followed by the Philippines (>20M); China (>15 M); Brazil, Vietnam, Brazil and the USA (>7 M). More than 20 countries had most of their population (>50%) living in low elevations and near reefs, which includes nations such as the Maldives, Palau, St. Kitts and Nevis, Grenada, Bermuda, Bahamas, and Bahrain. Global maps are accessible from www.network.coastalresilience.org.

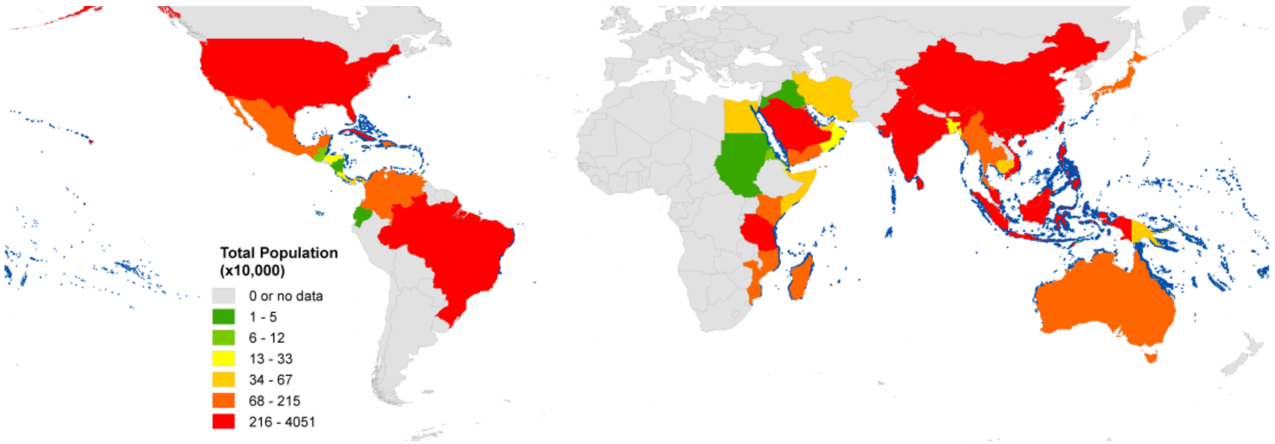

Figure 5 Coral reefs (blue) and at-risk people by country. The countries are grouped by the number of people living below 10 m elevation and within 50 km of a coral reef as indicated in the legend. Countries in gray either have no data or no people meeting these conditions.

Discussion

We provide the first quantitative meta-analysis of the role of coral reefs in reducing wave energy across reefs in the Indian, Pacific, and Atlantic Oceans. In combining results across studies, we show that coral reefs dissipate 97% of the wave energy that would otherwise impact the shoreline. Reef loss and degradation would be expected to result in large increases in wave height and energy impacting the coast (Sheppard et al. 2005).

Most (88%) of the wave energy was dissipated by the reef crest; this relatively high and narrow geomorphological area is the most critical in providing wave attenuation benefits. The reef flat dissipates approximately half of the remaining wave energy; most of the wave energy on the reef flat was dissipated in the first 150 m of the reef flat (i.e., closest to the reef crest). These results are consistent with both models and observations of coastal barriers that identified cross-shore bathymetric profile, and in particular the height of the barrier or reef crest, as the most important variable in coastal defense considerations (Smith et al. 2010, Hoeke et al. 2011, Sheremet et al. 2011, Storlazzi et al. 2011).

After bathymetry, another critical factor in wave attenuation is bottom friction, which is a function of bottom rugosity (Lowe et al. 2005b, Lowe et al. 2007). Coral reef degradation has had significant impacts on rugosity. For example the loss of branching Staghorn and Elkhorn corals (*Acropora* spp.) Caribbean-wide (Alvarez-Filip et al. 2009) affects both height and rugosity particularly on reef crests. The loss of these corals and the overall degradation of rugosity (Alvarez-Filip et al. 2009) has led to real increases in wave energy reaching coastlines (Sheppard et al. 2005). These considerations add weight to the concerns of coral reef managers about the ongoing loss of structural complexity (Alvarez-Filip et al. 2009) and the interaction of multiple stressors impacting coral reef rugosity (Blackwood et al. 2011).

The importance of the wave attenuation benefits provided by coral reefs intensifies as incoming wave energy increases. The data suggest, for example, that coral reefs would dissipate 92% of storm generated waves that are 3 m high or higher. These extrapolations are consistent with observations made during Hurricane Wilma (2005), where the Meso-American reef attenuated 99% of incoming wave height (Blanchon P et al. 2010). Moreover, the data are consistent with common observations (e.g., ubiquitous surfing photos) that large waves (>7 m) break and dissipate most of their energy on reef crests, resulting in relatively low wave energy on the inner portion of the adjacent reef flat. In this regard, coral reef crests exert some of the same functions as the inundated barrier islands that significantly dampened storm waves from Hurricane Gustav in 2008 (Smith et al. 2010).

Coastal barriers are critical not just for low-frequency, high-energy events (e.g., storms and cyclones), but also in shaping the erosion and accretion from the high-frequency (i.e., daily) events of wind and swell waves. We show that coral reefs are highly effective in dissipating the energy of the swell waves most relevant for coastal erosion.

Although coral reefs are one of the most well-studied marine ecosystems (e.g., >18,000 papers on reef ecology and geology in the last 20 years), we found only 182 papers that noted the role of reefs in wave attenuation, wave energy, or wave breaking. There were more than 5,000 papers that noted coral reef fish and fisheries. Given so little focus, it is not surprising that there are few direct measurements of the implications of reef degradation on wave impacts. In the Maldives, Red Sea, Cancun (Mexico) and Bali (Indonesia) there are inferred links between increases in coastal development, reef degradation, and investments in artificial defenses, but few direct studies on causality (Brown and Dunne 1988, Frihy et al. 1996, Knight et al. 1997, Sheppard et al. 2005, Moran et al. 2007). The effects of reef degradation on risk and vulnerability to coastal hazards need to be addressed in greater detail, which will require much greater collaboration among ecologists, engineers, geologists, and oceanographers.

Green Vs Gray Infrastructure

There are few direct economic analysis of the value of coral reefs for coastal protection, but four lines of evidence suggest that reef conservation and restoration are cost effective for hazard mitigation. First is the fact that coral reefs can deliver wave attenuation benefits similar or greater than common artificial structures designed for coastal defense such as low crested breakwaters (see results). Second, the costs of replacing just these wave attenuation benefits with artificial gray defenses (e.g. breakwaters) are very high. Building artificial breakwaters in tropical waters is expensive, with project costs ranging from \$1,300 m^{-1} to \$189,100 m^{-1} (Sargent et al. 1988, Berg et al. 1998, Wells et al. 2006); all \$ values reported are adjusted costs in 2012 US\$. The US Army Corps of Engineers provides the most comprehensive listing of projects (Sargent et al. 1988) and the median of these projects is \$40,055 m^{-1}. Third the costs of enhancing reef benefits through coral restoration are much cheaper and range from \$2 to \$900 m^{-2} (Cesar 2000, Fox et al. 2005, Goreau and Hilbertz 2005, Yeemin et al. 2006, Wells et al. 2010). Fourth, the insurance industry has identified that reef revival can be cost effective for risk reduction. They examined the costs and benefits of some 20 different approaches for coastal hazard mitigation, from reef restoration to new building codes, across eight Caribbean nations (Caribbean Catastrophe Risk Insurance Facility 2010). They found that reef restoration was one of the most cost effective strategies across seven of eight nations. Reef restoration was always substantially more cost effective than breakwaters across all eight nations, even though the only reef benefits considered were hazard risk mitigation not other benefits such as fisheries and tourism.

Conclusions and Recommendations

Reefs attenuate waves and reduce the wave energy impacting the shore. There are some 197 million people in villages, towns, and cities along the coast at low elevations who may receive risk reduction benefits from reefs or may have to bear costs if the reefs are lost or degraded.

Reefs offer many well-known benefits to coastal communities, but there has been relatively little focus on reef conservation and management for their risk reduction benefits. Indeed as coastal hazards increase and climate adaptation funds flow towards developing, tropical, coastal nations, there will be increasingly more funds spent on coastal hazard mitigation. For many nations, coral reefs are their first line of defense, and risk reduction funds may be best spent on conserving, managing, and restoring these benefits.

The conservation of existing reefs should be the preferred management option. Unhealthy reefs are more prone to erosion, which will lower reef crest height and allow more incident wave energy to propagate towards the shoreline (Sheppard et al. 2005). Many man-made defense infrastructure are expensive and will often further degrade coastal ecosystems (Nicholls 2011). Without improved management, the coastal protection value of coral reefs and other associated benefits will continue to decline. Healthy reefs, unlike artificial barriers, may be able to keep up with sea-level rise and to continue to supply sand to beaches, which adds further to their comparative cost effectiveness. A recent study showed that marine protected area (MPA) enforcement was a particularly cost-effective solution (Haisfield et al. 2010).

Reefs have faced growing degradation in the past few decades and some scientists question their viability in future centuries with climate change (e.g., (Hoegh-Guldberg et al. 2007)), but this view is too pessimistic (e.g., (Pandolfi et al. 2011)). The effects of climate change on reefs will be species and site-specific; there will be strong evolutionary pressure for coral climate resistance and resilience; and coral climate resilience can be enhanced by removing other stressors and preserving biogeochemical links with surrounding coastal habitats (Anthony et al. 2011, Pandolfi et al. 2011, Hughes et al. 2012, Manzello et al. 2012, Unsworth et al. 2012). Moreover, coral reefs are in better shape than most coastal habitats such as marshes, mangroves, and oyster reefs (Beck et al. 2011). They thus harbor even more options for conservation and restoration that is targeted for adaptation benefits for reefs and people. In terms of global climate change, most of the dire predictions about coral reef futures aim to influence climate mitigation discussions (e.g., slowing emissions) and lack sufficient consideration of adaptation opportunities.

Reef restoration will be needed in many areas. Restoration practices are advancing rapidly, can be cost-effectively targeted for risk reduction benefits, and there are funding flows that can support these adaptation efforts. In the last 20 years, many coral reef restoration approaches and technologies such as coral transplantation, Reef Ball, Biorock, and EcoReef modules have been developed. We have shown here how to focus these restoration efforts even more cost-effectively for coastal risk reduction benefits. Restoration or adaptation for hazard mitigation and adaptation should be focused along the reef crest, where the greatest wave energy reduction can be achieved. Coral reef scientists and managers must pay greater attention to the threats and opportunities that are already flowing with adaptation funds to tropical developing nations. These funds could be targeted appropriately for more reef restoration or can support more seawalls, groynes, and jetties. Hybrid measures that use reef-like artificial structures to deliver benefits to reefs and people should be preferable to options that have neutral or negative effects on reefs. Many governments and funders will demand projects with quick results and benefits for risk reduction, which makes direct restoration efforts more appealing than other equally useful reef management measures.

A management focus on reefs with the goal of providing hazard mitigation and risk reduction, however, will require changes in the approach that conservation and disaster risk reduction managers have taken to date. Conservationists will need to focus more attention on reefs closer to the people who will benefit from reef restoration and management instead of more remote and “pristine” reefs away from people and coastal property. Disaster risk reduction managers will have to focus more on prevention measures such as sustainable development and more on environmental conservation; both are recognized as important and cost effective by the disaster risk reduction community but rarely acted upon (UNISDR 2011).

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Supporting Information

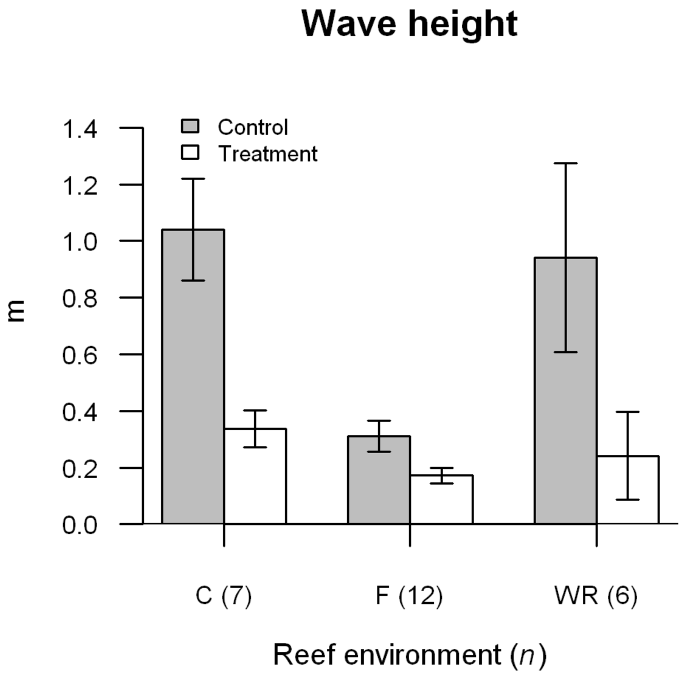

Figure S1 Wave height at control (seaward) and treatment (landward) sites for the three coral reef environment considered (C= reef crest, F= reef flat, WR= whole reef). Values are expressed as mean ± 1 standard error. Number of independent experiments (*n*) analyzed is reported in brackets.

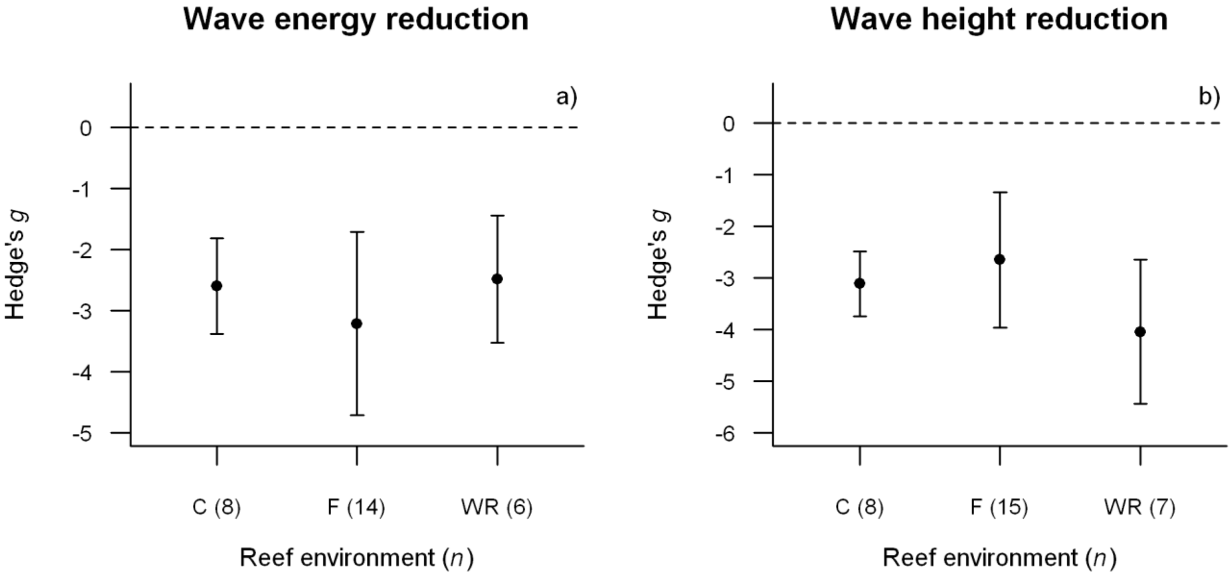

Figure S2 Meta-analysis of the wave attenuation service provided by coral reefs calculated as Hedge's *g* on (a) wave energy reduction and (b) wave height reduction. Average effect size and 95% confidence interval are reported for each coral reef environment considered (C= reef crest, F= reef flat, WR= whole reef). When confidence intervals do not overlap 0, averages are considered significantly different from 0. Number of independent experiments (*n*) analyzed is reported in brackets.

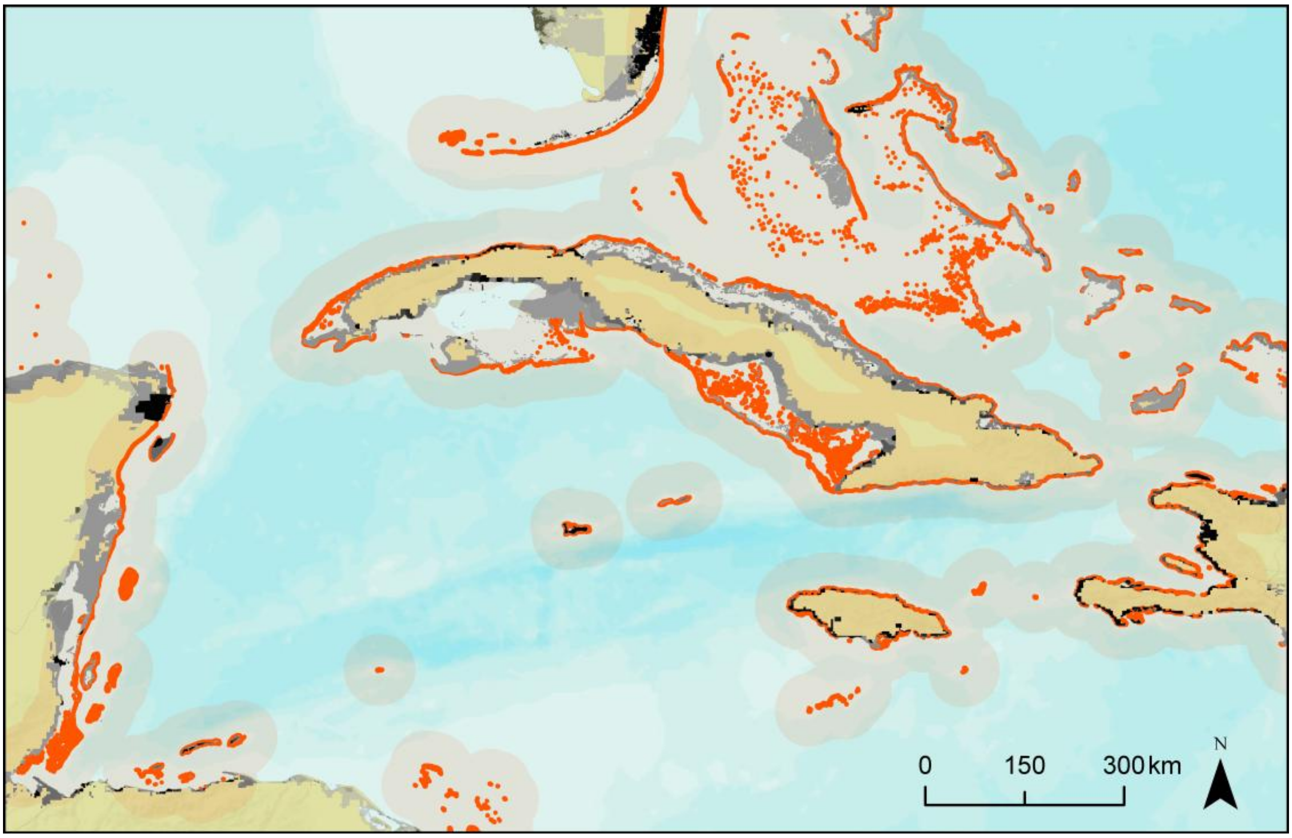

Figure S3 Detailed view of data sets used in our global estimate of the number of people in low lying areas near reefs focused on the Caribbean. Coral reefs are orange, 50km zone around reefs is light orange and population density (per sq km) ranges from grey (low) to black (high).

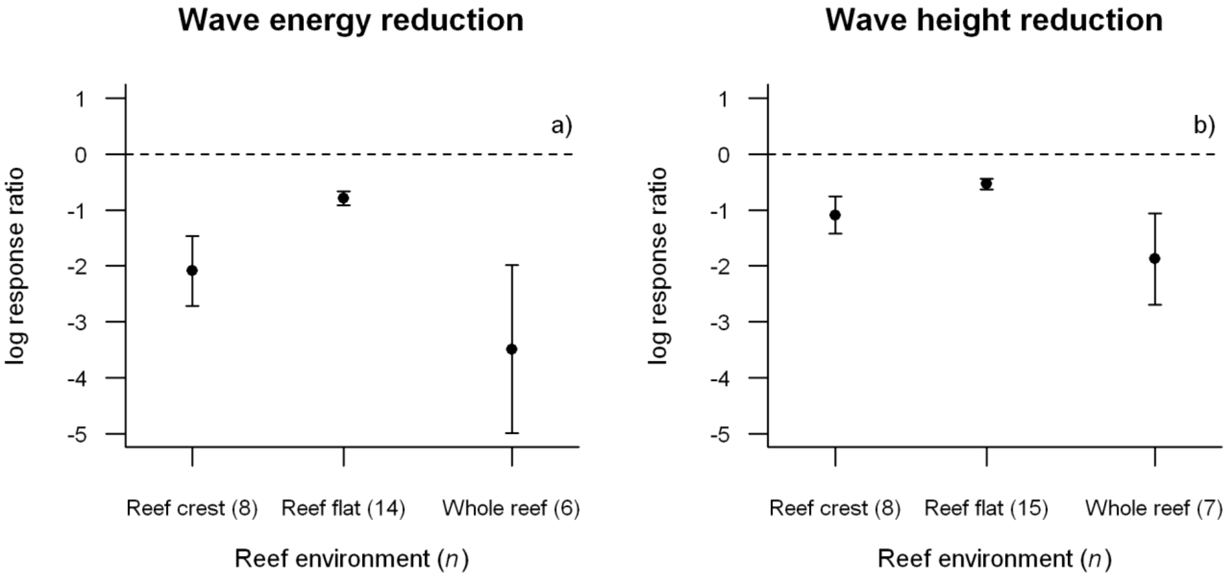

Figure S4 Meta-analysis of the wave attenuation service provided by coral reefs. Average effect sizes as log response ratios of a) wave energy reduction and b) wave height reduction due to each reef environment considered. Error bars represent 95% confidence interval. When confidence intervals do not overlap 0, averages are considered significantly different from 0 ($p<0.05$). Number of independent experiments analyzed (*n*) is reported in brackets.

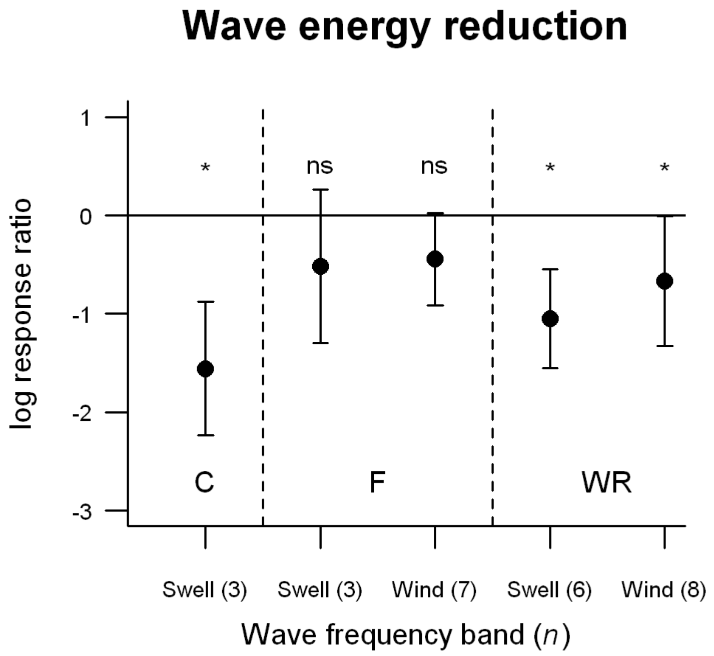

Figure S5 Average effect sizes calculated as log response ratios of meta-analyses on energy reduction for different wave bands: wind waves (T = 3-8 s, Wind) and swell waves (T = 8-20 s, Swell). Mean and 95% confidence interval are reported for different reef environments (C= reef crest, F= reef flat, WR=whole reef). When confidence intervals do not overlap 0, averages are considered significantly different from 0. Number of independent experiments (n) analyzed is reported in brackets. ns = non significant, * = p<0.05.

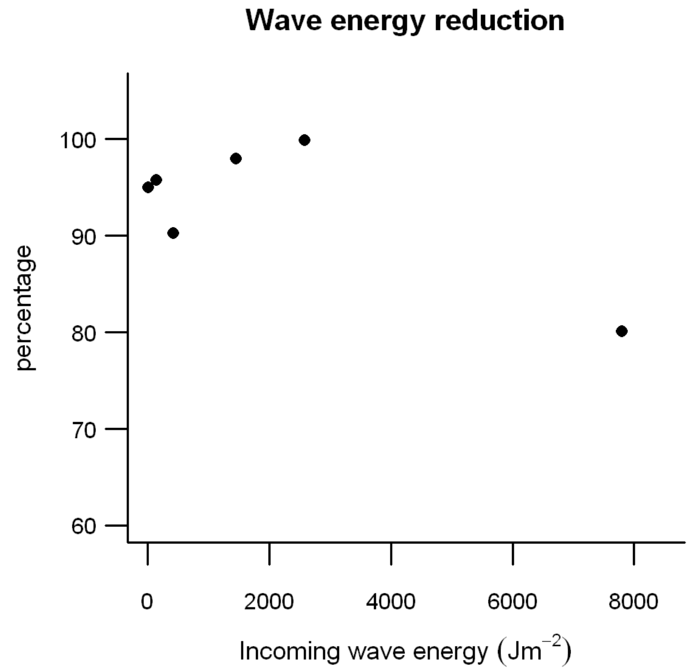

Figure S6 Wave energy reduction as function of energy of incoming waves. Each point represents the percentage of energy reduction computed for individual experiment considering the effect of the whole reef (N=6).

Text S1. *Estimating the total number of people living in low lying areas near reefs.*

To estimate the number of people that might benefit from the effects of coral reefs on wave energy, we examined the number of people globally in low lying areas (below 10m) near a reef (within 50 km). Using ArcGIS, we extracted all areas below 10m elevation from the Global Digital Elevation Model (ETOPO2) provided by the National Geophysical Data Center (NGDC). We used the resulting raster of low lying areas to clip the Global Rural-Urban Mapping Project (GRUMP) global population data set. GRUMP data provided by the Urban Extents Data Collection, Alpha Version, Center for International Earth Science Information Network (CIESIN), Columbia University. The resulting raster indicates total population residing in areas less than 10m elevation.

We mapped coral reefs using a global data set provided by World Resources Institute, *Reefs at Risk Revisited*, 2011. We applied a dissolved buffer of 50km to the global reef data to identify all areas within a 50km zone of coral reefs. We then intersected the 50km reef zone with the low lying population raster data set to generate a raster indicating low lying population near coral reefs. Figure S3 is a detailed view of the Caribbean showing a portion of the coral reefs, 50km zone, and low lying population raster used in our analysis. Using zonal statistics, we calculated the global estimate of the number of people in low lying areas near reefs. We also calculated separate totals per country using zonal statistics. Country zones were delineated by each country's land and maritime boundaries. Global country boundaries were provided by World Resources Institute, *Reefs at Risk Revisited*, 2011 and maritime boundaries were provided by VLIZ (2011) Maritime Boundaries Geodatabase, version 6.1, Flanders Marine Institute.

Table S1 Studies included in meta-analysis of wave energy dissipation and wave height reduction. For each reference is reported the sample size of both control and treatment for each independent experiment considered belonging to different coral reef environment (C= reef crest; F= reef flat;WR= whole reef).

Reference	**Reef location**	**Data[a] Source**	**Original response[b] variables ; unit**	**Sample Size**					
				Control			**Treatment**		
				C	**F**	**WR**	**C**	**F**	**WR**
Wave energy dissipation									
Falter *et al.* 2004	Kaneohe Bay, Oahu, Hawaii	DER	E ; J m^{-2}		3			3	
Storlazzi *et al.* 2004	Molokai, Hawaii	DER	E ; J m^{-2}			15			15
Lowe *et al.* 2005	Kaneohe Bay, Oahu, Hawaii	DER	E ; J m^{-2}	5	5	5	5	5	5
Lowe *et al.* 2009a	Kaneohe Bay, Oahu, Hawaii	DER	E ; J m^{-2}	10			10		
Lowe *et al.* 2009b	Kaneohe Bay, Oahu, Hawaii	DER	E ; J m^{-2}	25			25		
Gourlay 1994	Hayman Island, Australia (flume model)	DER	E ; J m^{-2}			17			17
Hardy and Young 1996	John Brewer Reef,Australia	DER	E ; J m^{-2}		10		10		
Brander *et al.* 2004	Warraber Island, Australia	SURV	Wave energy ; m^{2} Hz^{-1}		5 5 5 5			5 5 5 5	
Kench and Brander 2006	Australia	DER	Wave e. dissipation; %	9			9		
Jago *et al.* 2007	Lady Eliot Island, Australia	DER	E ; J m^{-2}		3			3	
Samosorn and Woodroffe 2008	Warraber Island, Australia	DER	E ; J m^{-2}		57			39	
Taebi *et al.* 2011	Sandy bay, Ningaloo Reef, Australia	DER	E ; J m^{-2}	15			15		
Péquignet *et al.* 2011	Ipan reef, Guam	DER	E ; J m^{-2}	50	50	50	50	50	50
Lugo-Fernandez *et al.* 1998a	Great Pond Bay, St. Croix, US Virgin Island	DER	E ; J m^{-2}	8	8	8	8	8	8
Lugo-Fernandez *et al.* 1998b	Tague Reef, St. Croix, US Virgin Island	DER	E ; J m^{-2}	110			110		
Kench *et al.* 2009	Hulhudhoo reef, South Maalhosmadulu atoll, Maldives	DER	E ; J m^{-2}		5 5 5 5			5 5 5 5	
Nakaza and Hino 1991	Minatogawa fishery port, Japan (flume model)	DER	E ; J m^{-2}			3			3

Zhu et al. 2004	Yongshu Reef, Nansha Islands, China	DER	Wave energy dissipation %		18 85			18 85	
Wave height reduction									
Falter *et al.* 2004	Kaneohe Bay, Oahu, Haii	SURV	H_s ; m		3			3	
Storlazzi *et al.* 2004	Molokai, Haii	SURV	H_s ; m			15			15
Lowe *et al.* 2005	Kaneohe Bay, Oahu, Haii	SURV	H_{rms} ; m	5	5	5	5	5	5
Lowe *et al.* 2009a	Kaneohe Bay, Oahu, Haii	SURV	H_{rms} ; m	10			10		
Lowe *et al.* 2009b	Kaneohe Bay, Oahu, Haii	SURV	H_{rms} ; m	25			25		
Gourlay 1994	Hayman Island, Australia (flume model)	EXP	H ; m			17			17
Hardy and Young 1996	John Brewer Reef,Australia	SURV	H_s ; m		10		10		
Brander *et al.* 2004	Warraber Island, Australia	SURV	H_s ; m		3			3	
Kench and Brander 2006	Australia	SURV	wave h. dissipation; %	6	6	6	6	6	6
Jago *et al.* 2007	Lady Eliot Island, Australia	SURV	H_s ; m		3			3	
Samosorn and Woodroffe 2008	Warraber Island, Australia	SURV	H_{m0} ; m		57			39	
Taebi *et al.* 2011	Sandy bay, Ningaloo Reef,Australia	SURV	H_s ; m	15			15		
Péquignet *et al.* 2011	Ipan reef, Guam	SURV	H_s ; m	50	50	50	50	50	50
Lugo-Fernandez *et al.* 1998a	Great Pond Bay, St. Croix, US Virgin Island	SURV	Significant wave h. m	8	8	8	8	8	8
Lugo-Fernandez *et al.* 1998b	Tague Reef, St. Croix, US Virgin Island	SURV	Significant wave h. m	110			110		
Kench *et al.* 2009	Hulhudhoo reef, South Maalhosmadulu atoll, Maldives	SURV	H_s ; m		5 5 5 5			5 5 5 5	
Nakaza and Hino 1991	Minatoga fishery port, Japan (flume model)	EXP	H_s ; m			3			3
Zhu *et al.* 2004	Yongshu Reef, Nansha Islands, China	DER	wave height dissipation %		18 85			18 85	

(a) Data Source indicate if data were collected during a survey in the field (SURV), resulted from experimental activity (EXP) or derived from other original measures (DER)

(b) Response variable as cited in the original study. E is wave energy calculated from eq. 1;Hs= significant wave height; Hrms = root-mean-square wave height; Hm0= significant wave height.

Chapter 3: Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures

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Abstract

With nearly two thirds of the human population concentrating along coastlines, coastal development and urbanized seascapes are inevitable. Proliferation of coastal and marine infrastructures such as breakwaters, ports, seawalls and offshore installations, is associated with loss of natural habitats. This calls for new strategies aimed at elevating the ecological and biological value of coastal infrastructures, while minimizing their ecological footprint. We explored the feasibility of using coastal defence structures as a scaffold for the conservation of threatened marine species. We experimented with fucoids, canopy-forming algae on Mediterranean coasts, in light of their declared conservation priority. We transplanted juveniles of *Cystoseira barbata* to a number of breakwaters and natural sites along the Adriatic Sea (Italy), and tested which factors could facilitate or inhibit its successful establishment. Survival of transplanted *C. barbata* was greater at most artificial and natural sites examined compared to the native sites where severe habitat loss was ongoing. Survival was greater at landward compared to seaward positions on the infrastructure, while no relevant effects of substratum characteristics (horizontal *vs.* vertical orientation, variable composition and increasing complexity) were observed. Lack of surrounding adult fronds did not impair the survival or growth of the transplants, suggesting a high transplantation potential also on novel infrastructures. Success of transplantation in areas remote from source population was limited by biotic disturbance which were more intense on coastal infrastructures in sedimentary environments compared to natural rocky sites. Harnessing coastal and marine infrastructures for enhancing desired species of conservation value (such as threatened canopy-forming algae) seems feasible. Nonetheless, in order to efficiently incorporate such strategies into management and conservation actions, a sound understanding of the different ecological functioning of these urban seascapes compared to natural habitats is required.

Keywords: Canopy-forming algae, Coastal infrastructures, Conservation, *Cystoseira*, Enhancement, Management, Transplantation, Urban seascapes.

Introduction

With nearly two thirds of the world's population concentrated in coastal areas (Creel, 2003), substantial coastal development is inevitable. The land-sea interface is exploited for various human uses including industry, transportation, energy, and recreation (Airoldi and Beck, 2007). These forms of coastal development are frequently associated with fragmentation and loss of natural habitats, damaged seascapes and reduced biodiversity (Airoldi and Beck, 2007; Crain et al., 2009; Dugan et al., 2011).

It is known that coastal infrastructures do not function as surrogates to natural habitats (Bulleri and Chapman, 2004; Jackson et al., 2008). Their vertical profile compresses the intertidal zones, and their homogenous surfaces combined with high frequency of disturbances tend to favor impoverished assemblages dominated by opportunistic and invasive species (Bulleri and Airoldi, 2005; Chapman et al., 2009; Airoldi and Bulleri, 2011).

As coastal infrastructures are expected to proliferate alongside with human population (UN, 2008), efforts should be made not only to minimize their detrimental impacts, but also to elevate their possible ecological value. This requires understanding of the types of assemblages or ecosystem functions that are desirable and feasible in these habitats. Initial steps in this direction have been made in highly urbanized areas in both temperate (Airoldi et al., 2005b; Chapman and

Blockley, 2009; Browne and Chapman, 2011), and tropical environments (Perkol-Finkel et al., 2006; Perkol-Finkel et al., 2008). Nonetheless, the notion of combining ecological principles to urban infrastructure is rather new (Mitsch, 1996; Bergen et al., 2001) and to date has been scarcely applied in marine environments.

We examined the feasibility of facilitating the growth of threatened fucoid macroalgae of the genus *Cystoseira* on coastal defense structures. Fucoids and kelps form diverse, structurally complex and highly productive canopy habitats along many temperate rocky coasts (Steneck et al., 2002). Canopies are suffering widespread habitat loss at global scales (Airoldi and Beck, 2007; Connell et al., 2008; Mangialajo et al., 2008). Decline in the Mediterranean Sea is well documented, and today six Mediterranean species of *Cystoseira* are listed as threatened in the Bern Convention and in the Mediterranean Action Plan. In the Mediterranean, the proximate cause for loss of *Cystoseira* is anthropogenic disturbance, largely in the form of urbanization (Benedetti-Cecchi et al., 2001). Recent experiments have shown the potential for recovery of canopy-forming macroalgae through various approaches, including transplanting or seeding macroalgae back to their original habitat (Correa et al., 2006; Susini et al., 2007; Perkol-Finkel and Airoldi, 2010), and the use of artificial reef for algal restoration is increasing (Terawaki et al., 2003; Falace et al., 2006; Park and Lee, 2010). Here, we explored the alternative possibility of gardening these important habitats-formers onto coastal infrastructures, deployed for other societal needs. This approach would enhance the ecological value of these infrastructures, without compromising their original function.

Relatively few studies have attempted to transplant canopy-forming macroalgae onto artificial substrata (Terawaki et al., 2003; Jonsson et al., 2006), and little is known about the factors enhancing the success of these interventions. We transplanted juveniles of *Cystoseira barbata* (Stackhouse) C. Agardh to a number of breakwaters and natural sites along the Italian North Adriatic Sea (Italy). Marine infrastructures offer atypical substrates for benthic assemblages in terms of orientation, exposure, structure, and surface texture (Vaselli et al., 2008; Burt et al., 2009;

Bulleri and Chapman, 2010), all of which are known to affect the recruitment, survival and growth of fucoids and other macroalgae (Harlin and Lindbergh, 1977; Wells et al., 1989; Airoldi, 2001; Jonsson et al., 2006). We tested whether the survival and growth of transplants differed between natural and artificial habitats, horizontal *vs*. vertical substrata, between landward *vs.* seaward sides of the breakwaters, or among substrata of different composition and increasing surface complexity. We also analysed whether lack of naturally occurring surrounding adult canopies on such infrastructures, which normally facilitate natural recruitment of canopies (Connell, 2005; Irving and Connell, 2006), limits successful transplantation. Finally, we used caging experiments to test the possible role of grazing pressure on success of transplantation, as this factor has been previously described as limiting for growth of macroalgae on coastal defense structures (Jonsson et al., 2006), and since pilot tests suggested the importance of this factor in our study system.

Methods

Study area and species

The study was conducted at the Monte Conero promontory (43° 33′ N, 13° 37′ E) and the surrounding urbanized sandy coastline of the North Italian Adriatic Sea (Fig. 1). The rocky promontory hosts some of the last-remaining scattered populations of the threatened genus *Cystoseira* along the central - northern Italian Adriatic coast (Perkol-Finkel and Airoldi, 2010). The fragmented state of these populations probably results from a synergistic effect of low substratum stability and competition with opportunistic species (Perkol-Finkel and Airoldi, 2010). We sourced *Cystoseira* from two sites “Due Sorelle” and “La Vela”. The algal assemblages at these sites were composed mainly of the species *Cystoseira barbata* C. Agardh (Fucales: Sargassaceae) that was found in varying densities from ca. 2 to 5 m depth. A detailed description of the study area, the biology of the species and historical changes in the distributions of macroalgal canopies can be found in Perkol-Finkel and Airoldi (2010).

Other rocky habitats in the area exist only in the form of detached breakwaters, two of which, at the localities named Urbani and Numana (Fig. 1) were used for the experiments. According to preliminary surveys, the natural bedrocks surrounding these breakwaters had a very sporadic appearance of naturally recruited *C. barbata*. We also transplanted juveniles onto breakwaters at the localities of Marotta, Lido Adriano and Punta Marina (ca. 50, 140 and 150 km north of Monte Conero), where no *Cystoseira* naturally occurs.

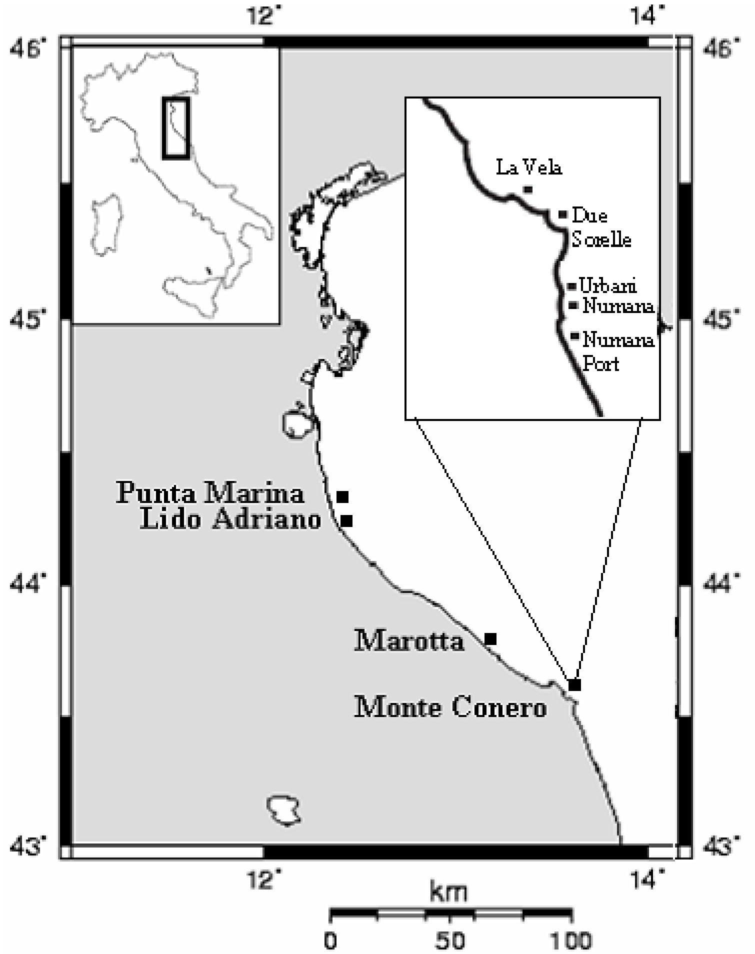

Figure 1: Map of the study sites along the north Adriatic Sea, and insert map of locations at the Monte Conero promontory.

Transplantation experiments

We transplanted juveniles (2-3 months old, 5 cm high) of *C. barbata* collected from loose boulders at Due Sorelle and La Vela in June 2008. Previous studies showed that recruits in these habitats have low survival probability due to severe substratum instability (Perkol-Finkel and Airoldi, 2010). The boulders were broken into small fragments holding 1-2 individuals which were transplanted onto the substrate into the new habitats using epoxy putty (Subcoat S. Veneziani) to form experimental plots comprising 5 transplanted individuals.

Such plots were transplanted in 4 habitat types (hereafter "Habitats"). These included: (1) "Native habitat", i.e. the loose boulder fields where the few juveniles naturally occurring in the area are found and from which they were initially collected, and 3 additional habitats (hereafter "Other Habitats") where natural recruitment of juveniles was not observed, including (2) Natural bedrock habitat (i.e. stable bedrocks represented by boulders > $10m^3$ in size or eroded rocky platforms), (3) Artificial habitat - seaward side, and (4) Artificial habitat - landward side. For each habitat, two replicated areas (hereafter "Areas") were established. For the Native and Natural habitats, one area was set at La Vela and another at Due Sorelle. For the artificial habitats, one area was set at Urbani and another at Numana. Within each area, 4 plots with transplants were created in each of the following positions (hereafter "Positions"): 1) Horizontally surrounded with naturally occurring adults (HA), 2) Horizontally without surrounding adults (HW), and 3) Vertically with no surrounding adults (V). Vertical positions with surrounding adults were not included due to the natural scarcity of adults on vertical surfaces. There were no comparable positions in the native habitat, which was represented by small, irregular, loose boulder fields with no consistent relief.

As the main goal of this experiment was to test the feasibility of enhancing fragmented communities of *C. barbata* by transplantation onto artificial structures and identify optimal conditions (i.e. position) for such transplantations, there was no need to include transplantation methodological controls (normally used when transplantation is used to explore aspects of the ecology of the species), as any effect of transplantation would be part of the hypothesis of interest.

Transplantation into the original native habitat and into stable rocky bedrocks served as a comparison to understand how successful would be the transplantation in artificial conditions compared to more natural conditions at natural bedrocks.

The height of the juveniles was recorded at the time of transplantation, and growth was monitored along with survival rates in September and October 2008 and in February 2009. At each date, we also measured the size of unmanipulated *C. barbata* juveniles naturally occurring at La Vela and Due Sorelle to explore whether transplanted juveniles had different growth rates from unmanipulated ones. For this, all juveniles were carefully removed from one random 6x6 cm plot on each of 3 randomly selected boulders, for subsequent measurements in the laboratory. Survival of unmanipulated juveniles from native habitats was known to be virtually nil (Perkol-Finkel and Airoldi, 2010), and no formal comparison was included.

Differences in the average survival and sizes of transplanted juveniles between habitats and positions were tested using asymmetrical permutational ANOVAs, including three factors: Habitat type (where the Native habitat was confronted with the three Other habitats: Natural bedrock, Artificial seaward, and Artificial landward; fixed factor), Area (2 areas, nested in each habitat; random factor), and Position (Horizontal surrounded with adults HA, Horizontal without adults HW, and Vertical V; fixed factor). These asymmetrical analyses involved partitioning components of variation through two sub-analyses (see: Winer, 1971). First, we ran two-way analyses testing for differences among the four habitats and areas, and contrasting the native habitat with the three other habitats irrespective of the possible different positions at the other habitats. Second, we ran three-way analyses, testing for effects of habitat, positions and areas at the other habitats only. We used the statistical package PERMANOVA+ for PRIMER (Anderson et al., 2008) to partition the variability and obtain F-statistics on a matrix of Euclidean distances calculated from the original raw data, and calculated all P-values using 9999 random permutations of the appropriate exchangeable units and Type III sums of squares to cope with the unbalanced design (Anderson et al., 2008). We used PERMANOVA (as opposed to a classic ANOVA test) due to ease of use with complex unbalanced design and to avoid the usual normality assumptions. The analyses were performed on data retrieved in October 2008, as this was the last date for which all plots remained intact; after this date some areas (one Natural bedrock and one Artificial seaward) were damaged by a storm in December 2008. Both survival and size data had homogeneous variances (Levenes' (1960) univariate test run using PERMDISP (Anderson et al., 2008), and there was no need for transformation. The average size of all surviving transplants at the end of the experiment, in February 2009, was also compared to the average size of naturally occurring juveniles using a t-test.

In order to test whether the conditions identified as optimal for the growth of *Cystoseira* also applied to more remote coastal infrastructures in sedimentary environments, we ran two additional transplantation experiments. The first was set at the seaward and landward sides of 2 breakwaters located at Punta Marina and Lido Adriano, simultaneously with the experiment set in the Monte Conero promontory (Fig. 1). Juveniles were transported by car to these locations as quickly as possible in 100 liter tanks. At each side of the breakwaters, 4 plots (with 5 individuals in each) were transplanted at each of the following positions: 1) Horizontally without surrounding adults (HW), and 2) Vertically with no surrounding adults (V). Some individuals were kept in tanks on land for approximately the same time of transportation and transplanted back at the original source location at Due Sorelle as procedural controls. All juveniles transplanted to breakwaters showed 100% mortality within a week of transplantation, and no further sampling was performed.

Because such a rapid loss of transplants was inconsistent with the results from the experiments done on breakwaters in the Monte Conero region, and not related to the transplantation procedure, the following year (June 2009) we ran a second experiment at the locality of Marotta (Fig. 1), which presented water conditions more similar to those at Monte Conero than the other two stations. Four small boulders (ca. 0.1x0.1 m) holding numerous recruits of *C. barbata* were transplanted from Due Sorelle and established horizontally without surrounding adults (HW) at the landward sides of two replicated breakwaters. Here too zero survival was recorded, as all transplants disappeared within three days.

Caging experiments

We used caging experiments to explore whether the loss of transplants observed at artificial habitats set on sedimentary shorelines was related to environmental factors (e.g., lower water quality or excess sedimentation along a sedimentary shoreline), biotic factors (i.e., pressure from grazers or other sources of biological disturbance) or a combination of both. In June 2009, we collected 32 small boulders (ca. 10 cm diameter) densely covered with naturally occurring juveniles of *C. barbata* from La Vela. The boulders were attached to the breakwaters, using epoxy putty, 8 at each of two sites randomly selected at Due Sorelle (natural sites on a stable bedrock) and on two breakwaters at Marotta (artificial sites on a sandy bottom setting). We did not include a comparison with artificial habitats in a rocky setting as we had already demonstrated in the prior transplantation experiment that survival and growth of transplants in this habitat was similar to that of transplants on natural bedrocks. We predicted that if loss of transplants at artificial sandy sites were related to biotic factors, their survival would increase below cages, which limit access to potential grazers. Conversely, differences in survival between the study locations would persist below cages under the prevailing effects of different local environmental conditions.

To unravel the two mechanisms, 4 boulders selected at random at each area were protected by 40x15x15 cm plastic mesh cages (hole size 1x1 cm) which excluded possible macro-grazers (i.e., fish and sea-urchins), while the remaining 4 were left un-caged as controls. Because all transplants (both caged and non-caged) in Marotta were lost within 48 h, the experiment was repeated using 1x1 mm mesh cages, in order to exclude both macro and mesograzers, while control plots were left uncaged. We did not include a partial caging control as we did not know jet the nature of eventual grazers (see Discussion). However, to minimize possible environmental alterations by the cages (e.g., sedimentation or wave action), we conducted the experiment under calm sea conditions. In this experiment, the transplanted units were marble plates (10x10x2 cm) densely covered with *C. barbata* juveniles. The plates had been placed at La Vela in March 2009, at the start of the reproductive season, to measure patterns of recruitment and had not been manipulated in any way before this experiment. The density and cover of juveniles were measured for each plate prior to transplantation, and subsequent changes were monitored 4 and 8 days after transplantation. This short interval was sufficient to detect a clear response while limiting possible longer-term artifacts related to the use of fine-mesh cages. Differences between treatments were analyzed by permutational ANOVA (using the statistical package PERMANOVA as illustrated previously) on data from day 8. The model included the factors: Biotic pressures (caged vs. un-caged, fixed factor), Local Environment (Natural bedrock vs. artificial sandy, fixed factor), and Site (random factor nested within Local Environment).

Recruitment experiments

As the feasibility of successfully rearing *C. barbata* on coastal infrastructures will ultimately depend on its ability to proliferate and recruit onto the artificial substrata following active transplantation, we analyzed the effects of small scale complexity on settlement of *C. barbata* using clay settlement plates (10x10x2 cm). Six plates were prepared for each of 3 levels of complexity: Low (smooth surface), Medium (surface with crevices 1-2 mm deep), and High (surface with crevices ca. 5 mm deep), and set randomly at La Vela in March 2009. Complexity was imprinted onto the moist clay using pieces of natural rock, to mimic natural features. Plates were attached to natural substratum close to adult fronds of *C. barbata* at La Vela during March 2009, at about 3 m depth, using epoxy putty. Recruits of *C. barbata* were counted at the end of June and August 2009. Differences between levels of complexity (fixed factor) were tested separately for each time by permutational ANOVA (Anderson et al., 2008).

We also analyzed the effects of different materials often used for the construction of marine infrastructures, i.e., limestone (marble) concrete, and clay. Six replicated plates (10x10x2 cm) of each material were set randomly at La Vela in March 2009. Recruits of *C. barbata* were counted at the end of June 2009. No further sampling was possible as these plates were lost during a storm. Effect of material (fixed factor) was tested by permutational ANOVA (Anderson et al., 2008).

Results

Transplantation experiments

Juveniles of *C. barbata* transplanted to both natural bedrocks and artificial habitats had significantly greater survival relative to those transplanted back to their native (source) habitat (Fig. 2 and Table 1A, contrast Native *vs.* Other Habitats). While virtually no transplants survived after October 2008 in the native habitat (due to boulder overturning and disturbance), many transplants in the other habitats survived until February 2009. Survival was highest in landward artificial habitats, with average survival > 30%, in comparison to ca. 20% in the natural bedrock habitats and 9% in the seaward artificial habitats (Fig. 2). Nonetheless, differences among these other habitats were not significant (Table 1). Variability among individual replicated plots was high, and some plots had 100% survival throughout the experiment while others had no surviving transplants. There were no consistent detectable effects in relation to position in none of the three other habitats where it was tested (Fig. 2 and Table 1, effects of Position within Other Habitats contrasts).

No significant differences in the size of transplanted juveniles were found between native and other habitats (Fig. 3 and Table 1B, contrast Native *vs.* Other Habitats). However, all survived transplanted juveniles had on average a greater size than naturally unmanipulated juveniles in the study region. These differences were significant (t-test, $P < 0.01$) at the last monitoring date (February 2009) when transplanted juveniles had an average size of 10.79 ± 6.08 cm (mean ± 1 SD, n=83) while natural unmanipulated juveniles sized only 8.27 ± 3.88 cm (mean ± 1 SD, n=49). Moreover, some transplanted thalli that survived to the following spring (2009) both in natural bedrocks and artificial habitats were observed to have grown to adult sizes and hold reproductive structures. In fact, during the summer first generation recruits were observed in close proximity to these transplants. While at the natural sites it is possible that these new recruits originated from other adults in the area, this was unlikely at the artificial sites where very few adults occurred naturally.

None of the juveniles transplanted onto breakwaters at Punta Marina, Lido Adriano or Marotta survived longer than 2-3 days. During these experiments the sea was calm, leading to exclude a possible dislodgment by waves, and there were no signs of vandalism.

Table 1: Asymmetrical analysis of the effects of Habitat type and Position on A) percentage survival and B) size of transplanted *C. barbata* recruits in October 2008. Factors are: Habitat type (were Native boulder habitats were confronted with three Other habitats, namely Natural bedrocks, Artificial seaward, Artificial landward, fixed), Area (2 random areas, nested in Habitat type), and Position (Horizontal surrounded with adults HA, Horizontal without adults HW, and Vertical V, fixed factor) orthogonal to the Other habitats only. The analysis is split in two parts, one (upper) contrasting Native *vs.* Other habitats and the other (lower) examining survival within Other habitats in relation to the different positions. We used the statistical package PERMANOVA to partition the variability and obtain F-statistics on a matrix of Euclidean distances from the original raw data, and calculated all P-values using 9999 random permutations of the appropriate exchangeable units (Anderson et al 2008). * P < 0.05

A. Source of variation	Df	MS	*F*
Habitat	3		
Native *vs.* Other Habitats	1	6796.35	7.77 *
Area (Habitat)	4	874.35	0.73
Residual	72	1189.5	
Among Other Habitats:			
Other Habitats	2	190.3935	0.20
Area (Other Habitats)	3	961.6329	0.84
Position	2	271.8759	0.11
Position x Other Habitats	4	1496.8456	0.59
Position x Area (Other Ha)	6	2547.6733	2.22
Residual	54		
B. Source of variation	**Df**	**MS**	***F***
Habitat	3		
Native *vs.* Other Habitats	1	1.1544	0.007
Area (Habitat)	4	161.19	14.34
Residual	180	11.24	
Among Other Habitats:			
Other Habitats	2	72.72	0.55
Area (Other Habitats)	3	190.31	18.78 *
Position	2	37.865	0.8322
Position x Other Habitats	4	48.315	3.4807
Position x Area (Other Ha)	6	13.921	1.373
Residual	162		

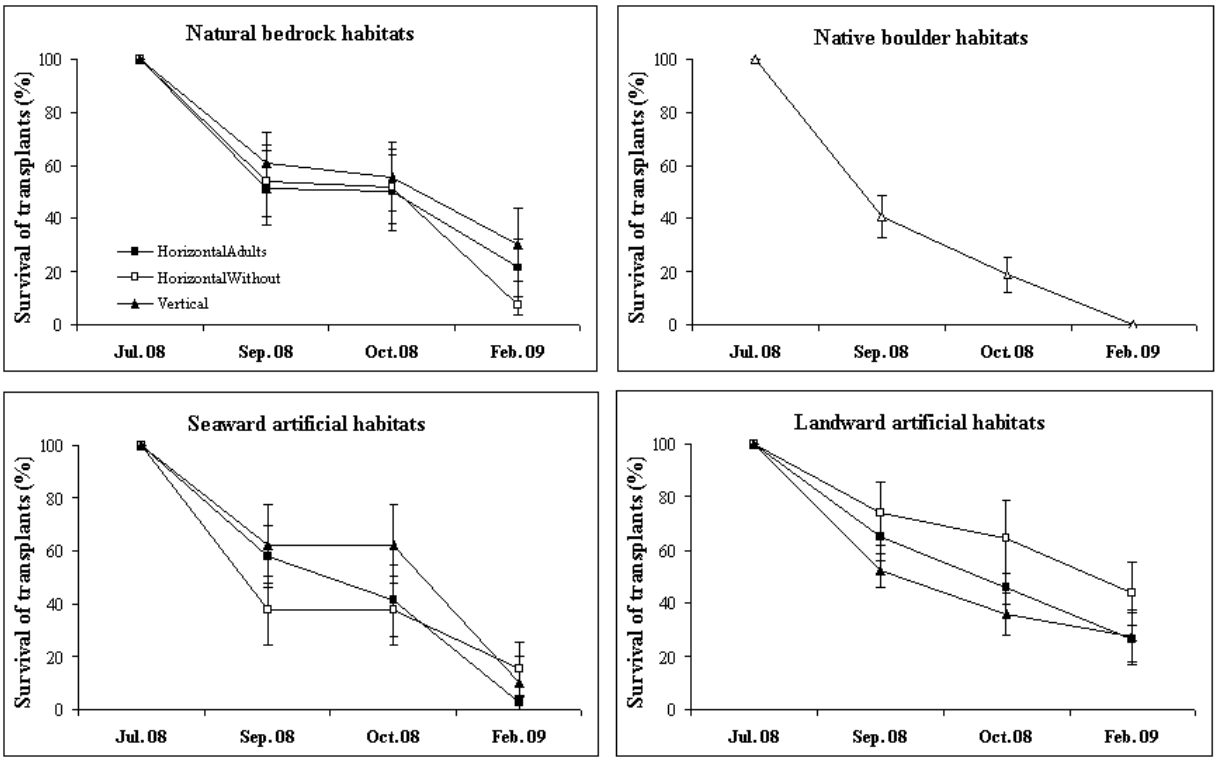

Figure 2: Percentage (average ± 1SE, n = 8, i.e. 4 plots for each of 2 areas) of recruits survived out of those transplanted (5 per plot) in July 2008 at 4 habitats (Natural bedrock, Seaward artificial, Landward artificial, and Native boulder) in Sep. 08, Oct. 08 and Feb. 09, and 3 Positions (Horizontal with surrounding adults = black squares, Horizontal without surrounding adults = white squares, Vertical = black triangles). Native habitat (white triangles) had no comparable positions (see text for further explanation). Data of natural habitats have been presented in part in Perkol-Finkel and Airoldi (2010).

Caging experiments

At the natural bedrock sites, caging did not influence the survival or the cover of juveniles, and all transplants remained equally intact both inside and outside of the cages (Fig. 4A-B). At the artificial sites in Marotta, uncaged transplants showed severe decline, with nearly 80% of the coverage lost within 8 days. These losses persisted when large mesh cages were used. Conversely, both survival and cover of transplanted juveniles at the artificial sites significantly increased when fine mesh cages were used (Table 2A-B, PERMANOVA, significant Treatment x Habitat interaction, $F_{(df = 1,18)} = 5.8739$ $p<0.05$ for cover and $F_{(df = 1,18)} = 47.459$ $p<0.05$ for survival). In these treatments, after 8 days both cover and survival matched the values measured at the natural bedrock sites (Figure 4A-B).

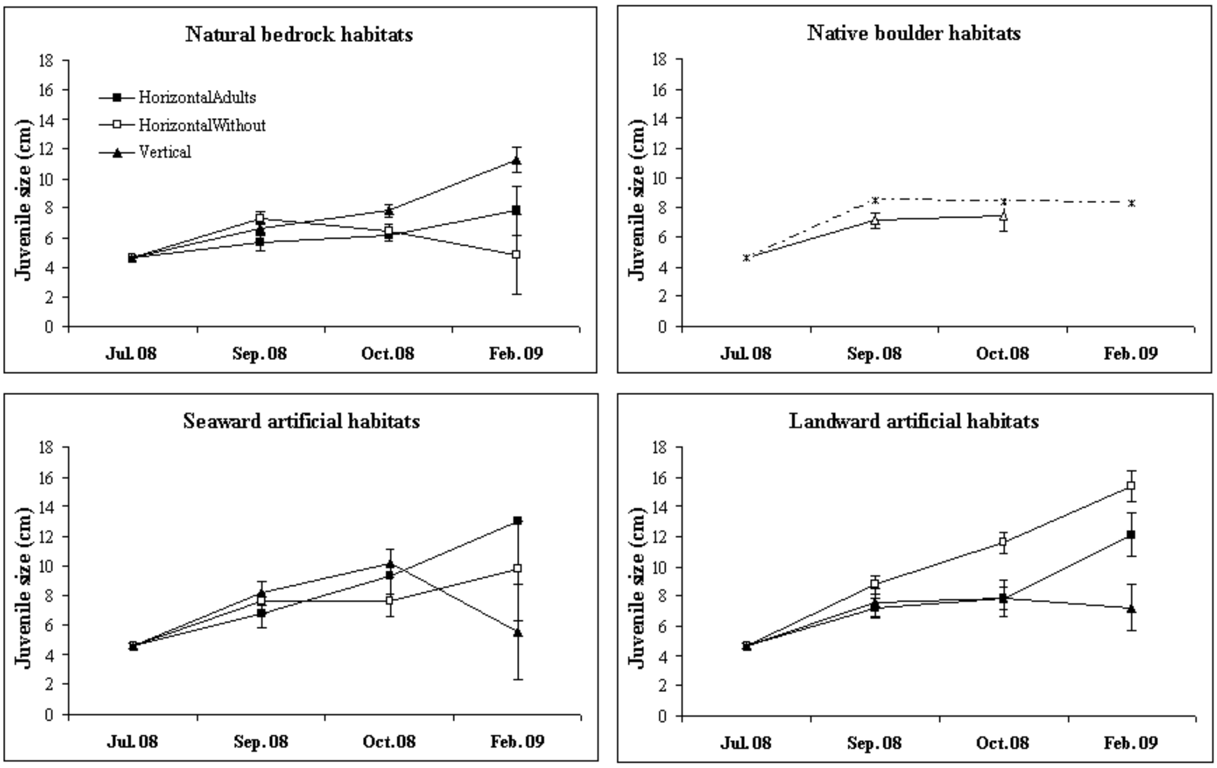

Figure 3: Size of transplanted recruits at 4 habitats (Natural bedrock, Seaward artificial, Landward artificial, and Native boulders) and 3 Positions (Horizontal with surrounding adults = black squares, Horizontal without surrounding adults = white squares, Vertical = black triangles). Native habitat (white triangles) had no comparable positions (see text for further explanation). Plotted are also sizes of natural, un-manipulated recruits in the study areas in July 08, Sep. 08, Oct. 08 and Feb. 09. Data for transplanted recruits are averages (±1SE, n = 8, i.e. 4 plots for each of 2 areas) of the mean sizes of survived thalli within each plots (no measures were available for Feb 09 for control habitats because no transplants survived by that time). Data for natural un-manipulated recruits (= black stars) are averages (± 1ES) over 80 recruits from 3 different boulders sampled from natural habitats at each time point. Data of natural habitats have been presented in part in Perkol-Finkel and Airoldi (2010).

Recruitment experiments

By the end of the reproductive season (June 2009) all settlement plates had some juveniles of *C. barbata*. The density of recruits was highly variable among individual plates, ranging from 6 to 64 individuals. Initially, complexity appeared to have a significant influence on settlement (PERMANOVA: $F_{(df\ =\ 2,14)} = 3.893$, $P < 0.05$), and densities of settlers on plates with medium complexity were on average almost double than those with low and high complexities (Fig. 5). Two months later, average densities on plates with medium complexity was still the highest, but differences between complexities were no longer significant (PERMANOVA: $F_{(df\ =\ 2,14)} = 2.72$, $P >$

0.05). The density of recruits was lower on cement than on limestone and clay (Fig 6), but there was a large variability among plates, and substratum composition did not appear to significantly affect settlement of *C. barbata* (PERMANOVA: $F_{(df = 2,13)} = 1.684$, $P > 0.05$).

Table 2: Results of tests for **A.** Relative cover and **B.** Percentage survival (in relation to initial cover/count respectively) of Caged (1 mm mesh size cage) and Un-caged recruits transplanted onto two breakwaters at two Sandy Artificial sites *vs.* two Natural bedrock sites. Factors are: Treatment (Cages *vs.* Un-caged), Habitat (Artificial Sandy *vs.* Natural Bedrock), Site (nested in habitat: two breakwaters at Marotta and two areas in La Vela). N = 4 plates covered with *C. barbata* recruits per treatment and site within each Habitat. The tests were carried out 4 days following transplantation. We used the statistical package PERMANOVA to partition the variability and obtain F-statistics on a matrix of Euclidean distances from the original raw data, and calculated all P-values using 9999 random permutations of the appropriate exchangeable units (Anderson et al 2008). * P < 0.05

A. Source of variation	**Df**	**MS**	***F***
Caging	1	3327.5	5.8739 *
Habitat	1	3869.1	4.7762
Site (Habitat)	2	812.3	2.5831
Caging x Habitat	1	3327.5	5.8739 *
Caging x Site (Habitat)	2	567.62	1.805
Residual	18	314.46	
B. Source of variation	**Df**	**MS**	***F***
Caging	1	4494	24.604 *
Habitat	1	17626	17.181
Site (Habitat)	2	2057.4	2.6137
Caging x Habitat	1	8670.5	47.459 *
Caging x Site (Habitat)	2	363.51	0.4618
Residual	18	7084.3	

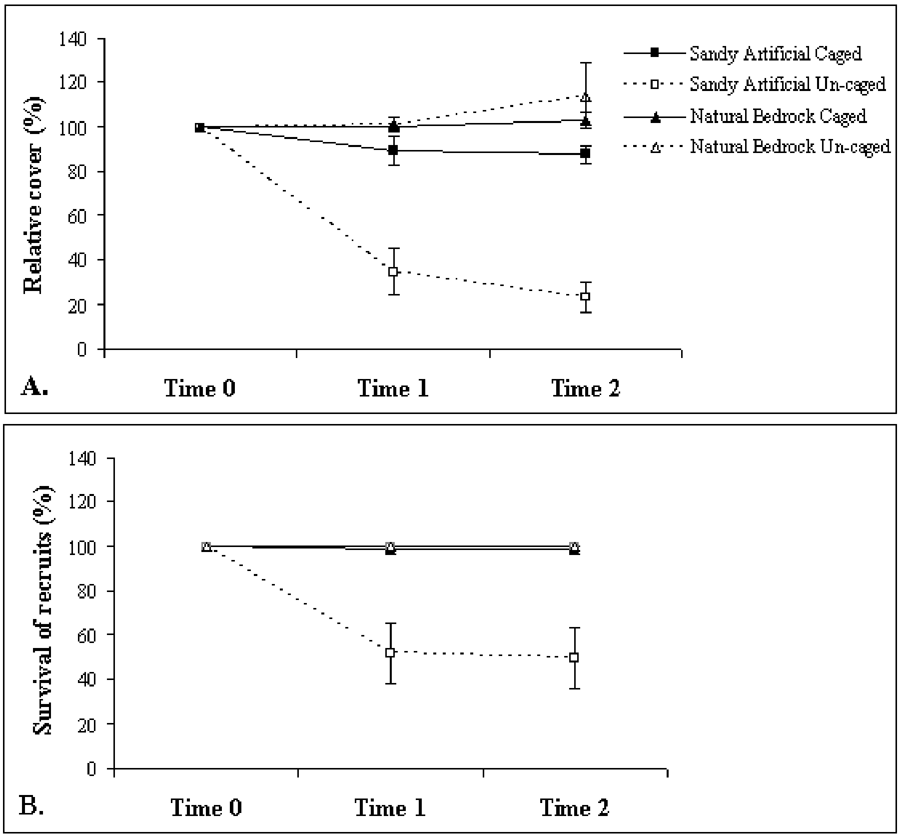

Figure 4: A. Relative cover and **B.** Percentage survival (in relation to initial cover/count respectively, Avg. ± 1SE) of Caged (1 mm mesh size cage, full symbols) and Un-caged (open symbols) recruits transplanted onto two breakwaters at Marotta (Sandy Artificial - black squares), *vs.* two natural bedrock areas in La Vela (Natural bedrock - black triangles). N = 4 plates covered with *C. barbata* recruits per treatment and site within each habitat. Values are presented as 100% when transplanted (Time 0) and then 4 and 8 days following transplantation (Time 1, Time 2 respectively).

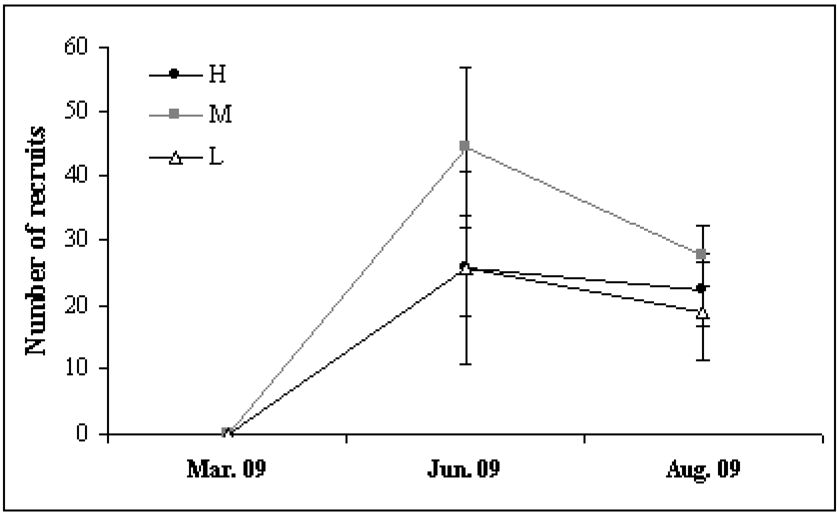

Figure 5: Number of *C. barbata* recruits (Avg. ± 1SE, n=6) on clay plates of different complexity levels: L – low, M – medium, H – high. Plates were set on March 2009 and counted in June and August 2009. Superimposed circles represent significant differences by SNK test (M > H = L, P < 0.05).

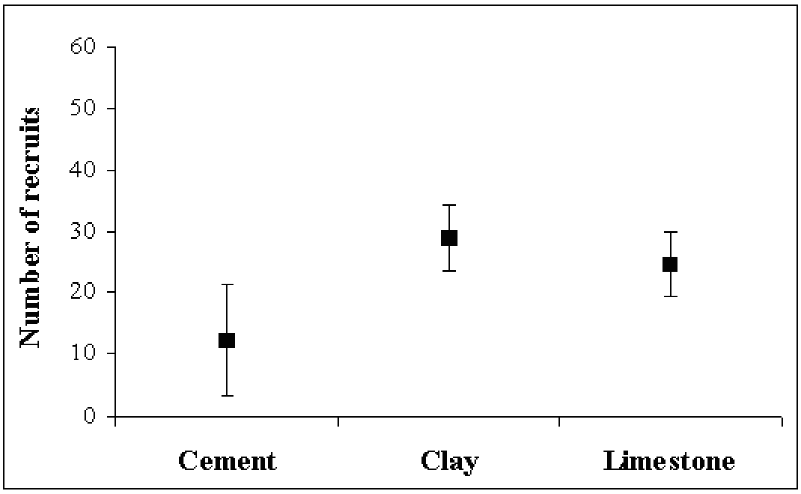

Figure 6: Number of *C. barbata* recruits (Avg. ± 1SE, n=6) on plates of different composition: cement, clay and limestone. Plates were set on March 2009 and counted in June 2009.

Discussion

Transplanting *C. barbata* juveniles proved technically feasible on both natural bedrocks and man-made habitats in the area of Monte Conero, indicating the potential of coastal infrastructures to provide a suitable habitat for the growth of this threatened species. Overall, landward, sheltered rocky artificial habitats seemed most successful, regardless the presence of surrounding adults. Furthermore, the chances for survival and growth of transplanted individuals in the study area were greater than those measured in the native habitats, where this species is threatened due to long-term recruitment failure related to increasing instability of the substrata (Perkol-Finkel and Airoldi, 2010). Assisted re-introduction or translocation can facilitate recovery of damaged populations (Lotze et al., 2011). Therefore, developing simple techniques to garden *C. barbata* on suitable habitats, either natural or artificial, could enhance the recovery potential of locally endangered populations of this species.

Transplanted juveniles showed no consistent survival patterns that relate to substratum orientation. This suggests that coastal infrastructures such as seawalls, breakwaters and pilings could provide potentially adequate habitats despite the greater proportion of inclined surfaces compared to natural habitats (Bulleri et al., 2005; Chapman and Blockley, 2009). Moreover, the survival of transplants was not impaired by lack of surrounding adults, suggesting that this would not be a limiting factor when managing assemblages on newly built man-made infrastructures that would obviously lack adult canopies.

Transplantation success was greater on landward, sheltered sides compared to exposed seaward sides of the breakwaters. This is in agreement with findings from Jonsson et al. (2006) who demonstrated that the higher flow speed on seaward compared to landward sides of breakwaters induced greater dislodgment of fucoid macroalgae. Indeed, the different sides of marine infrastructures provide distinct habitats to the growth of a variety of macroalgae and invertebrate species (e.g., Bacchiocchi and Airoldi, 2003; Bulleri and Airoldi, 2005; Burt et al., 2009). This ecological characteristic of many coastal infrastructures must be considered if we are to design and manage these structures for achieving desired secondary management goals and for enhancing their contribution to local biodiversity and ecosystem functions.

While several transplants survived and reproduced for over a year post-transplantation, we did not establish a substantial self sustaining population (which was beyond the scope of the current research). Nonetheless, as most of the receiving habitats had relatively high levels of survivals several months after deployment, much of the mortality can be attributed to rough sea conditions and not as an immediate reaction to the transplantation procedure. Moreover, out transplantation efforts were limited in scale and only small sized recruits were transplanted. Future work should explore whether a larger scale transplantation effort onto sheltered portions of coastal infrastructures would be self-sustaining, and whether using larger transplants would increase their survival and thus facilitate establishment of viable populations.

While transplantation of *C. barbata* proved successful onto coastal infrastructures along a rocky coastline, survival was not as promising when the structures were located along sedimentary coastlines, a typical setting of many coastal defense infrastructures (Airoldi et al., 2005b). The results of the caging experiment suggested that lack of survival of *C. barbata* transplants along sedimentary coastlines was not related to environmental factors (e.g., reduced water quality or excess sedimentation). Instead biotic disturbance was a determinant factor limiting the survival of *C. barbata* in these habitats. Our tests with cages of different mesh sizes initially suggested that such biotic disturbance could be related mainly to the activity of small sized organisms (0.1 - 1 cm). However, preliminary results of ongoing experimental work by our group (aiming at clarifying the nature, distribution and generality of such biotic disturbance with the aid of UW video cameras) suggest that loss of *Cystoseira* at some structures is related to a complex of both consumptive and non-consumptive disturbance by a variety of organisms of different sizes, ranging from small crabs to mullets (Ferrario et al., unpublished data). Some of these organisms are also present at natural rocky sites, but at lower densities and they do not show the same degree of interaction with the *Cystoseira*. Coastal infrastructures set on sedimentary shorelines represent "oasis" of hard bottoms in a soft bottom environment (Airoldi et al., 2005a). As such, they might attract a greater abundance of predators compared to nearby natural habitats, similarly to what is thought to occur in other oasis systems such as seamounts (Rowden et al., 2010a; Rowden et al., 2010b). This unexplored aspect of the ecology of marine infrastructures deserves further attention.

Substratum composition and complexity have a strong influence on settlement, recruitment, and survival of benthic fauna and flora in both natural (Harlin and Lindbergh, 1977; Wells et al., 1989; Johnson and Brawley, 1998; Guarnieri et al., 2009) and artificial substrata (Spieler et al., 2001; Chapman, 2003; Burt et al., 2009). Coastal infrastructures, such as seawalls, breakwaters, and jetties may be constructed of stone, concrete, wood, steel or geotextiles (Dugan et al., 2011), and may be designed to incorporate greater habitat complexity (Moreira et al., 2007; Chapman and Blockley, 2009). For example, subtle change in infrastructure complexity, at small scale (e.g., addition of pits to a seawall as in Martins et al. (2010) or at medium scale (e.g., addition of holes to concrete wave energy foundations as in Langhamer and Wilhelmsson (2009) can significantly increase the ability of the infrastructure to sustain greater abundance of organisms. Our tests with concrete and limestone (the most common materials in our study region) and clay (a potentially practical substratum for transplantation) showed similarly high levels of recruitment. Settlement was initially double on surfaces with medium complexity in comparison to simple or highly complex ones, yet this facilitation was apparently transient, probably due to post-settlement processes related to natural self thinning (Reed, 1990; Kendrick and Walker, 1995; Johnson and Brawley, 1998). Moreover, it is possible that engineering species like *Cystoseira* (Sales, In Press), modify their immediate environment once established in terms of e.g. hydrodynamic/sedimentation patters, thus masking further effect of complexity. This suggests that the artificial substrata in the study area provide potentially suitable substrata for this canopy forming alga, and that other biological or ecological factors (such as those suggested by the caging experiment) limit its natural recruitment on the infrastructures.

Understanding how man-made habitats function in urbanized seascapes is fundamental if we are to design and manage these habitats in a way that enhances their contribution to marine biodiversity and flow of ecosystem services (Airoldi et al., 2005a; Chapman and Blockley, 2009; Bulleri and Chapman, 2010). We demonstrate that managing assemblages on marine infrastructures for desirable secondary management goals can be feasible, but requires a good understanding of the different ecology of these artificial systems. This is in agreement with Moschella et al. (2005) concluding that infrastructures can be modified to influence the abundance and species composition of epibiota to achieve desired management goals such as controlling growth of nuisance algae or promoting diversity of habitats and species for recreational activities. This emerging approach complements the evolving paradigm of ecological engineering (Mitsch, 1996), aimed at integrating ecological, economic and social needs into the design of man-made ecosystems.

In conclusion, the current study contributes to bridging the gap between growing societal needs of coastal development and the need for conserving the marine environment (Mitsch, 1996; Chapman and Blockley, 2009; Inger et al., 2009; Bulleri and Chapman, 2010). The ability to utilize coastal infrastructures as scaffolds for recovery of threatened species or for enhancement of desirable species has concrete applications for the conservation of biodiversity in globally expanding coastal urban environments. For example, current restoration or enhancement efforts based on the construction of artificial reefs (Reed et al., 2006; Schmidt et al., 2007; Dupont, 2008) could be best replaced by utilizing existing infrastructures. This approach could be more sustainable in the long term, and be efficiently incorporated into marine spatial planning.

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Chapter 4: Unequal ecological performance of artificial vs natural rocky habitats and underlying ecological processes.

Abstract

Constructed artificial structures represent the only habitat that is rapidly and globally expanding in marine seascapes as a result of the burgeoning coastal populations, pressing development and greater risk of coastal hazards from climate change, storm surges and sea level rise. Although numerous studies suggest that created artificial habitats can be very poor compared to natural habitats (e.g. low species and genetic diversity, dominance by invasive and opportunistic species) the ecological processes underlying the different performance of artificial habitats compared to natural reefs are still not fully understood. Here we documented the suitability of artificial structures compared to natural rocky reefs to support native canopy forming algae of the genus *Cystoseira* and clarified the potential underlying drivers by either experimentally manipulating and filming the interactions between macroalgae and faunal assemblages. Canopy forming algae thrived on natural rocky reef but their survival was impaired on man-made structures where both fishes and crabs were involved in either consumptive and non-consumptive interactions with algal thalli. We demonstrated a consistent role of the biotic disturbance (mainly grazing) in determining the different ecological performance of artificial and natural habitats. Unraveling of the functioning of systems associated with artificial habitats is the key to allow environmental managers to identify proper mitigation options and to forecast the impact coastal development plans at a seascape scale.

Keywords: canopy-forming algae, biotic disturbance, grazing, artificial habitats, natural habitats, *Cystoseira*, ecological processes.

Introduction

Constructed artificial structures represent the only habitat that is rapidly and globally expanding in marine seascapes. Seawalls, breakwaters, dykes, groynes jetties, pilings, bridges, artificial reefs, offshore platforms, and marine energy installations, are increasingly built to protect coastal population and assets, exploit marine resources and provide alternative energy sources. It is expected that armoring will further increase as a result of burgeoning coastal populations, greater threats from climate change, storm surges and sea level rise, and pressing demand for renewable marine energy installations (Inger et al. 2009, Dugan et al. 2011). Although significant fisheries and local economic benefits related to recreational fishing and diving are attributed to the construction of these artificial habitats, there are open questions about the ecological performance and value of marine infrastructures as habitat for marine fauna and flora. Indeed numerous studies suggest that created artificial habitats can be very poor compared to natural habitats (e.g. Perkol-Finkel et al. 2006, Burt et al. 2009, Miller et al. 2009), supporting structurally different assemblages with low species and genetic diversity (Johannesson and Warmoes 1990, Chapman 2003, Fauvelot et al. 2009) and dominance by opportunistic and invasive species (Bacchiocchi and Airoldi 2003, Bulleri and Airoldi 2005, Glasby et al. 2007). Even in the comparatively rare situations when artificial structures have been purpose designed to mimic natural habitats and enhance species of recreational, commercial or naturalistic value (e.g. artificial reefs), there has been no consistent evidence that these aims have been achieved (Svane and Petersen 2001, Perkol-Finkel et al. 2006, Burt et al. 2009, Miller et al. 2009).

The ecological processes underlying the different performance of artificial habitats compared to natural reefs are still not fully understood. Current knowledge suggests that divergence of benthic assemblages is not simply attributable to incomplete succession, but appears to be a persistent, possibly stable state (Perkol-Finkel et al. 2006, Miller et al. 2009). Several co-occurring factors could contribute to maintain these differences, including the effects of construction materials (Burt et al. 2009, Espinosa et al. 2011, Feary et al. 2011, Green et al. 2012), the unique habitat characteristics (Bacchiocchi and Airoldi 2003, Perkol-Finkel and Benayahu 2007, Vaselli et al. 2008, Irving et al. 2009, Perkol-Finkel and Benayahu 2009), the unnaturally high disturbances (Benedetti-Cecchi et al. 2001, Bulleri and Airoldi 2005, Moschella et al. 2005, Mangialajo et al. 2008, Airoldi and Bulleri 2011), the fragmented nature and isolated location and the complex interactions of these factors with the native physical and biotic environments. For example, differences in building material seemed to affect limpet species on seawalls in Sydney harbor through both direct effects on recruitment and indirect effects on competitive outcomes (Ivesa et al. 2010). The greater cover of bryozoans on kelps growing on pier-pilings than in surrounding natural reefs was explained by the combined effects of unnatural levels of shade and lower grazing pressure by sea urchins (Marzinelli et al. 2009, Marzinelli et al. 2011). The greater cover of non-indigenous species observed at numerous artificial structures has been attributed to the combined effects of unnaturally high levels of disturbance and interactions (positive and/or negative) with the native assemblages (Dafforn et al. 2012). It has also been demonstrated that, whether or not specifically planned for the scope, artificial structures affect the distribution of fish assemblages by providing enhanced nursery grounds, refugia (depending on 3dimensional features) and feeding areas (Brickhill et al. 2005, Thanner et al. 2006, Clynick et al. 2007, Leitão et al. 2007, Leitao et al. 2008, Pizzolon et al. 2008, Edelist and Spanier 2009, Hackradt et al. 2011, Simon et al. 2011) therefore potentially altering grazing pressure on native assemblages. Whilst some information exists, our ability to make generalizations is restricted, as most work in these habitats is still conducted at limited spatial scales and with little consideration to ecological interactions (but see Moschella et al. 2005).

Canopy-forming macroalgae of the genus *Cystoseira* (Fucales) are a “foundation” component (sensu Dayton 1972) on rocky reefs in the Mediterranean Sea (Giaccone 1973, Ballesteros 1992). They are functionally analogous to kelps, forming dense forests that play a key role in primary production and nutrient cycling, modify both physical and biological factors, sustain a variety of epiphytic assemblages and offer shelter and habitat to a great variety of species (Bulleri et al. 2002, Steneck et al. 2002, Maggi et al. 2009, Sales and Ballesteros 2012). Canopies of *Cystoseira* are sensitive to a variety of natural and anthropogenic stressors (Benedetti-Cecchi et al. 2001, Devescovi and Ivesa 2007, Sales and Ballesteros 2009, Falace et al. 2010, Perkol-Finkel and Airoldi 2010) and have suffered widespread regressions (Thibaut et al. 2005, Mangialajo et al. 2008, Fraschetti et al. 2011, Sales et al. 2011). Indeed the Mediterranean Action Plan, adopted within the framework of the Barcelona Convention, identifies the conservation of *Cystoseira* belts as a priority (UNEP/MAP 2005 and following amendments). Artificial structures could potentially offer favorable hard substrata for the establishment of these species and provide a scaffold for their conservation in face of increasing loss of natural habitats (chapter 3, hereafter 'Perkol-Finkel et al. 2012'). However, most often this is not the case, and occurrence of species of *Cystoseira* on artificial substrata is scattered (Falace et al. 2010, Perkol-Finkel et al. 2012). The ecological factors behind the unequal success of canopy-forming algae on artificial structures vs natural reefs are at present unknown. Experimental work done on coastal defense structures in the North Adriatic sea has shown that the growth of *Cystoseira* in these habitats is not limited by the characteristics of the substrata: these species have the potential to grow on substrata of different materials, substratum complexities and orientations, and successful transplantations can be obtained even in the absence of surrounding adult canopies (Perkol-Finkel et al. 2012). The different success of native canopy-forming algae on artificial structures compared to natural reefs might therefore depend on a more complex interaction of biotic and/or abiotic factors.

In a time of urbanization unprecedented in rate of growth and geographic scope, understanding factors potentially enhancing the ecological performance of urban structures is a pressing challenge to preserve native coastal biodiversity and fundamental ecological processes. Here we document the suitability of coastal artificial structures compared to natural rocky reefs to support native, ecologically relevant, habitat-forming canopy algae, and through experiments clarify the potential underlying drivers. Specifically we determined: 1) the differential distribution of canopy-forming algae between artificial and natural habitats along about 500 km of coasts of the North Adriatic sea, 2) whether any difference in the survival of canopy forming algae in the two habitats was primarily related to local environmental conditions (e.g., lower water quality or excess sedimentation along a sedimentary shoreline) or biotic factors (i.e., pressure from grazers or other sources of biological disturbance) or an interaction of both, and 3) whether any different response observed was consistent between different canopy-forming species and locations. We also 4) carried out extensive field work to identify and document the variety of biotic interactions acting on canopy forming algae in artificial habitats compared to natural reefs. The results of this latter work will be presented in extended in a subsequent paper (chapter 5), and the main findings will be only summarized here.

Method

Study area

The research was carried out at several locations along the two sides of the north Adriatic Sea (Fig. 1). The Italian side comprises a prevailingly sedimentary coastal system and is severely urbanized (Cencini 1998). The source natural study site was located on the Monte Conero promontory (43° 33′ N, 13° 37′ E). This area is predominantly composed of marls and limestone rocks extending to a depth of ca. 8m. The rocky promontory hosts some of the few scattered populations of the threatened genus *Cystoseira* along the central - northern Italian Adriatic coast (Perkol-Finkel and Airoldi 2010), with only two species remaining (*C. barbata* and *C. compressa*) out of 7 described in the 1960ies. The current fragmented state of these populations has likely resulted from a synergistic effect of increasing loss of suitable stable substrata and competition with opportunistic species of lower structural complexity such as turf algae and mussel beds (Perkol-Finkel and Airoldi 2010). The natural site “La Vela” was used as the source of *Cystoseira* juveniles used in all the experiments along the Italian coast, being the only site remaining with sufficient natural recruitment of *Cystoseira* at the time of the present research. The artificial sites were located along about 200 km of coast extending to north of Monte Conero, namely three locations at Marotta, Cesenatico and Punta Marina. The sites were characterized by the presence of breakwaters built with large blocks of quarried rock (1 - 3 m across), deployed at ~ 200 - 300 m from the shore, with an average length of 100 -150 m, and extending to ~ 2 - 3 m in depth. No *Cystoseira* occurred naturally at any of these sites. A detailed description of both artificial and natural habitats in this region can be found in (Bacchiocchi and Airoldi 2003, Perkol-Finkel and Airoldi 2010, Perkol-Finkel et al. 2012).

The Croatian side comprises a prevailingly rocky coast, and compared to the Italian side is far less urbanized, with large natural areas still devoid of marine infrastructures. In this region 7 species of *Cystoseira* are still naturally present. For our work we selected 3 natural rocky sites: Faborso (45° 7' 8.46''N, 13° 36' 53.58''E) is a natural bay embedded in the natural area of “rt Kritz”, Kuvi (45° 3' 47.32''N, 13° 37' 59.12''E) located in the “rt Zlatni” national park and Stari Grad (45° 5' 2.69''N, 13° 37' 43.78''E). The first two are located north and south of Rovinj, respectively, whereas Stari Grad is a natural rocky site close to the old city of Rovinj. These sites are characterized by a gently sloping rocky bottoms densely forested and variously covered by coarse sand and granular gravel. In Faborso *Cystoseira barbata* is the most abundant species, while *Cystoseira crinita and C. compressa* are dominant respectively in Kuvi and Stari Grad (Iveša et al. 2009). The artificial sites were interspersed with the natural sites. Valalta (45° 7' 29.76''N, 13° 37' 14.40''E) was characterized by breakwaters delimiting the landing place of a resort village, Bolnica (45° 5' 36.24''N, 13° 38' 28.62''E) presented an artificial structure attached to the shore protecting a coastal street while in Marina (45° 4' 29.94''N, 13° 37' 59.16''E) breakwaters defend the touristic port of Rovinj. All artificial structures at these sites were built with boulders of quarried rock. Whilst only *Cystoseira compressa* has been reported to be present at these sites in spring and summer its presence remain uncertain during fall and winter, the thalli being absent or undetectable.

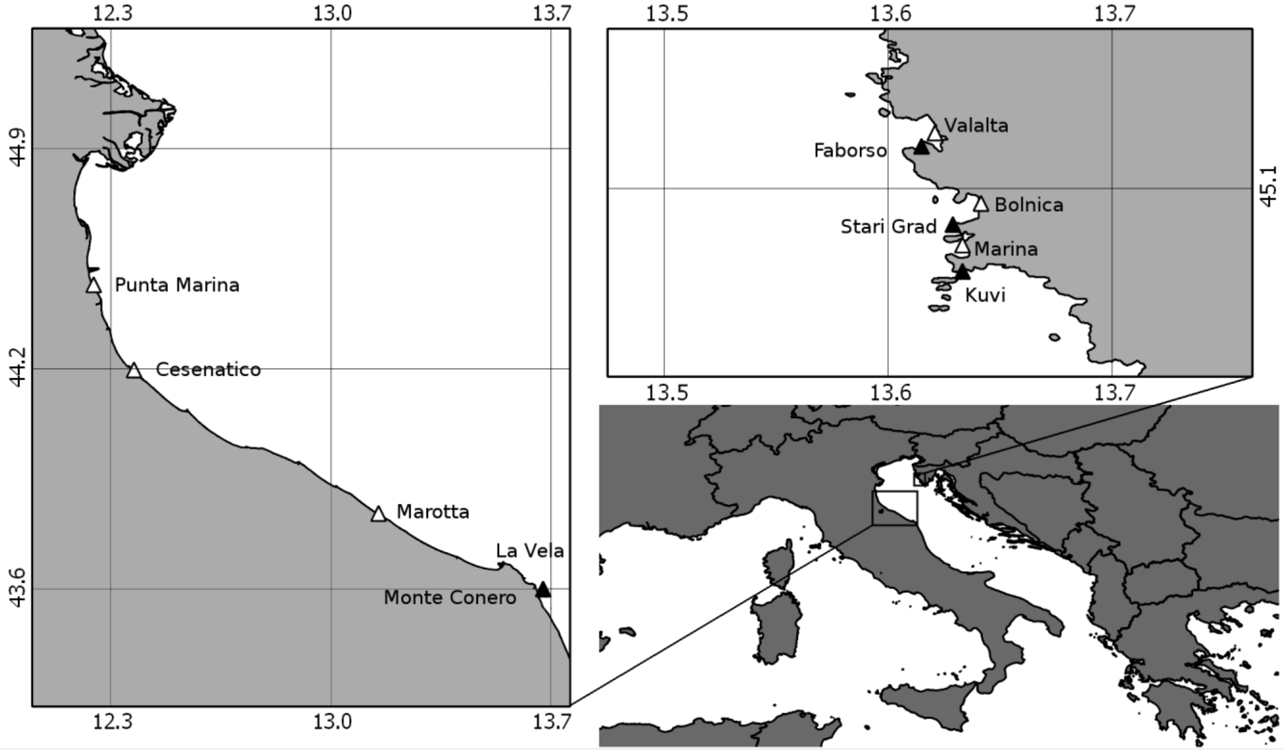

Figure 1 Map of the study region in the Adriatic Sea. Insert maps of the study sites along the Italian coast (on the left) and along the Croatian coast (on the right). Site at natural (black) and artificial habitats (white) are represented.

Distribution of canopy forming algae at artificial and natural sites

The distribution of canopy forming algae at artificial and natural sites along the Italian coast had already been characterized previously(Perkol-Finkel and Airoldi 2010, Perkol-Finkel et al. 2012). Two species of *Cystoseira, C. barbata* and *C. compressa,* are present on natural rocky reefs in Monte Conero (Perkol-Finkel and Airoldi 2010), covering < 15% of the bedrocks between 2 and 4 m. No *Cystoseira* has even been observed on any artificial structure in the region, except for some sparse specimens occurring on some artificial structures built on rocky bottoms along the Monte Conero promontory.

In October 2010 we quantified the distribution of *Cystoseira* sp. at both natural and artificial sites along the coast of Croatia. At each site we estimated the total percentage cover of dominant *Cystoseira* species in 5 replicated quadrats (25 x 25 cm), by using the visual method (Benedetti-

Cecchi et al. 1996). A frame divided into a grid of 25 small squares was used, and a score from 0 to 4 % was given to the coverage of *Cystoseira* in each square.

Pilot caging experiments

To explore whether the consistently sparse to nil presence of canopies of *Cystoseira* observed at the artificial sites is dictated by local environmental conditions (e.g., low water quality or excess sedimentation) or is mediated by different biotic pressure in these habitats (from e.g. grazers or other non-consumptive disturbance), we conducted a first pilot caging experiments at Marotta in July 2010. Due to the lack of *Cystoseira* at these coastal defence structures, the juveniles (about 2-3 months old, 5 cm high) of *Cystoseira barbata* used in the experiment were collected from loose boulders at La Vela. Recruits in these loose habitats have naturally low survival probability due to severe substratum instability (Perkol-Finkel and Airoldi 2010), therefore their use for our experiments did not damage the source population. The boulders were broken into small fragments holding 1-3 individuals that were glued on to marble tiles (10x10x2 cm) by using epoxy putty (Subcoat S Veneziani) to form experimental plots comprising 5-6 juveniles. The tiles with the juveniles were transported by car to the experimental site in Marotta as quickly as possible in 100 liter tanks.

We hypothesized that if growth of *Cysoseira* at the artificial habitats was mainly limited by local environmental conditions, no difference would occur in the survival of juveniles between caged and uncaged treatments, while the opposite would occur if the main limiting factor was related to biotic disturbance. As we had no hypotheses about the potential sources of biotic disturbance at the artificial structures, we used cages of different mesh sizes to explore different possibilities: 10mm mesh (hereafter MA) to exclude potential macrograzers and 1mm mesh (hereafter ME) to also exclude potential mesograzers. Cages (12x12x25 cm) were built using a plastic-coated iron wire mesh with a 10mm squared grid. The more selective cages were obtained by wrapping the MA cage with a mosquito net. We used epoxy putty (Subcoat Veneziani) to attach them to the rock.

We attached 15 experimental tiles at the breakwater by using epoxy putty and we randomly assigned five replicate tiles to each of three levels of the factor Exclusion: ME, MA and uncaged. We did not include a partial cage as control for artifacts because at this stage we had no clues about the potential sources of biotic disturbance, which could drive our design of such a partial control. However, the experiment was run during two weeks of very calm sea conditions, and was set up at the sheltered, landward side of one breakwater. Previous work has shown that *Cystoseira barbata* grows potentially well under sheltered conditions, and the combination of shelter and sea calm conditions would have reduced the risks of artifacts potentially related to modifications of hydrodynamics by the cages. The height of each juvenile was measured at the beginning and at the end of the experiment by using a ruler. The experiment was run for 13 days, as responses to treatments were very rapid. After checking for the absence of any evident pattern in initial conditions, we used the final juveniles height as the response variable. Data were analyzed by permutational one-way ANOVA with 9999 permutations performed on the between replicate Euclidean distance matrix using PERMANOVA+ for PRIMER 6.0 software. The model included the factor Exclusion (three levels: MA, ME, uncaged).

As the previous experiment had excluded a role of mesograzers, in August 2010, we ran a second caging experiment by using two different mesh sizes to discriminate between small and large macrograzers and at the same time test for generality of results at replicated sites. We built cages using the same 10 mm mesh as before, but in one of the treatments we cut openings (6x7cm) on each side and on the top of the cage allowing for access to small macrograzers (LMA treatment).

At each of three replicated sites (Marotta, Cesenatico and Punta Marina), we attached 15 experimental tiles on the landward side of one breakwater following the same procedure described previously. After 15 days we assessed the status of juveniles. Because this time the losses in uncaged treatments were even more severe than in the previous experiment, we measured responses as percentage survival rather than length of juveniles. Data were analyzed by permutational two-way ANOVA with 9999 permutations performed on the between replicate Euclidean distance matrix. The model included factors Exclusion (3 levels: ME, LMA and uncaged) and Site (3 levels: Marotta, Cesenatico, Punta Marina).

Variable effects of biotic disturbance on different canopy algae in artificial vs natural habitats

In October 2010 we started a larger caging experiment to clarify the relative importance of biotic pressure in controlling the different distribution of canopy-forming algae in artificial vs natural habitats. We hypothesized that the different distribution of canopies of *Cystoseira* sp. in the two habitats was related to a greater biotic control on artificial structures compared to natural reefs.

The experiment was set up along the coasts of Croatia, where, unlike along the Italian coastline, it is possible to correctly intersperse replicated artificial and natural sites and therefore test for generality of responses. Because only *C. compressa* is known to possibly occur on the artificial structures, while several species of *Cystoseira* were found in the natural reefs, we also hypothesized that the responses would differ between species of *Cystoseira*, with *C. compressa* showing a greater tolerance to biotic disturbance in artificial habitats.

For this experiment we used marble tiles (10x10x2 cm) densely covered with juveniles of either *C. barbata* or *C compressa* (we initially attempted to create also tiles with *C. crinita* but they have been lost or irremediable damaged while in the field during the recruitment season). The tiles had been placed at a depth of 3 – 4 meters in Faborso and Bonica, at the start of the reproductive season, to intercept natural recruitment and had not been manipulated in any way before this experiment. In October 2010, eight tiles for each of *C. barbata* and *C. compressa* were fixed at each of three replicated natural rocky sites (NAT: Faborso, Starigrad, Kuvi) and three artificial sites (ARS: Valalta, Bolnica, Marina) interspersed along 7 km of coast, for a total of 96 tiles Four tiles for each species were caged using the same 10mm mesh size cage described previously (MA) while the remaining 4 were left uncaged. Although this experiment was set at less sheltered sites than those used in the pilot experiments, and although the experiment lasted longer (therefore experimenting the occurrence of more hydrodynamic conditions) we did not use partial controls for potential caging artifacts (on hydrodynamics or light) as by the start of this experiment our observations had clearly indicated that biotic pressure on *Cystoseira* was exerted by a wide range of species of different sizes. A control for artifacts should therefore have included large openings on both the sides and the top of the cage, which basically prevented the possibility to build a proper partial control. However, we directly measured biotic pressure on *Cystoseira* at both artificial and natural sites (see next paragraph), to see whether it supported the results of this and the previous experiments. We also regularly cleaned the cages from fouling to prevent alteration of lightening conditions and water movement.

The experiment was sampled at the start in October 2010 (Time 0), and subsequently in December 2010 (Time 1), April 2011 (Time 2) and October 2011 (Time 3). At each sampling time we took digital pictures of the tiles. The pictures were analyzed in the laboratory by superimposing a digital grid (10x10 squares) and by counting the number of quadrats occupied by each species of *Cystoseira*. The response variable was expressed as the total percentage cover of each species of *Cystoseira* on each tile. Due to significant differences in the initial cover obtained on tiles for *C, barbata* and *C. compressa*, we decided to analyze the two species separately. We also decided to analyze the different times separately from one another. Data were analyzed by means of permutational ANOVA with 9999 permutation performed on the between replicate Euclidean distance matrix. The model included factor Substratum (fixed; 2 levels: Artificial vs Natural), Site (random and nested in Substratum) and Exclusion (fixed; 2 levels: MA vs uncaged).

Biotic pressure on canopy forming algae in artificial vs natural habitats

In summer 2011 we used remote underwater video cameras (RUVs) to identify the variety of biotic interactions acting on canopy forming algae in artificial habitats compared to natural reefs and quantify their relevance in both natural and artificial habitats. Two plots of three experimental tiles with 4-5 *Cystoseira* juveniles each (prepared as described in the pilot experiments, see paragraph *Pilot caging experiments*) were fixed at La Vela and on one breakwater in Marotta at a depth of 1.5-2.0 meters. The plots were located several meters apart, and a RUV was positioned at a distance of about 40-50 cm in front of each plot. The RUV consisted in a GoPro® HD Hero, equipped with a flat lens and an additional battery pack, mounted on a weighted square base (10x10x2 cm; 1 kg). The RUVs were deployed at the same time at the two sites and filmed contemporaneously for 3-4 hours during daylight (late morning - early afternoon). The whole procedure was replicated on two different days. The videos were analyzed to identify all possible species directly interacting with *Cystoseira* and quantify the number and duration of interactions in the two habitats, natural and artificial. We defined interaction the contact or a continuous series of contacts between a single organism and the algae. We quantified the duration of each interaction as the time occurring between the first and the last contact of the series. To prevent possible bias due to the presence of the diver we started analyzing the videos five minute after the diver exit from the shot. Organisms were identified from the video to the lower possible taxonomical level and their size estimated using the tile as a reference. The response variable was expressed as the number of interactions per taxon in each video.

To examine the generality of our findings, in summer 2012 we repeated the study, and replicated it at a variety of natural and artificial sites and during several days. The results from this work (about 146 hours of filming) were qualitatively similar to our pilot observations and will be reported in a subsequent paper.

Results

Distribution of canopy forming algae at artificial and natural sites

Similarly to what previously observed along the Italian coast of the North Adriatic sea (Perkol-Finkel et al 2012), *Cystoseira* species were absent on coastal structures located along the coastline of Croatia. Conversely, dense stands of *Cystoseira* were supported at all natural reefs at Faborso, Stari Grad and Kuvi . *C. barbata*, *C. compressa* and *C. crinita* were present in Faborso (cover = 24 ± 2.1 %, mean ± SE), Stari Grad (73 ± 4.,6 %) and Kuvi (27.4 ± 5.1%) respectively. It must be considered that at this time of the year only the thalli were visible as the fronds are lost at the end of the summer. Thus the cover will further increase during the growing season when new fronds will develop.

Pilot caging experiments

Caging significantly influenced the survival and growth of juveniles of *Cystoseira barbata* at the artificial sites, where uncaged juveniles showed severe declines compared to caged juveniles. In the first pilot experiment in Marotta, the length of thalli of uncaged *C. barbata* juveniles declined by 77% of the original length (which was on average 3.45 ± 0.21 cm, mean ± SE) within two weeks, while length did not change or slightly increased in the two exclusion treatments. At the end of the experiment the length of *C. barbata* juveniles was significantly lower in the uncaged plots compared to the two caged treatments, while there were no differences between MA and ME plots with different cage sizes (Fig. 2, Table 1), indicating that the decline of *Cystoseira* could not be related to effects from mesograzers.

The trend observed in Marotta was substantially confirmed in the second pilot experiment, where survival of juveniles was significantly enhanced in caged plots compared to uncaged ones (Fig. 3 and Table 2). This trend was rather consistent among artificial structures independently of their location. On average, two weeks, after the start of the experiment, 89 % of caged juveniles survived in ME plots compared to only 55 % in uncaged plots (Fig. 3). Survival of juveniles in LMA plots, where openings were present, was statistically similar to that measured in uncaged plots (Fig. 3, Table 2), suggesting an important biotic pressure from organisms of intermediate size. Indeed during the sampling we observed the presence of several crabs in LMA treatments, in particular at Punta Marina where we recorded the lowest survival of juveniles in this treatment.

Table 1 Effect of biotic pressure vs environmental factors on the performance of *Cystoseira barbata* juvenile thalli on a breakwater in Marotta. Response variable: height of juveniles at the end of the experiment (13 days). Factor Exclusion has three levels: Mesograzers exclusion (ME), Macrograzers exclusion (MA), no exclusion (Uncaged). Data were analyzed by permutational one-way ANOVA with 9999 permutations on the Euclidean distance matrix. We used the statistical package PERMANOVA+ for PRIMER 6.0 software. Responses judged as significant are in bold.

Source	df	MS	Pseudo-F	P
Exclusion	2	18.0	61.46	**0.00**
Res	9	0.3		
Pair wise within Exclusion		t	P(perm)	
MA vs. ME		1.42	0.09	
Uncaged vs. MA		11.77	**0.01**	
Uncaged vs. ME		8.93	**0.02**	

Table 2 Relevance of grazers of different size on the performance of *Cystoseira barbata* juvenile thalli. Response variable: survival of juveniles at the end of the experiment (15 days). Factor are as follow: Exclusion [Mesograzers exclusion (ME), Large Macrograzers exclusion (LMA), no exclusion (Uncaged)] and Site (Marotta, Cesenatico, Punta Marina). Data were analyzed by permutational ANOVA with 9999 permutations on the Euclidean distance matrix. We used the statistical package PERMANOVA+ for PRIMER 6.0 software. Responses judged as significant are in bold.

Source	df	MS	Pseudo-F	P
Exclusion	2	4504	4.23	**0.02**
Site	2	168	0.16	0.86
Exclusion x Site	4	1896	1.78	0.17
Res	32	1065		
Pair wise within Exclusion		t	P	
LMA vs. ME		2.35	**0.03**	
Uncaged vs. LMA		0.36	0.72	
Uncaged vs. ME		3.13	**0.00**	

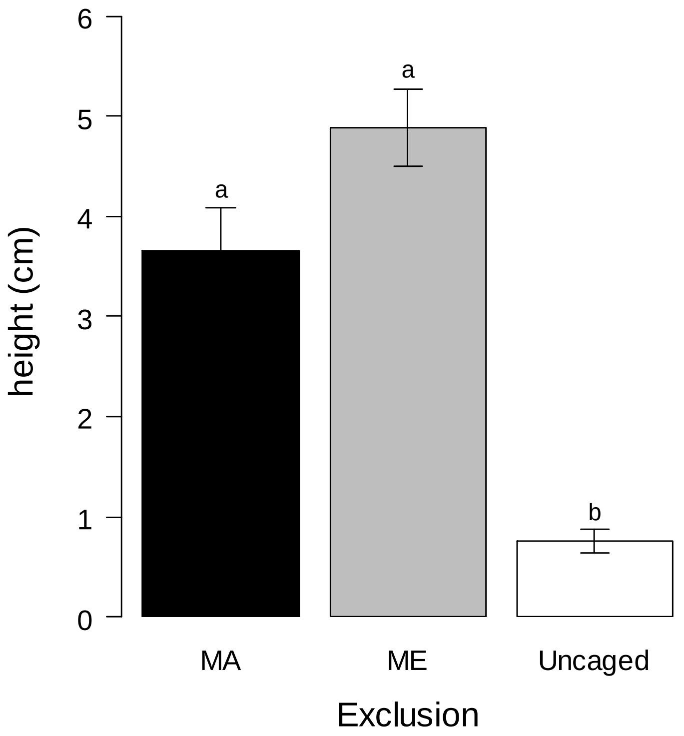

Figure 2. Average height (± SE) in cm of thalli of *Cystoseira barbata* juveniles in treatments macrocgrazers exclusion (MA, black; N=20), mesograzers exclusion (ME, grey; N=16) and uncaged (white; N=21) two weeks after the start of the experiment in Marotta (July 2010). Different letters indicate statistical significance.

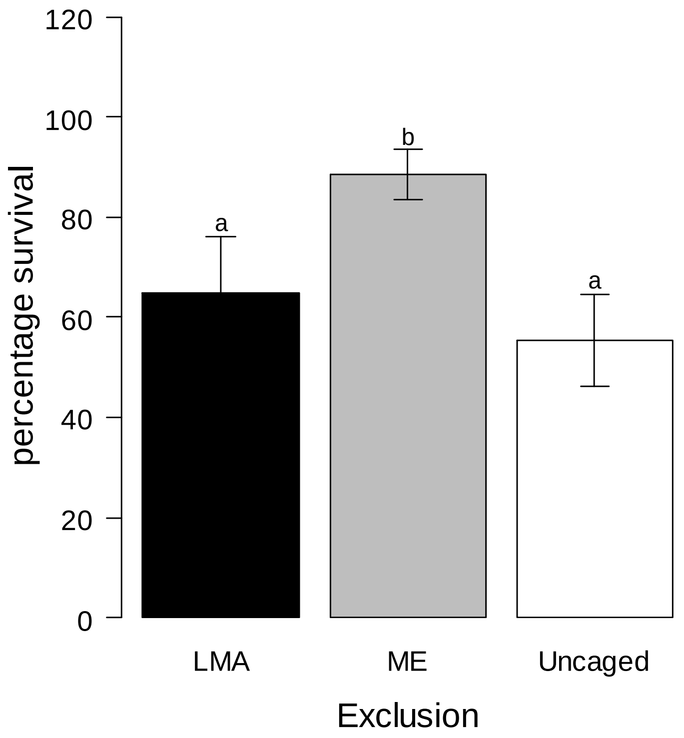

Figure 3. Average percentage survival (± SE) of *Cystoseira barbata* juveniles at the end of the experiment for the treatments LMA (Large macrograzers exclusion), ME (Mesograzers exclusion) and Control (No exclusion).

Variable effects of biotic disturbance on different canopy algae in artificial vs natural habitats

Caging had profoundly different effects on the coverage of *Cystoseira* between artificial and natural habitats (Table 3,4). At the natural rocky sites limited to no differences were observed between caged and uncaged treatments during the first 6 months of the experiment (Fig. 4), suggesting that cages did not introduce particularly relevant artifacts on e.g. light or hydrodinamics. This was particularly true for *C. barbata*, which grew undisturbed in both caged and uncaged treatments on rocky reefs until April 2011 (Fig. 4a), while cover of *C. compressa* was generally slightly lower in uncaged plots compared to caged ones (Fig. 4b). At the last sampling time, in October 2011 a slight decline of both species of *Cystoseira* was observed at uncaged plots at the natural sites.

On the artificial structures caged plots showed similar growth patterns to those measured in both caged and uncaged plots on natural rocky reefs during the first 6 months of experiment, reaching covers greater than 70% for both species of *Cystoseira*. Even in October 2011 when cover of both species of *Cystoseira* decreased in uncaged treatments on rocky shores, cover in caged plots remained equally high in both habitats. Conversely, cover of *Cystoseira* notably deteriorated in uncaged plots (Fig. 4; Table 3,4), where *Cystoseira* decreased to covers below 10%. This trend of loss was substantially consistent between the two species considered (*C. barbata* and *C. compressa*) and among locations. Similarly to what observed in previous pilot experiments run along the Italian coastline, the loss of uncaged canopies of *Cystoseira* on the artificial structures was rather rapid, being clearly detectable at the first sampling time two months after the start of the experiment. Since that time, differences between caged and uncaged plots on artificial structures maintained consistent.

Table 3 *Cystoseira barbata.* Relative importance of biotic pressure in controlling the different distribution in artificial vs natural habitats. Response variable: total percentage cover of juveniles on marble tiles. Factor are as follow: Habitat (Hab, Artificial sv natural), Site (nested in Hab: natural rocky reefs at Faborso, Stari Grad, Kuvi and breakwaters at Valalta, Bolnica and Marina), Exclusion [Macrograzers exclusion (MA) vs no exclusion (Uncaged)]. The experiment started October 2010 and sampled in a) December 2010, b) April 2011 and c) October 2011. Separate analysis were performed for each sampling time. Data were analyzed by permutational ANOVA with 9999 permutations on a Euclidean distance matrix. We used the statistical package PERMANOVA+ for PRIMER 6.0 software. Responses judged as significant are in bold.

Source	(a) December 2010				(b) April 2011				(c) October 2011			
	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
Habitat	1	5347	5.43	0.17	1	8074	16.93	0.09	1	2256	4.92	0.10
Exclusion	1	11559	33.34	**0.00**	1	19849	95.54	**0.00**	1	26693	26.88	**0.01**
Site (Hab)	4	998	7.96	**0.00**	4	480	1.59	0.20	4	461	1.51	0.23
Hab × Excl	1	4297	12.39	**0.03**	1	15440	74.32	**0.00**	1	2757.8	2.78	0.18
Site (Hab) × Excl	4	350	2.79	**0.04**	4	206	0.68	0.60	4	1007	3.28	**0.02**
Res	34	125			34	301			33	306		
Pair wise MA vs Uncaged within			t	P			t	P				
Artificial habitat			6.21	**0.03**			13.65	**0.01**				
Natural habitat			1.71	0.23			0.77	0.52				

Table 4 *Cystoseira compressa.* Relative importance of biotic pressure in controlling the different distribution in artificial vs natural habitats. Response variable: total percentage cover of juveniles on marble tiles. Factor are as follow: Habitat (Hab, Artificial sv natural), Site (nested in Hab: natural rocky reefs at Faborso, Stari Grad, Kuvi and breakwaters at Valalta, Bolnica and Marina), Exclusion [Macrograzers exclusion (MA) vs no exclusion (Uncaged)]. The experiment started October 2010 and sampled in a) December 2010, b) April 2011 and c) October 2011. Separate analysis were performed for each sampling time. Data were analyzed by permutational ANOVA with 9999 permutations on a Euclidean distance matrix. We used the statistical package PERMANOVA+ for PRIMER 6.0 software. Responses judged as significant are in bold.

Source		(a) December 2010				(b) April 2011				(c) October 2011		
	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
Substratum	1	6191	60.24	**0.00**	1	15507	39.22	**0.00**	1	3341	4.23	0.11
Exclusion	1	19494	33.52	**0.00**	1	23062	27.17	**0.01**	1	34100	118.19	**0.00**
Site (Hab)	4	103	0.41	0.80	4	395	0.76	0.55	4	796	2.22	0.09
Hab × Excl	1	2705	4.65	0.11	1	7826	9.22	**0.04**	1	1186	4.11	0.12
Site (Hab) × Excl	4	582	2.30	0.08	4	849	1.64	0.18	4	288	0.80	0.52
Res	35	253			35	517			32	358		
Pair wise MA vs Uncaged within							t	P				
Artificial habitat							9.54	**0.01**				
Natural habitat							0.29	0.36				

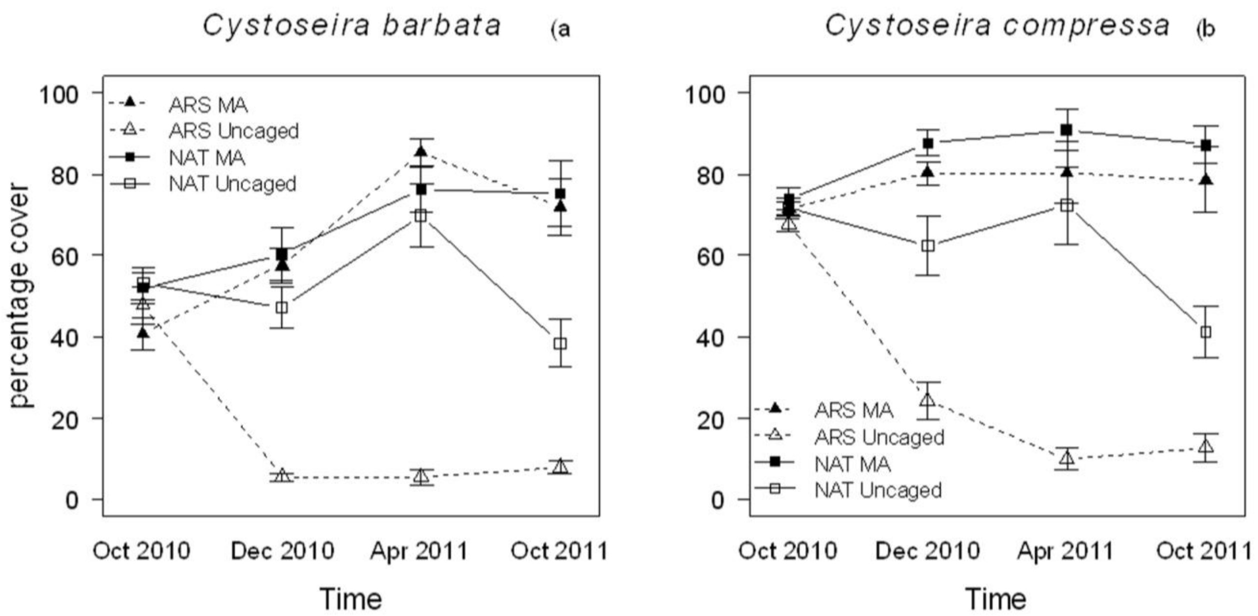

Figure 4 Percentage cover of a) *Cystoseira barbata* and b) *Cystoseira compressa*. Values are reported as the average ± SE of the mean for October 2010, December 2011 , April 2011 and October 2011. Depicted symbols identify levels of the interaction between factors Substratum (artificial= ARS, triangles and dashed lines; natural= NAT, squares and solid lines) and Exclusion (Macrograzers exclusion= MA, solid symbols; Uncaged, open symbols).

Biotic pressure on canopy forming algae in artificial vs natural habitats

We identified two major categories of interactions between algal transplant and benthonic and nektonic species using RUVs. We defined a first suite of interactions as “consumptive” when interacting species showed a feeding behavior (e.g. biting) whereas we defined “non-consumptive” any mechanical (e.g. handling or frictions) interactions potentially damaging algal thalli. In general, fishes were responsible only for consumptive interactions whereas decapods accounted for both categories sometimes contemporary. We also observed different types of interactions depending on the taxon. For examples, mullets (*Mugilidae*, size >10cm) typically attacked the top of the juveniles with fast and vigorous bites during short interactions (median of interaction length = 3 sec). Wrasses and seabreams (*Sypmphodus* sp. and *Diplodus* sp., size <10 cm) interactions were longer (median of interaction length = 25 sec) with bites equally distributed during this time without a clear preference for any specific parts of the thallus. Crabs (*Pachygrapsus marmoratus*, size 5-10cm) handled juveniles thalli using claws, sometimes clearly bending them, for minutes. Hermit crabs (size <5 cm) spent considerable time (tens of minutes) moving on the juveniles. In the artificial habitat, we filmed fishes (*Mugilidae*, *Boops boops*, *Symphodus* sp., *Diplodus annularis*) and crabs (*Pachigrapsus marmoratus*) interacting with *C. barbata* juveniles. In this habitat we counted the highest number of interactions (N= 366), mainly due to *Symphodus* sp. (N=287), *Diplodus annularis* (N=37) and Mugilidae (N=34). In the natural habitat, although we filmed both fishes (*Diplodus vulgaris*, *Diplodus annularis* and *Parablennius zvonimiri*) and decapods (*Pachigrapsus marmoratus*, Paguridae, *Majidae*) we only counted few events (N=32) mainly due to *Diplodus vulgaris* (N=14) and Paguridae (N=12).

Discussion

Artificial structures performed very poorly compared to natural habitats in supporting native population of canopy forming algae. At all sites considered in this study along about 500 km of the North Adriatic coastline, species of *Cystoseira* failed to grow or only sparsely occurred on artificial structures. This result is consistent with work on artificial structures also from other sites in the Mediterranean sea, where rarely the presence of these relevant, native, habitat-forming algae has been reported as an important component of the epibenthos (Falace and Bressan 2002, Bacchiocchi and Airoldi 2003, Bacchiocchi 2004, Vaselli et al. 2008).

Previous experiments have demonstrated that the failure of canopy-forming algae to grow on the artificial structures is not related to some unique, unfavorable, structural characteristics of these artificial substrata. In fact species of *Cystoseira* have the potential to settle and recruit on a variety of artificial surfaces of different materials, complexity and orientations (Perkol-Finkel et al. 2012). Our results also suggest the poor performance of canopy-algae cannot be even clearly related to particularly unfavorable local environmental conditions at the artificial sites compared to the natural reefs. Indeed, although poor water quality, stress from enhanced nutrient and sediment loads, and high temperatures from stagnant conditions [all factors that are known to negatively affect canopy - forming algae (Airoldi 2003, Gacia et al. 2007, Connell et al. 2008, Mangialajo et al. 2008, Perkol-Finkel and Benayahu 2009, Sales et al. 2011) were likely to be more severe at artificial sites compared to natural reefs, whenever *Cystoseira* was experimentally protected by cages its performance consistently increased on artificial structures, becoming similar to that measured at nearby natural rocky sites. This clearly suggests that although water quality and related environmental parameters at the artificial structures were likely not optimal for the growth of *Cystoseira* (Munari et al. 2011), they were not the main limiting factor at artificial sites at least during our study.

Biotic disturbance (both consumptive and non consumptive) appeared to be the most relevant factor limiting the survival and growth of *Cystoseira* at the artificial structures. While caging generally had limited to no effects on canopy forming algae in the natural habitats, at the artificial structures both *Cystoseira barbata* and *C. compressa* persisted only if biotic disturbance was prevented by caging. Although we could not include a proper control for artifacts related to caging, we believe that the differences observed between caged and uncaged plots reflect a true effect of biotic disturbance, rather than alterations of other environmental parameters. First, on rocky reefs caging had limited to no effects on survival and growth of *Cystoseira*. Second, the responses observed where consistent across all experiments and sites, therefore spanning a variety of hydrodynamic and other environmental conditions: in particular the first pilot experiments were purposely run at a time when hydrodynamics was extremely low, which leads to exclude that cages might have enhanced survival of *Cystoseira* by offering shelter to wave action. Third if any artifact had occurred either reducing light or water exchange in cages, this should have impaired juveniles of *Cystoseira* rather than enhance them: therefore results should be interpreted as conservative, further reinforcing the interpretation of the importance of biotic disturbance. Fourth, our subsequent video measures of direct biotic interactions with *Cystoseira* clearly confirmed biotic pressure is much higher at the artificial structures than at the rocky reefs.

The role of herbivory in shaping and regulating the benthic algal community is known from a variety of systems, spanning from temperate to tropical regions (Miller and Hay 1996, Haggitt and Babcock 2003, Hughes et al. 2007, Verges et al. 2009, Taylor and Schiel 2010). In temperate regions in particular, evidence from both mesocosm- and field-based experiments has shown that different organisms can be involved, including mesograzers, e.g. amphipods, (Duffy and Hay 2000{Haggitt, 2003 #685, Kotta et al. 2006, Taylor and Brown 2006, Andersson et al. 2009), crabs and hermit crabs (Ruesink 2000, Cannicci et al. 2002), and fishes (Miller and Hay 1996, Verges et al. 2009, Taylor and Schiel 2010). By using cages of different sizes we could exclude a relevant controlling effect by mesograzers (< 1cm) at our artificial structures. We also observed that both small and large macrograzers were actively interacting at the artificial habitats effectively limiting the growth of canopy-forming algae. RUV observations clearly indicated that the biotic disturbance on *Cystoseira* was likely the result of a suite of “consumptive” and “non-consumptive” interactions from a wide range of species, comprising both fishes and crabs of different sizes. All the fishes showed consumptive interactions, directly biting the juveniles of *Cystoseira* in our experimental plots. Conversely crustaceans showed non-consumptive interactions, clipping the *Cystoseira* but not directly biting it, which possibly might reflect the need to handle the thallus before feeding on it. Interestingly, none of the interacting species is considered a true herbivore, being rather classified as omnivores (Stergiou and Karpouzi 2001). For example bogues in the southern Mediterranean increased the algal contribution in their diet during summer and autumn (Derbal and Kara 2008). Mullets feed primarily on benthic organisms but also on filamentous algae and microalgae (Cardona 2001, Whitfield et al. 2012). The crab *Pachigrapsus marmoratus* is considered a true omnivore with a selective feeding and equal intake of animal and plant materials (Cannicci et al. 2002). Interestingly some of the organisms interacting with *Cystoseira* on the artificial structures were also observed at the natural rocky sites, but they did not show the same degree of interaction with the *Cystoseira*, which indeed was generally not particularly limited by grazing during our experiments at the natural sites. It is possible that at the natural sites pressure by grazing is diluted over a much greater abundance and variety of algal specie, including much more palatable ones. Conversely coastal infrastructures set on sedimentary shorelines represent “oasis” of hard bottoms in a soft bottom environment(Airoldi et al. 2005). As such, they might attract a greater abundance of predators compared to nearby natural habitats, similarly to what is thought to occur in other oasis systems such as seamounts (Rowden et al. 2010). This unexplored aspect of the ecology of marine infrastructures deserves further attention.

Our results showing a significantly different biotic control on artificial vs natural structures add to the growing body of evidence that biological factors such as recruitment (Bulleri 2005), competition and predation (Ivesa et al. 2010, Marzinelli et al. 2011) substantially differ between artificial and natural habitats. For example, the convergence of benthic assemblages on artificial reefs towards their natural coral reefs counterpart in Florida was impaired by the a much greater growth of macroalgae and algal turf on the artificial substrata, exerting a deterrent effect on coral recruitment (Miller et al. 2009), and these differences appeared to be extremely stable over time, persisting even on artificial reefs older than 12 years. The reasons behind this different functioning deserve urgent attention. Provision of hard substrata by artificial structures can in fact facilitate the expansion of a number of hard-bottoms species, including those that are non-indigenous , in areas that otherwise lack suitable habitats (Glasby and Connell 1999, Davis et al. 2002, Bacchiocchi and Airoldi 2003, Bulleri and Airoldi 2005, Glasby et al. 2007, Airoldi and Bulleri 2011), with important implications for biodiversity at local and regional scales (Airoldi et al. 2005). In our study region artificial structures appear to be dominated by filamentous algae, mussels and other opportunistic species, while valuable habitat forming species such as canopy forming algae seem to be severely impaired. The foreseen expansion of artificial habitats (Inger et al. 2009, Dugan et al. 2011) could then entail a table increase in the relative proportion of opportunistic species along the the coasts, leading to increasing homogenization of coastal communities and loss of native biodiversity and associated ecosystem services.

Nearly all current research into the ecological design of artificial structures focuses on construction material, substratum complexity and other structural components or on the improvement of local water quality. However our results clearly suggest that the different ecological performance of artificial structures compared to natural reefs is probably a much more complex phenomenon, likely involving a completely different ecological functioning of the artificial systems, leading to different trophic structure, different species interactions and different population dynamics. Future work should be explore the reasons behind the different ecological functioning of artificial and natural habitats and possibly unravel the factors and mechanisms which cause it. Indeed, the comprehension of the functioning of systems associated with artificial habitats is the key to allow environmental managers to identify proper mitigation options and to forecast the impact of alternative coastal development plans.

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Chapter 5:The quality of marine infrastructures as habitats for epibiota: Different grazing pressure on canopy forming algae in artificial structures and natural reefs.

Abstract

Marine infrastructures are predicted to increase in abundance to cope with the quest for land, energy and food. Yet, the ecological consequences of the expansion of coastal artificial habitats (e.g. coastal defense structures) remain uncertain. Therefore, interest is a growing in understanding the ecological processes driving the functioning of artificial structures and how this can be influenced by different seascape context (e.g. sedimentary vs rocky). These information can improve the success of bioengineering options in mitigating the impacts of marine infrastructures, and enhancing their ecological value, without compromising their original function. Caging experiments showed that the growth of canopy-forming algae was limited on marine infrastructures, due to greater biotic disturbance at artificial compared to natural habitats. Using remote underwater video cameras, we quantified grazing intensity and tested if it differs between the two habitats types and within artificial structures in different seascape contexts. We also evaluated possible causal relationships with other ecological factors (e.g. differences in composition of grazers and/or algal assemblages). We show that grazing intensity was greater in artificial than in natural habitats and that between artificial habitats it was greater in those in a sedimentary than in a rocky context. The ecological functioning of artificial habitats, especially those in a sedimentary context, is therefore the result of a complex interplay of both biotic interaction between species inhabiting these habitats and the seascape context.

Keyword: Grazing pressure, artificial habitat, natural habitat, seascape context

Introduction

Globally, artificial marine structures are increasing in coastal seascapes (Dugan et al. 2011). The purposes of these structures vary greatly, the most important being defense of coastal infrastructures, such as marinas and seaside property. Others include oil and gas rigs, renewable energy plants, offshore aquaculture facilities and artificial reefs to enhance local fisheries or for recreational goals. Future scenarios will likely see an increase of marine infrastructures to cope with the demand for land, energy and food, leading to important alterations of the nature, quality and distribution of habitats patches and associated communities within marine seascapes (Airoldi et al. 2005, Bulleri 2005, Lundholm and Richardson 2010, Bostrom et al. 2011). Most marine infrastructures are built in areas which would otherwise be sedimentary. Thereby, they cause the fragmentation and loss of native sedimentary habitats on one side, (Martin et al. 2005) and introduce new intertidal or subtidal hard substrata not previously available, on the other side (Dethier et al. 2003, Airoldi et al. 2005). Though at first glance, coastal infrastructures seem to adequately represent natural reef habitats (e.g. Thompson et al. 2002, Pister 2009), there is growing and consistent evidence that artificial structures substantially differ structurally and functionally from natural reef habitats (Airoldi et al. 2005, Bulleri and Chapman 2010, Feary et al. 2011, chapter 3, hereafter 'Perkol-Finkel et al. 2012'). Benthic communities colonizing most artificial structures differ in both species richness and abundance from those on nearby natural rocky bottoms (Chapman and Bulleri 2003, Vaselli et al. 2008, Wilhelmsson and Malm 2008, Burt et al. 2011). In many cases, such differences are remarkably persistent, being observed even after a considerable submersion time of the structures (Perkol-Finkel et al. 2006, Zintzen and Massin 2010, Genzano et al. 2011). Artificial structures also tend to favor the spread of opportunistic and invasive species that have been shown to easily colonize artificial habitats and their secondary biogenic substrata (Dethier et al. 2003, Bulleri and Airoldi 2005, Vaselli et al. 2008, Zintzen and Massin 2010, Airoldi and Bulleri 2011, Dafforn et al. 2012, Marzinelli 2012). The causes of these differences are not yet fully understood and require urgent attention, as the projected expansion of armoring and other structures is expected to alter the quality and functioning of marine habitats ultimately leading to biotic homogenization (Sax and Gaines 2003, Airoldi et al. 2008, Airoldi et al. 2009, Fauvelot et al. 2009).

Manipulative experiments have helped identifying some of the most relevant biotic and abiotic factors shaping communities in these habitats. For example, differences in seawall building material seemed to affect the recruitment of two limpet species in Sydney harbor by altering competitive outcomes (Ivesa et al. 2010). The greater cover of bryozoans on leaves of kelps growing on pier-pilings than in the surrounding natural rocky bottom resulted from the increased shading provided by artificial reef structures and the lower grazing pressure of sea urchins in this habitat (Marzinelli et al. 2009, Marzinelli et al. 2011). Colonization of non-indigenous species on artificial structures has been shown to be favored by the very large natural and anthropogenic disturbances (from e.g. sedimentation, maintenance and harvesting) that are unique to these habitats (Airoldi et al. 2005, Airoldi and Bulleri 2011, Dafforn et al. 2012). Understanding these mechanisms is fundamental to identify bioengineering options that mitigate the impacts and enhance the ecological value of marine infrastructures, without compromising their original function. Past examples include the adding of morphological features to seawalls and breakwaters such as tidal pools, crevices, rough or complex surfaces (Airoldi et al. 2005, Moschella et al. 2005, Chapman and Blockley 2009) to reproduce as much as possible the structural complexity of natural habitat. Another approach is to reduce or manage the impacts from the severe disturbances from maintenance (Airoldi and Bulleri 2011). Finally, the growth of ecologically valuable benthic communities can be promoted through direct “gardening” of important native habitat-forming species (Falace et al. 2006, Susini et al. 2007, Perkol-Finkel et al. 2012). The potential success of these options relies on a deep understanding of the ecological processes and factors controlling the ecological performance of artificial habitats.

Previous work done in both, artificial reefs and coastal defense structures suggests that one of the most relevant factors controlling the development of epibiota on marine infrastructures may be related to altered biotic pressure from a variety of species that find in these habitats particularly favorable as nursery grounds, refugia and feeding areas (Brickhill et al. 2005, Thanner et al. 2006, Leitão et al. 2007, Leitao et al. 2008, Pizzolon et al. 2008, Edelist and Spanier 2009, Hackradt et al. 2011, Simon et al. 2011). For example, caging experiments have shown that the growth of ecologically relevant, native habitat-forming species (i.e. canopy-forming algae) was consistently limited on marine infrastructures along the coast of the North Adriatic sea by greater biotic disturbance at these artificial habitats compared to natural reefs (chapter 4 of this thesis). These effects were greatest if structures were built along sedimentary coastlines rather than on rocky bottoms (Perkol-Finkel et al. 2012). Focusing on these ecological interactions and how the effects of changing habitat quality in human-dominated seascapes may cascade through whole assemblages is critical to predicting the impacts of marine structures. Here, we quantify grazing pressure at artificial structures and natural rocky reefs along the North Adriatic coastline by using field experiments and videos. We also document, how the regional-scale distribution of canopy forming algae and other dominant epibiota related to the different distributions of a variety of grazers in natural and artificial habitat patches. Specifically, we tested: 1) whether grazing pressure on canopy forming algae differed between artificial structures and natural reefs; 2) whether grazing pressure differed between artificial structures built along sedimentary or rocky coastline. We hypothesized, that structures embedded in a sedimentary context would act as an “oasis” of hard substrata, attracting mobile fauna from surrounding sediments (Einbinder et al. 2006, Clynick et al. 2007, Wehkamp and Fischer 2013), therefore resulting in much greater grazing effects than occur at structures built along rocky coastlines. Thirdly, we analyzed the composition of mobile fauna and dominant epibiota on artificial structures and natural reefs. With this analysis, we explored, whether the differences observed in grazing pressure between habitats related to any differences in the composition of the potential pool of grazers or in the composition of the epibenthic communities.

Method

Study area

The study area spans along the Adriatic coast between the municipalities of Marotta and Porto Recanati (Fig. 1). The coastline is mainly characterized by sandy beaches with the exception of the Monte Conero promontory (43° 33′ N, 13° 37′ E; in proximity of Ancona) that represents the only natural rocky stretch of coast. The area is heavily urbanized and attracts mass-tourism during the summer season. For this reason, beaches have been extensively protected by breakwaters deployed at a distance of 100-300 m from the shore. We identified two study sites for each of the three habitats of interest: reefs at 'La Vela' and 'Due Sorelle' located about 1 km apart along Monte Conero, were selected as natural rocky habitats (Nat). 'Urbani' and 'Numana', located about 500 m apart, along Monte Conero were selected as sites with artificial habitats (breakwaters) set in a rocky context (Rar). 'Marotta' (north of Monte Conero) and 'Porto Recanati' (south of Monte Conero) were selected as sites with artificial habitat in a sedimentary context (Sar). Detailed descriptions of the study areas and region can be found Perkol-Finkel et al. (2012) and in chapter 4.

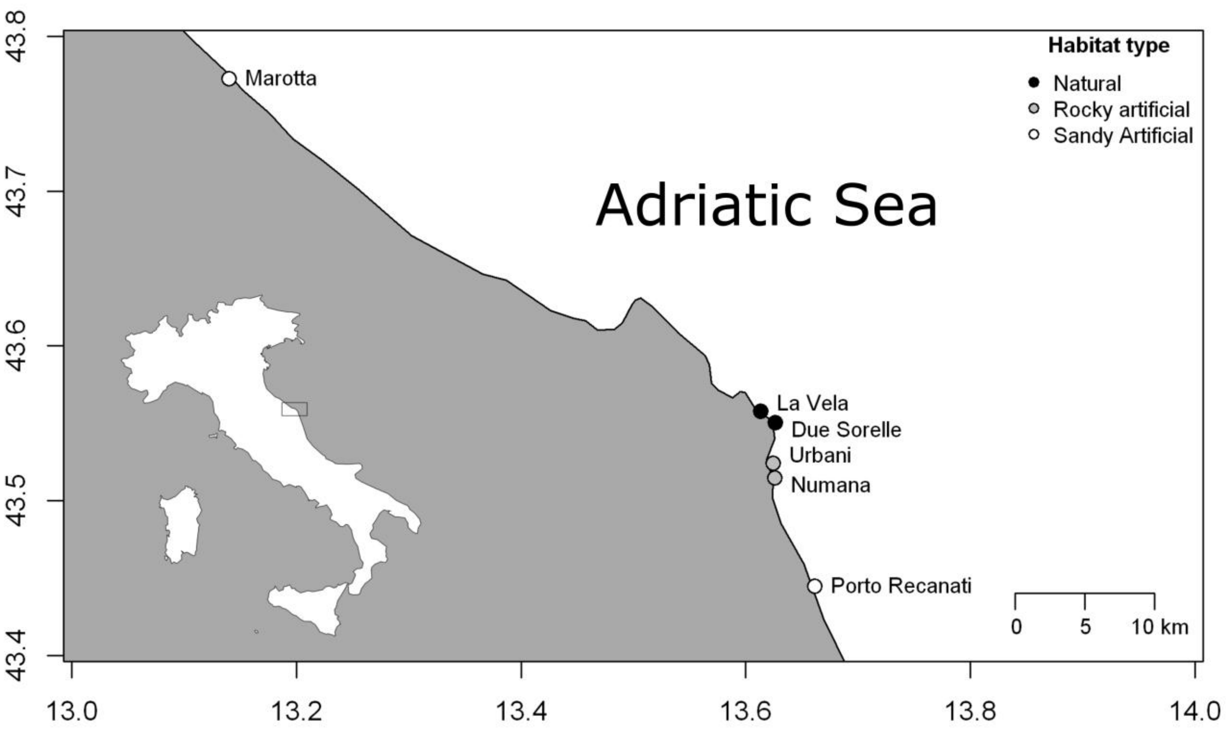


Figure 1 Map of the study sites along the north Adriatic Sea. The three habitat types are represented: natural reef (black circles), artificial habitat in a rocky context (gray circles) and artificial habitat in a sedimentary context (open circles).

Video quantification of grazing pressure in artificial and natural habitats

To quantify grazing pressure and biotic disturbance on juveniles thalli of the canopy forming algae *Cystoseira barbata* in the three different habitats, we used remote underwater video cameras (RUVs) to film interactions between a variety of invertebrates and fishes and thalli *of C. barbata* in the three different habitats.

Each RUV consisted of a GoPro® HD Hero, equipped with a flat lens and an additional battery pack, mounted on a weighted square base made out of marble (10x10x2 cm). Cameras were set at the resolution ‘r2’ (HD, 1280x720, 30 fps), allowing 4 hours of continuous filming. RUVs were always oriented towards the open sea.

Marble tiles, carrying 3-5 *Cystoseira barbata* juveniles, were placed in front of the RUVs at a distance of 0.5 m. Tiles (each one was one experimental unit, hereafter “unit”) were placed on horizontal boulders at a water depth of 1.5 – 2.0 m. This procedure allowed setting identical experimental conditions at all study sites, including the artificial structures, where no *Cystoseira* occur naturally. The juveniles (about 3-4 months old, 6 cm high) of *Cystoseira barbata* used in the experiment, were collected from loose boulders at La Vela. Recruits in these loose habitats have naturally low survival probability due to severe substratum instability (Perkol-Finkel and Airoldi 2010), therefore their use for our experiments did not damage the source population. The boulders were broken into small fragments holding 1-2 individuals that were glued on to marble tiles (10x10x2 cm) by using epoxy putty (Subcoat Veneziani) to form experimental units comprising 3-5 juveniles. The tiles with the juveniles were preserved in laboratory aquaria (in aerated tanks at controlled temperature and light condition) for 2-3 days until use in the experiment to guarantee equal starting conditions, and transported by car to the experimental sites as quickly as possible in 100 liter tanks.

In summer 2011, we ran preliminary pilot measurements by placing two replicate RUVs at the rocky reef in La Vela (Monte Conero) (Nat) and at one breakwater in Marotta (Sar), where previous studies suggested high grazing pressure on *Cystoseira*. At each site, the two RUVs were set several meters apart from each other and filmed biotic interactions with *Cystoseira* on three tiles, sitting next to each other to measure interactions on a larger sample of juveniles. Videos were recorded on two replicate days, on the 1st (3 h from 14.00 to 17.00) and 5th of August (4 h from 11.15 to 17.15). Each time the filming was synchronized by two operators to occur at the same time interval, to reduce possible differences related to temporal variability between study sites. Differences in grazing pressure at the artificial and natural sites (Marotta and La Vela) were analyzed by 2-way ANOVA, including factors Habitat (fixed, artificial vs. natural) and Day (2 days, random, orthogonal to habitat). Pooling procedures for factor Day where used to increase the power of the test for Habitat (Underwood 1997). We used the statistical package PERMANOVA+ for PRIMER (Anderson et al. 2008) to partition the variability and obtain F-statistics on a matrix of Euclidean distances calculated from the original raw data, and calculated all P-values using 9999 random permutations of the appropriate exchangeable units.

There were no replicated sites for each habitat in this pilot study, which limited the possibility to generalize the results and unequivocally interpret them in terms of differences between habitats. However, the large differences observed between the artificial and natural sites stirred interest in running further analyses. In summer 2012, we ran a second extensive and replicated study to confirm the generality of the differences in grazing pressures between artificial and natural habitats found during the pilot study. Also, the aim was to further explore possible differences between artificial structures set in different environmental contexts (sedimentary vs. rocky). For each of the three habitats identified, (Nat, Rar and Sar) video recording of biotic interactions with *Cystoseira* was replicated at two different sites (see *Study area*), and at each site filming was replicated at three different days between 27 June and 7 August 2012 (4 hours for each RUV). To optimize logistics, we measured biotic interactions at two randomly chosen sites on each sampling date. For each combination of Site and Day, we deployed two replicated tiles holding about 5 juveniles of *Cystoseira*. The tiles were prepared by collecting juveniles at La Vela as described for the pilot study. In this case, however, all juveniles were collected at the start of the experiment and were preserved in laboratory aquaria (in aerated tanks at controlled temperature and light condition) until use in the experiment to guarantee equal starting conditions at each measurement. We prepared each tile the day before use by gluing the small rock fragments with juveniles to marble tiles, using epoxy putty (up to 5 juveniles per tile). Each time, the tiles prepared were transported by car to the experimental sites as quickly as possible in 100 liters aerated tanks. Each tile was used only once to guarantee independence of the measurements.

Tiles were set in place several meters apart and one RUV was deployed in front of each at a distance of 0.5 m. Filming was carried during daylight because of the lack of illumination systems. Even if data from preliminary trials suggested that interaction rates are relatively constant during the day, we restricted the video recording to the central hours of the day, between 12 a.m. and 4 p.m., to minimize any possible differences related to light conditions.

We quantified grazing pressure on canopy-forming algae as number of interactions involving the contact between *C. barbata* juveniles and animal species. We defined as interaction the contact, or a continuous series of contacts, between a single organism and the algae. For each interaction we recorded the type of interacting organisms to the lowest possible taxonomical level (hereafter 'taxa'), the type of interaction [consumptive (evident feeding behavior, e.g. biting) or non-consumptive (mechanical, e.g. handling or frictions)] and the initial and final time of interaction. For fishes, we also recorded the size class as 1 (less than 5 cm), 2 (between 5 and 10 cm) and 3 (more than 10 cm) using the known size of the tiles as a reference.

To prevent possible bias due to the presence of the diver we started analyzing the videos five minutes after the video cameras were switched on. In total, we recorded 144 hours of video. After an initial random screening of some of the videos (which showed that the interactions were relatively homogeneously distributed during the four hours of recording) we decided to subsample each video by extracting 12 random sequences of 5 minutes (1 hour total, see *Supplementary Information*).

For each video sequence, we calculated the number of interactions per hour (independently of the interacting taxa and type of interaction) as a proxy for grazing pressure intensity, and tested for any difference between habitats by using Permutational three-way ANOVA with 9999 permutations. The analysis included the factors 'Hab' (fixed with 3 levels: Nat, Rar and Sar) , "Site" (random, two levels nested in Hab), and "Day" (random, 3 levels nested in "Site"). The analysis was run by using PERMANOVA+ for PRIMER 6.0 software as described previously. We checked for homogeneity of dispersion of the data using PERMDISP and applied a square-root transformation when needed.

Analysis of mobile fauna and dominant epibiota in the different habitats

We used the videos recorded in 2012, to analyze the overall composition of mobile fauna at the different habitats and study sites. In each video sequence, we counted the number of individuals of different taxa present or passing through the frame. Following Cappo et al. (Cappo et al. 2004), we considered the maximum number of individuals of the same taxon seen in a single sequence in a video as a proxy for the abundance. We referred to this variable as ‘max pass through number per taxon’ (hereafter *MaxPTN*) to avoid confusion with the *MaxN* metric used in Cappo et al. (2004). We used *MaxPTN* to minimize the chance of an overestimation due to counting the same individuals in more than one video sequence. We used non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity matrix to detect dissimilarities in species composition and abundance of faunal assemblages (the potential grazers) between habitats. Additionally, we used univariate ANOVA and SNK post-hoc tests to assess differences in abundance of single taxoa in the different habitats. We checked data for normality using the Shapiro-Wilk test, and for homogeneity of the variance using the Cochran test. When assumptions were not met, we transformed data as suggested by the boxcox method. We performed statistical analyses using the ‘MASS’, ‘outliers’ and ‘agricolae’ packages in version 2.15.0 of R software (Team 2009).

We also investigated the composition of the dominant epibenthos colonizing the hard substrata at each site for each of the three habitats studied. In summer 2012, we deployed three transects 50 m long at a depth of 1.5 – 3.0 m parallel to the coast in the natural reefs or along the main length of the breakwaters at the artificial sites (due to limited breakwater length only two transect were deployed in Urbani). Along each transect, we photographed 11 quadrats (identified by a steel frame of 20x20 cm) spaced at 5 m intervals, starting from the origin of the line. By using the software Vidana 1.1, we calculated the percentage cover of 10 categories (hereafter taxa): *Mytilus galloprovincialis* (hereafter *Mytilus*), *Mytilus* juveniles, *Ulva* sp., *Cystoseira* sp., other coarsely branched algae (hereafter CB,), *Sabellaria* sp., turf (comprising a dense layer of mixed filamentous algae that entrapped sediments), and bare rock (comprising rock not covered by any macroscopic visible species or patches of sand , hereafter R&S). We also quantified any unreadable areas to adjust the estimation of the percentage covers of each taxa to the real sample surface. We used non-metric multidimensional scaling (nMDS) based on centroid distances derived from Bray-Curtis similarity matrix to detect dissimilarities between habitats. We undertook the SIMPER (similarity percentage) analysis to identify the discriminating community components between pairs of habitats using PRIMER 6.0 software.

Results

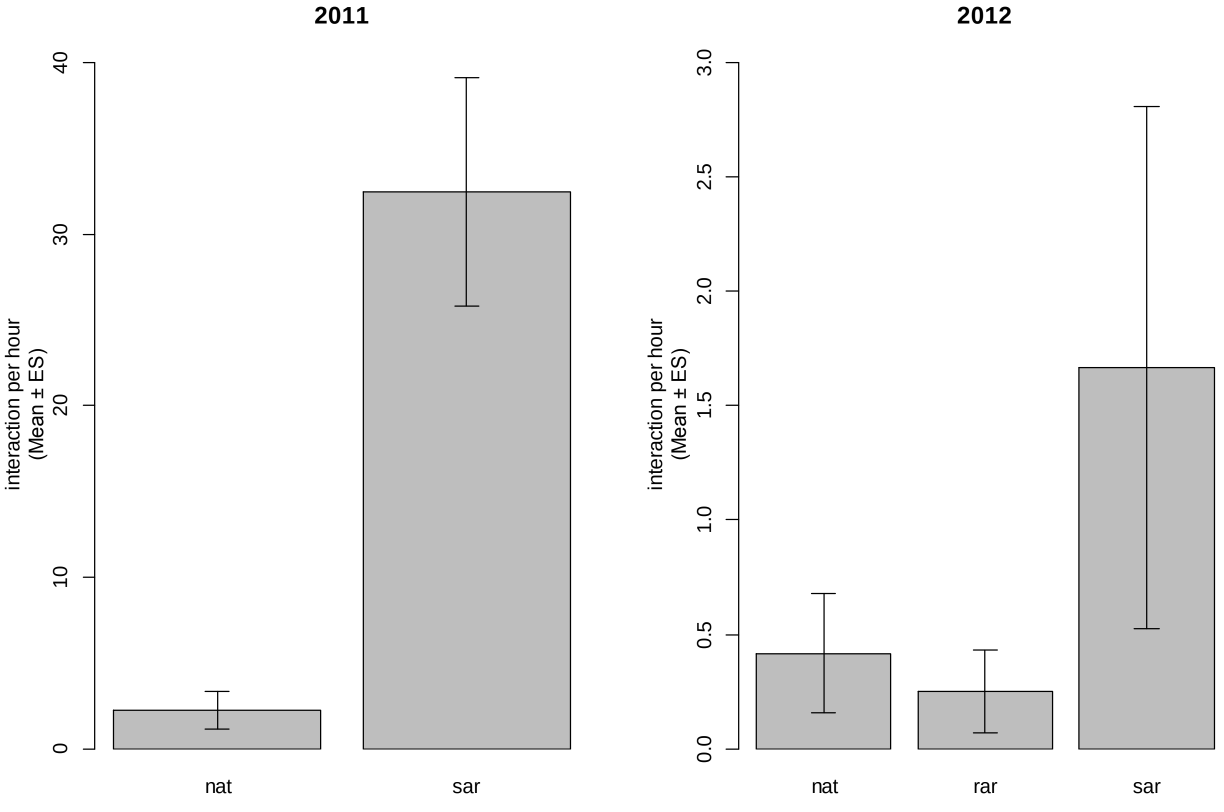
Grazing pressure

During the pilot study in August 2011, we observed a total of 366 interactions with juveniles of *Cystoseira* at the breakwaters in Marotta and 32 at the natural rocky reef in La Vela. The average amount of interactions per hour at Marotta was more than ten times greater than at La Vela (33 ± 7 and 2 ± 1, respectively, Fig. 2a), which was detected as significant after pooling the factor 'Day' (F($_{df\ 1,6)}$= 30.8; p<0,05).

During 2012, the number of interactions measured was much smaller compared to 2011, which probably reflected unusual environmental conditions at the study sites (see *Discussion*). Overall, we observed 20 interactions in artificial habitats on sand, three in artificial habitats on rock and five in natural habitats, which reproduced very closely the pattern observed in the pilot study in 2011 (Fig. 2b). However, due to the large variability and high number of zeroes in the data set, the differences between habitats were not statistically significant.

In both years, fishes were in the majority responsible for interactions in both, artificial habitats on sand and natural habitats. In particular, in 2011, *Symphodus sp.* accounted for 26 ± 9 interactions per hour in artificial habitats on sand, followed by *Diplodus annularis* (4 ± 3) and *Mugilidae* (2 ± 2, size class 3). In Nat, *Diplodus vulgaris* was the major grazer (1 ± 1 interactions per hour). Among crustaceans, the major grazer in Sar was the crab *Pachygrapsus marmoratus* (0.5 ± 0.4) whereas, Paguridae were dominant in Nat (0.7 ± 0.7). In 2012, the sparid *Boops boops* (size class 3) were responsible for 15 of the 20 interactions observed in Sar, whereas in Nat three interactions out of five involved *Sarpa salpa* (size class 3).

Fish interactions were always consumptive, as they bit the juveniles. Different feeding behaviors were recognizable between taxa and size classes. In general, bites of small and medium fishes were small and repeated those of bigger fishes (size class 3) were more aggressive and rapid. Crustaceans showed both, consumptive and non-consumptive interactions. Crabs (*Pachygrapsus* *marmoratum*) were seen bending thalli and they possibly fed on them. Other crabs, mainly Paguridae and Maijdae occasionally climbed juveniles.



a) **b)**

Figure 2. Number of interactions per hour observed between *Cystoseira barbata* juveniles and grazers in the natural (nat), rocky artificial (rar) and sandy artificial (sar) habitats in a) 2011(2 replicate videos recorded in 2 different days at 1 site per habitat, N=4) and b) 2012 (2 replicate videos recorded in 3 different days at 2 sites per habitat, N=12). Values are reported as the Mean ± 1 Standard Error.

Faunal composition and abundance

We did not observe relevant dissimilarities between natural and artificial habitats in the multivariate structure of faunal assemblages (Fig. 3). Fourteen fish taxa of the 24 filmed, were observed in all of the three habitats. Of these, *Boops boops* was the most abundant taxon, while other taxa were relatively sparse. *Atherina* sp. was common at both artificial habitats, whereas it was never observed at natural sites. *Sarpa salpa* was abundant only once at the natural site Due Sorelle.

Taxa abundance was significantly different (*MaxPTN*, Fig. 4) for Mugilidae ($F_{df(2,32)}$=5.1, $p<0.05$; SNK failed to detect difference between habitats), *Diplodus vulgaris* ($F_{df(2,32)}$=4.6, $p<0.05$, SNK Rar > Nat = Sar) and *Diplodus sargus* ($F_{df(2,32)}$=4.3, $p<0.05$, SNK Sar>Nat=Rar) , while the abundance of the other taxa were significantly different between the three habitats.

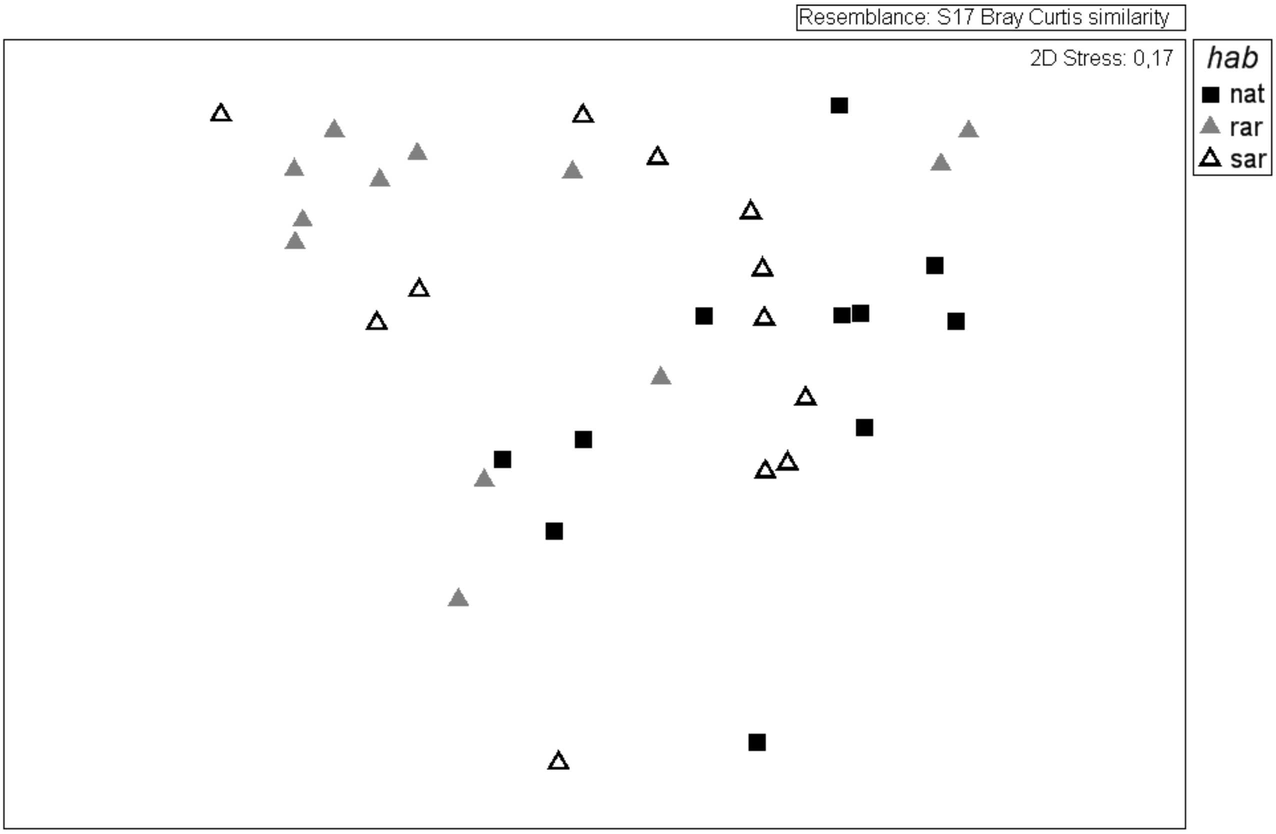


Figure 3 Non metric Multidimensional Scaling (nMDS) of faunal assemblages associated with the three habitats. Habitats are: rocky natural (nat, black squares), artificial habitats in a rocky context (rar, grey triangles) and artificial habitats in a sedimentary context (sar, white open triangles). Depicted points are replicate videos.

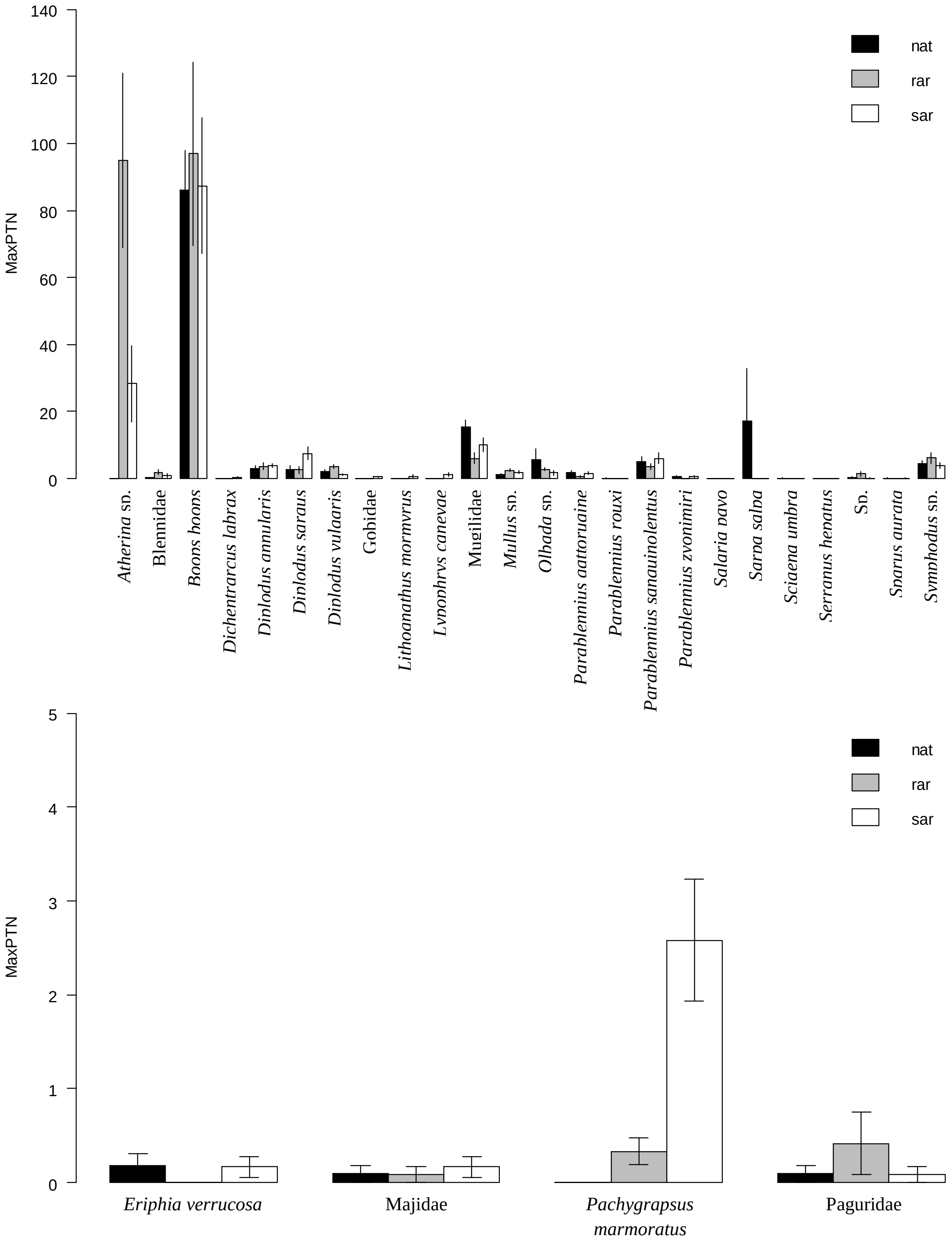


Figure 4 Taxa Abundance per habitats for fish (upper panel) and crustacean (lower panel). *MaxPTN* (i.e. maximum number of individual of the same taxon seen in a single sequence in a video) is used as proxy for the abundance Habitats are: rocky natural (nat, black), artificial habitats in a rocky context (rar, gray) and artificial habitats in a sedimentary context (sar, white). Values are reported as the Mean ± 1Standard Error.

Distribution of dominant epibiota

The composition of benthic assemblages differed among habitats. CB, *Cystoseira* sp. and turf were the most abundant taxa in natural habitats (percentage cover 26 ± 4%, 26 ± 4 %, 20 ± 3% respectively; mean ± standard error). Turf was dominant in artificial habitat in a rocky context, followed by CB (36 ± 4% and 24 ± 3%). In artificial habitats on sand, CB and *Cystoreira* were virtually absent, while the other taxa were rather homogeneously represented, with percentage covers ranging on average between 13 and 19 %.

The nMDS ordination (Fig. 5) revealed, that natural habitats and those artificial habitats in a sedimentary context were more similar to each other than to rocky artificial habitat in a rocky context. Differences between natural habitats and artificial substrates on sand were mainly driven by *Cystoseira* and CB (30% of dissimilarity). These taxa were the two most abundant components at the natural habitat whereas they were virtually missing at artificial habitats on sand (Fig. 6). On the other hand, *Mytilus*, both adults and juveniles, were more abundant in artificial habitats on sand than in natural reefs. Turf and CB were the two taxa differentiating the most rocky artificial habitats from both natural and artificial habitats on sand, turf being the most represented benthic taxa in rocky artificial sites. Differently from artificial habitats on sand, *Cystoseira* occurred at those artificial substrates in a rocky context, even if with much lower percentage cover (rarely exceeding 5%). Finally, cover of CB was similar in artificial habitats in a rocky context and in natural reefs.

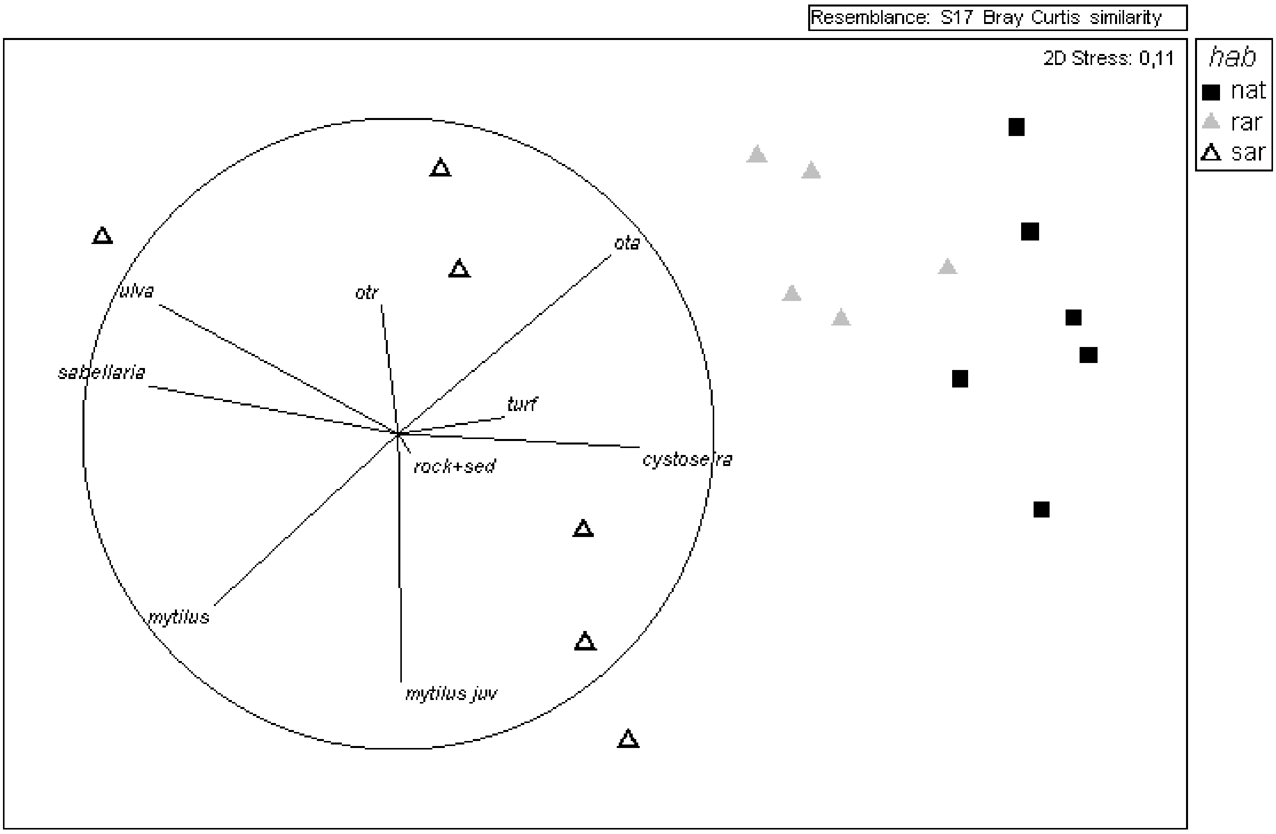


Figure 5. Non metric Multidimensional Scaling (nMDS) of benthic assemblages in natural (nat, black solid squares), artificial habitat in a rocky context (rar, gray solid triangles) and artificial habitat in a sedimentary context (sar, white open triangles) based on centroid distances derived from Bray-Curtis similarity matrix. Vectors represent the contribution of the different taxa in determining the multivariate ordination pattern. Depicted symbols are replicate transect at two different sites per habitat (N=6) sampled in summer 2012.

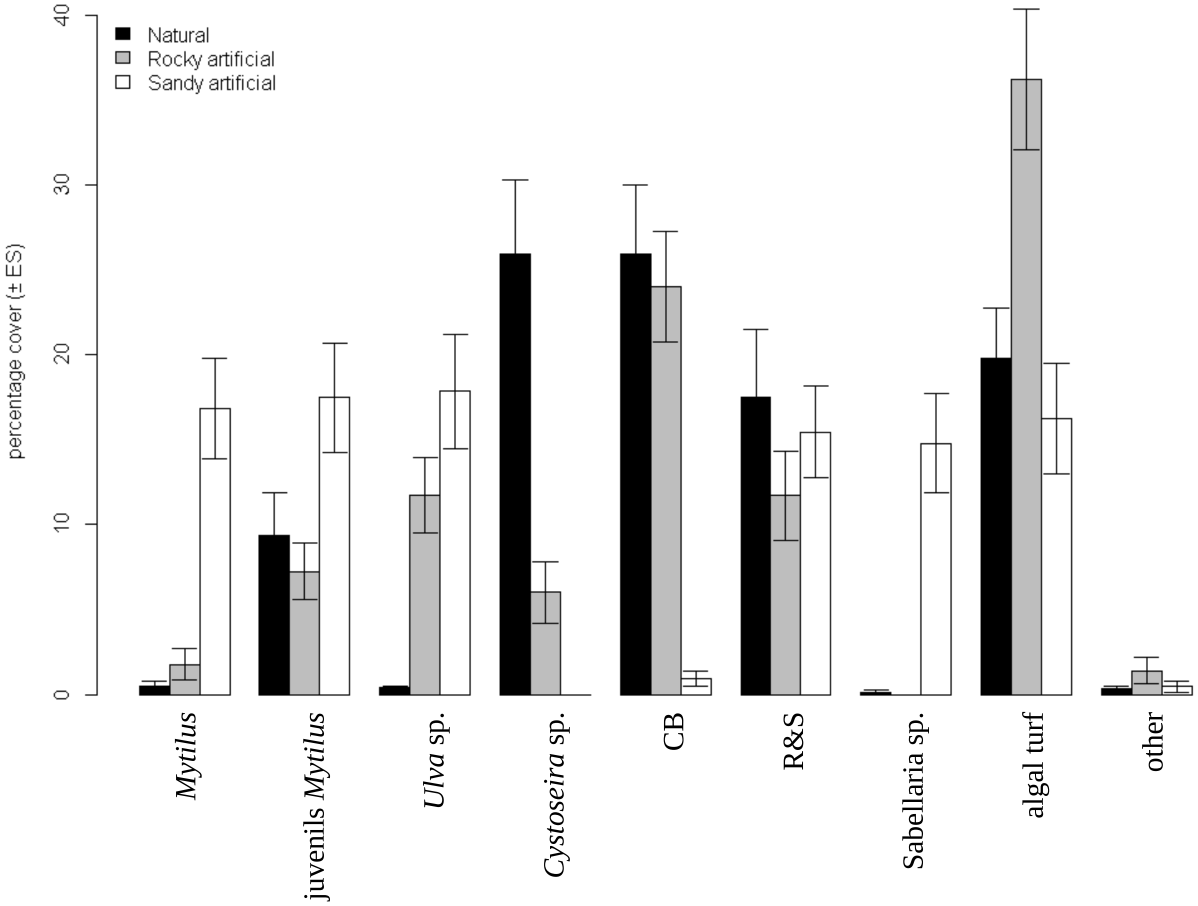


Figure 6 Composition of benthic assemblages in natural (black, N=65), rocky artificial (gray, N=55) and sandy artificial (white, N=64) habitats. Bars represent the average percentage cover of benthic taxa sampled at two site per habitat. Taxa are *Mytilus*, juvenils *Mytilus*, *Ulva* sp., *Cystoseira* sp., coarsely branched algae (CB), bare rock with sediment patches (R&S), Sabellaria sp., algal turf, other. Values are reported as the Mean ± 1 Standard Error.

Discussion

Grazing pressure on the canopy forming alga *Cystoseira barbata* was greater in artificial than in natural habitats. Moreover, grazer impact was higher at those artificial structures that were built along a sedimentary coastline compared to artificial structures built along a rocky coastline. This result is coherent with previous experimental evidence which highlighted a poor growth potential of canopy forming algae of the genus *Cystoseira* on artificial structures compared to natural reefs, particularly at artificial structures built in a sedimentary context (Perkol-Finkel et al. 2012 , chapter 4).

The same trend of larger grazing pressure on *C. barbata* on artificial habitats built along a sedimentary coastline compared to natural reefs was observed during both 2011 and 2012. However, the intensity of grazing pressure at the sandy artificial habitats was much greater in 2011 than in 2012. This difference could possibly be related to the larger abundance of the green alga *Ulva* sp. observed in 2012. Ephemeral macroalgae belonging to the genus *Ulva* are rather common on artificial structures in the study area, and they show large temporal fluctuations in abundance (Bacchiocchi and Airoldi 2003). *Ulva* sp. almost absent on artificial structures in Marotta during 2011, but was abundant in 2012 (personal observation). In 2012, we could see from the videos that some of the grazer species, such as *Boops boops*, fed on nearby thalli of *Ulva* sp. rather than on our experimental *Cystoseira*. Green algae, and *Ulva* in particular, are considered palatable species to many omnivorous species (Hay 1986). For example, different mullet species either regularly or preferentially fed on filamentous green algae in a Mediterranean lagoon where algal community comprised also red algae (Cardona 2001). On the contrary, brown macroalgae, such as Fucoids, are considered scarcely palatable to grazing fishes (Miller and Hay 1996, Duffy and Hay 2000, Taylor and Steinberg 2005). Thus, it seems reasonable to hypothesize that when *Ulva* sp. is abundant it might represent a preferable resource compared to *Cystoseira barbata*, which could explain the lower grazing pressure measured at the artificial structures in 2011 compared to 2012.

Grazing pressure differed not only between artificial and natural habitats, but also between artificial habitats built along a sedimentary or a rocky coastline. This result is consistent with previous observation and experiments on the distribution of *Cystoseira* in the study region. Indeed, *Cystoseira* has never been observed at artificial structures in sandy habitats, while it can be sparsely present on artificial structures along the rocky coasts of Monte Conero or Croatia (Perkol-Finkel and Airoldi 2010, Perkol-Finkel et al. 2012, chapter 4 in this thesis). Moreover, the survival of Cystoseira sp. transplanted on artificial structures in sedimentary environments was virtually nil if protection against macrograzers was not provided (chapter 4 in this thesis), while it had good growth potential on structures built along Monte Conero (chapter 3 in this thesis). Therefore, results of our RUV observations strengthen interpretation of previous assessment of *Cystoseira* distribution, and confirm that different macrograzers, namely fishes and crabs, cause biotic disturbance that severely limit its distribution at the artificial sites, particularly in sedimentary environments.

Different explanations could be hypothesized to explain the different grazing pressure observed between artificial vs. natural habitats and among artificial structures in different environmental context. Firstly, it could have been possible that potential grazer pools differed between the three habitat types as a consequence of unequal composition of faunal assemblages (Thanner et al. 2006, Clynick 2008, Andersson and Ohman 2010, Hackradt et al. 2011). However, we did not detect any particular dissimilarity between habitats on the basis of multivariate ordination of mobile faunal assemblages (Fig. 3). Moreover, the only true herbivore species, *Sarpa salpa* (Stergiou and Karpouzi 2001), has been observed exclusively at natural habitats. The other taxa, omnivores with varying preference for plant material (Stergiou and Karpouzi 2001), showed similar abundance at the different sites. Secondly, structures embedded in a sedimentary context could represent “oases” of hard substrata, attracting potential grazers from surrounding sediments thus exacerbating the grazing pressure (Einbinder et al. 2006, Clynick et al. 2007, Wehkamp and Fischer 2013). Similar effect are thought to occur in other oasis systems such as seamounts (Rowden et al. 2010a, Rowden et al. 2010b). Additionally, it has been shown that, the diet of *Diplodus sargus*, sampled in the proximity of an artificial reef, was more associated with benthic community colonizing the structure rather than that of the surrounding soft-bottom (Leitão et al. 2007). The grazer abundance was similar in all three habitats studied, but the hard bottom area available at sandy artificial structures was much lower than that available at the other two habitats. In fact, both natural and nearby artificial habitats at the Monte Conero promontory, were embedded in the same wide rocky matrix. Therefore, grazer pressure at artificial habitats in a sedimentary context was possibly higher than at both natural and artificial habitat in a rocky context. Thirdly, because diversity of prey species influences the strength of top-down regulation (Helmut and Bradley 2004, Duffy et al. 2007, Edwards et al. 2010), local algal diversity could have affected grazing pressure at the different habitats. In our study region, artificial structures in a sedimentary context supported benthic assemblages dominated by invertebrate fauna (e.g. mussels and tube worms), whereas algae were mainly represented by ephemeral, opportunistic species, such as green algae of the genus *Ulva* (this work). On the contrary, both natural habitats and rocky artificial habitats supported more diverse algal communities, comprising *Cystoseira* sp. and other coarsely branched algae (category CB) in addition to *Ulva* sp.. An increase in algal diversity may result in a decrease in 'prey risk' for the focal species, *Cystoseira barbata* in our case, following a "dilution" effect (Narwani and Mazumder 2010). Further, in a more diverse community, it could be more likely to find algae that are more palatable than the *Cystoseira* simply because of a sampling effect. If this was the case, a "preference" effect could occur, with grazers consuming relatively more of a preferred resource when is available (Narwani and Mazumder 2010). Fourthly, food availability at artificial habitats in a sedimentary context could be limited. Total algal cover was lower in these habitats compared to those in rocky context (Fig. 6). Additionally, abundance of infaunal organisms at sandy artificial reef could be influenced by sediment composition (Danovaro et al. 2002, Martin et al. 2005) while resource depletion can be induced by predation in the surrounding area (Langlois et al. 2005, Galvan et al. 2008, Edelist and Spanier 2009, Simon et al. 2011). This could have induced some grazer species to widen their trophic niche to include algal material. For example, a similar reaction to shortage in the organic matter content of sediment has been observed in mullet species inhabiting a Mediterranean coastal lagoon (Cardona 2001). Testing these hypotheses exceeds the aims of our work, thus further investigation will be required to discriminate which mechanisms are more relevant.

It has been suggested that artificial substrata may adequately represent natural habitats (e.g. Thompson et al. 2002, Pister 2009) or may, in fact, compensate for loss of habitat elsewhere (e.g.

Iannuzzi et al. 1996), or even create additional valuable habitat (e.g. Iverson and Bannerot 1984). This approach to conservation should, however, be treated with caution, as our results clearly highlight that artificial structure do not function as rocky reefs, and their value as habitat for native epibiota can be very variable depending on local environmental and biological factors. Fucoid canopy-forming algae are some of the most important habitat formers on Mediterranean rocky reefs, dominating benthic assemblages, and greatly influencing both biodiversity and the physical environment (Benedetti-Cecchi et al. 2001, Maggi et al. 2009). The lowest ecological performance of artificial structures compared to natural reefs in supporting these species has therefore profound implications for the functioning of these systems and the maintenance of coastal native biodiversity. Whilst most research on the ecological design of artificial structures tends to focus on the effect of differences in building material or substratum complexity (Moschella et al. 2005, Burt et al. 2009, Ivesa et al. 2010, Espinosa et al. 2011, Green et al. 2012), we advocate that more attention should be devoted to incorporate knowledge of the different ecological functioning of these systems into the design of these structures.

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Supplementary Information

Video Sub sampling

The video camera GoPro® HD Hero, when working in ‘video’ modality, saves one or more different files on the memory card depending on the filming duration. The length of the individual files can be different (likely depending on memory used for each file in relation to filming condition). Therefore what we called ‘a video’ was actually formed by two or more successive videos depending on how many files were saved by the camera.

In order to extract the desired number of sequences of five minutes length to be analyzed, we needed to respect several procedural constrains:

1. the fist sequence of the first file can be extracted starting from 5 after the operator exit from the framing.
2. For each file sequences must be extracted randomly
3. Sequences must not overlap
4. One sequence must not be split on two successive files

As manual sub sampling is tedious and time consuming, we compiled the following function using R Gui to perform the sub sampling automatically and in a matter of seconds.

```
sampling<-function(dat, n.seq, dur.seq, m.inizio,s.inizio, nomefile){
        label<-as.character(dat[,1])
        hs<-dat[,2]*3600
        ms<-dat[,3]*60
        ss<-dat[,4]
        dat$durss<-hs+ms+ss
        inizio<-(m.inizio*60)+s.inizio
        p.iniziali<-c(inizio,rep(0,nrow(dat)-1))
        seqxfile<-rep(0,nrow(dat))
                 repeat {if (sum(seqxfile)==n.seq) break
                    seqxfile<-sample(1:n.seq,nrow(dat), replace=T)}
        elenco.inizio<-0
        elenco.inizio<-list(elenco.inizio)
        for (j in 1:length(seqxfile)){
          cont<-10^9
          repeat { if (cont <= dat$durss[j]) break
               elenco.inizio[[j]]<-sort(
         (sample(0:dat$durss[j],seqxfile[j],replace=F)+p.iniziali[j]))
           ifelse( length(elenco.inizio[[j]])<2,elenco.inizio[[j]],{
              dif<-0
              sdif<-sum(dif)
              repeat { if (sdif==length(elenco.inizio[[j]])-1) break
                    for (w in 1: (length(elenco.inizio[[j]])-1)) {
                       dif[w]<- elenco.inizio[[j]][w+1]-elenco.inizio[[j]][w]
                           }
                    dif<-(dif>=dur.seq)
```

```
                    sdif<-sum(dif)
                    ifelse ( sdif==length(elenco.inizio[[j]])-1,
                                  elenco.inizio[[j]],
                       elenco.inizio[[j]]<-sort(
(sample(0:dat$durss[j],seqxfile[j],replace=F)+p.iniziali[j]))  )
                     }
               elenco.inizio[[j]] })
             cont<-elenco.inizio[[j]][seqxfile[j]]+ dur.seq
              }
}
        c1<-rep(0,n.seq)
        c2<-rep(0,n.seq)
        tab<-cbind(c1,c2)
        tab<-as.data.frame(tab)
        n1<-1
        for (j in 1:length(seqxfile)){
              n2<-sum(seqxfile[1:j])
              tab$c1[n1:n2]<-rep(label[j],seqxfile[j])
              tab$c2[n1:n2]<-elenco.inizio[[j]]
              n1<-n2+1
              }
        hf<-(tab$c2/3600)
        h<-trunc(hf)
        mf<- (hf-h)*60
        m<-trunc(mf,0)
        sf<-  (mf-m)*60
        s<-trunc(sf,0)
        tab$c3<-tab$c2+dur.seq
        fhf<-(tab$c3/3600)
        fh<-trunc(fhf)
        fmf<- (fhf-fh)*60
        fm<-trunc(fmf,0)
        fsf<-  (fmf-fm)*60
        fs<-trunc(fsf,0)
        tab$h.inizio<-h
        tab$m.inizio<-m
        tab$s.inizio<-s
        tab$h.fine<-fh
        tab$m.fine<-fm
        tab$s.fine<-fs
        tab$st<-paste(h,':',m,':',s)
        tab$fn<-paste(fh,':',fm,':',fs)
        tab<-tab[,c(1,10,11)]
        names(tab)<-c('file','start','end')
        write.table(tab,paste(getwd(),'/',nomefile,'.txt',sep=''),row.name=F
                     ,quote=F, sep='\t')
        return (tab)

         }
```

The arguments to be specified are:

`dat`	a dataset containing the information relative to each video file. The dataset must contain the file name in the first column and the relative duration (expressed as ‘number of hours’, ‘number of minutes’, ‘number of seconds’) in the following columns.
`n.seq`	number of sequences to be extracted (e.g. 12 for the present study)
`dur.seq`	length of a sequence in seconds (e.g. 300 sec = 5 mins)

`m.inizio`	minute of the position on the first file from which the video was analized.
`s.inizio`	second of the position on the first file from which the video was analized.
`nomefile`	specify the name to give to the .txt output file listing the sequences to be analyzed per file. The file will be saved in the working directory that R is using. Use getwd() to visualize it.

Example of use:

```
sampling(data, n.seq= 12, dur.seq= 300, m.inizio=10, s.inizio= 0, 'lav1b')
```

Chapter 6: Regeneration potential of Mediterranean canopy forming algae *Cystoseira barbata* (Stackhouse) C.Agardh.

Abstract

Coastal populations well being relies on services provided by marine ecosystems, such as coastal and shoreline protection, recreational use, carbon and nutrient sequestration and support to both fish and shellfish fisheries. The conservation and rehabilitation of threatened coastal systems is urgent and essential to ensure the continuous supply of their services. Canopies created by fucoid algae originate structurally complex and highly productive systems on temperate coasts. In the Mediterranean Sea, species of *Cystoseira* are the main canopy-forming algae, but they are severely threatened by increasing habitat loss. Here, we explore the regeneration potential of *Cystoseira barbata* by means of *in vitro* propagation and its possible application for restoration on natural and artificial substrata. We assessed regeneration potential of *C. barbata* fragments in relation to different temperature, light irradiance, sterilization protocol and culture medium. We show that *Cystoseira barbata* has the potential for in vitro propagation and we identify the combination of factors that could enhance its growth.

Keywords: algal tissue culture, micropropagation, *Cystoseira barbata*, regeneration, restoration

Introduction

Marine ecosystems sustain coastal populations and their economical development by providing many services such as coastal and shoreline protection, recreational use, carbon and nutrient sequestration and support both fish and shellfish fisheries (Barbier et al. 2011). For example, fisheries and recreation accounted for more than half of the United States ocean sector GDP in 2004 (Kildow et al. 2009). Coastal wetlands buffer storm surges and stabilize shorelines (Wamsley et al. 2009, Gedan et al. 2010, Shepard et al. 2011, Zhang et al. 2012) seagrasses actively sequestrate carbon dioxide and buffer ocean acidification (Fourqurean et al. 2012, Unsworth et al. 2012). The relationship between degradation of ecosystems created by habitat-forming species and decline of fishery dramatically emerged in different systems such as kelp forests and coral reefs (Hughes et al. 2005, Jackson 2008). Thus, the conservation and rehabilitation of threatened systems is needed to ensure the continuous supply of their services.

Efforts of conservation scientists provide valuable theoretical and practical knowledge of the ecological factors promoting ecosystem resilience, management strategies and restoration attempts to foster recovery of natural resources and reverse negative trends (Hughes et al. 2005, Lotze et al. 2011). In particular, active restoration techniques have been developed and their feasibility proven in different systems. For example, there has been attempts to restore environmental parameters (i.e. elevation and tidal regime) in degraded wetlands to an optimal value (Zedler and Kercher 2005). Artificial reefs have been used with various success for algal restoration (Terawaki et al. 2003, Falace et al. 2006, Park and Lee). While coral recruitment has been promoted by stabilizing hard substrata (Fox et al. 2005). Manual transplantation of either adult or juvenile individuals of the focal species is increasingly common (Zedler and Kercher 2005, Edwards 2010). However, sourcing transplant material from natural stocks could cause collateral damages to otherwise healthy populations. To avoid unintended negative impacts on donor populations, a positive example of good practice comes from coral reef restoration where more often transplanted colonies are being reared in coral nurseries, taking advantages of the corals asexual reproduction potential (Edwards 2010).

In the Mediterranean Sea, the brown macroalgae of the genus *Cystoseira* C. Agardh (Fucales) are a major habitat-forming species in the shallow subtidal rocky reefs (Giaccone 1973, Ballesteros 1992) creating dense canopies. Similarly to kelp forests (Steneck et al. 2002), *Cystoseira* is a habitat “engineer” on temperate reefs, as its canopies modify local environmental conditions and provide habitats and refugia to a wide range of benthic and nektonic species (Bulleri et al. 2002, Maggi et al. 2009, Maggi et al. 2012, Sales and Ballesteros 2012, Sales et al. 2012). Species of *Cystoseira* have suffered widespread habitat loss, and today six species are listed as threatened in the Bern Convention and in the Mediterranean Action Plan (UNEP/MAP 2005). To achieve restoration and conservation of these macroalgae some transplantation techniques have been tested (Falace et al. 2006, Susini et al. 2007). However, these mainly rely on sourcing for adult thalli in natural systems, thus potentially damaging donor populations. Recently, the feasibility of transplanting juvenile thalli in both natural and artificial habitats has been demonstrated (Perkol-Finkel and Airoldi 2010, and chapter 3 of this thesis, hereafter ‘Perkol-Finkel et al. 2012'). In that case juveniles were sourced from unstable boulders and cobbles or were intercepted by using artificial tiles which reduced the impacts on source populations (Perkol-Finkel et al. 2012). Still this technique required relevant efforts, and also relies on natural recruitment potential which can be very variable.

Techniques for culture in the laboratory have been developed for many types of algae, and commonly used in aquaculture. In contrast, techniques for supplementary seeding of early stages in the field are poorly developed and they are currently not developed for species of *Cystoseira* or other canopy forming algae in the Mediterranean sea. Further their application to experimental work in the field or restoration efforts is limited. Here we explore the regeneration potential of *Cystoseira barbata* by means of *in vitro* propagation and its possible application for the creation and maintenance of algal stocks. We also explored which combinations of factors can enhance the development of this species. The settlement of *Cystoseira barbata* germlings can be affected by light and temperatures (Irving et al. 2009). Additionally, the performance of cell calluses of different macroalgae from axenic tissues (i.e. non-contaminated by other living organisms) exposed can be inhibited by excess irradiance (Polnefuller and Gibor 1987, West and Andersen 2005). Therefore we specifically tested whether the regeneration of algal structures (i.e. lateral branches) from fragmented macroalgal thalli was affected by variations in light irradiance, temperature or an interaction of the two.

Axenic culture conditions are a requisite for seaweed tissue culture, similar to clonal propagation in superior plants. These can be obtained by means of both mechanical removal of visible epiphytes and chemical sterilization (Baweja et al. 2009). The actual composition of the culture media used is less critical than their physical state in determining the tissue culture outcomes: solid culture media favor the induction of disorganized calluses, whereas liquid media foster regeneration of the explants, i.e. new thallus growth (Baweja et al. 2009). To our knowledge, this is the first attempt to apply clonal propagation techniques to the species *C. barbata,* thus we could not find an already optimized culture protocol in the literature. We therefore tested, 2) how the regeneration outcomes were affected by testing three alternative sterilization procedures and two alternative liquid culture media.

Methods

Algal collection, explants and preparation of the experimental replicates

Twenty adult thalli of *Cystoseira barbata* were collected by SCUBA diving in November 2010 at the natural site “La vela” along the Monte Conero promontory (43° 33′ N, 13° 37′ E) in the Adriatic Sea. In this period, seawater temperature was 14°C and algal individuals had not completely lost their fronds. In the lab, we excised lateral branches and cleaned each single thallus by carefully removing detritus, mussels and other visible epiphytes using soft brushes, sterile gauzes and lancets. After a resting period of 12h in aerated seawater in a cold temperature room held at 4°C, thalli were transversally cut into 1.5 cm long fragments (hereafter 'explants'). All the explants (N=192) were placed in one single container filled with sterilized seawater (SSW) for 1 hour . This allowed us to haphazardly assign explants to different treatments avoiding pseudo-replication. All water used from this step to the end of the experiment (e.g. for preparing solutions, agar gels and culture media) was natural seawater filtered on fiber glass filter (1.2 μm) and autoclaved for 20 minutes at 120°C. Explants were haphazardly divided in three groups (N=64) and assigned to one of the three sterilization protocols: EtOH [1 minute in ethyl alcohol 70%, based on (Gusev et al. 1987)], PC (20 minutes in a 0.1% ProClin® 200 preservative, Sigma-Aldrich) and RR (Repeated Rinsing: 10 repeats of one rinse of 60 minutes in 250 ml glass flasks filled with 200 ml SSW on a magnetic shaker). Explants were treated under laminar airflow chamber. At the end of each procedure, explants were rinsed twice with SSW (1 min) and left undisturbed for 1 hour in a glass flask with SSW under laminar airflow chamber. Two liquid culture media were prepared: sterilized natural seawater (hereafter 'seawater') and Von Stosch (Grund) medium, commonly used for macroalgae (Harrison and Berges 2005). Von Stosch (Grund) medium falls into the category of 'natural seawater media' for macroalgae and consists ofseawater enriched with minerals and vitamins (Harrison and Berges 2005), see Table S1 and S2 for the recipe. One sterilized explant and one of the two culture media were then added in sterile test tubes (25ml) into which a 5 ml agar gel which provided a solid substratum, into which to place the explant. Test tubes were closed with a screw cap and considered experimental replicates.

Experimental design and data analysis

We tested the effects of light, temperature, sterilization protocol and culture medium on 1) regeneration of structures from fragmented thalli of *C. barbata* and 2) culture sterility by exposing explants to two levels of irradiance, 10-20 µmol $m^{-2}s^{-1}$ ('low') and 70-80 µmol $m^{-2}s^{-1}$ ('high'), in two controlled temperature rooms at 18°C and 25°C, respectively. For each combination of temperature and light, two replicate plots were set up, each one carrying 4 replicates for each combination of sterilization protocol and culture medium (i.e. 2 temperature [Te, fixed] × 2 lights [Li, fixed] × 2 plots [Pl, random and nested in Te×Li] × 3 sterilization protocol [St, fixed] × 2 culture media[Me, fixed] × 4 replicates). We randomly allocated plots at the same heights from the ground on shelves in each room and within plots we randomized replicates and distributed them evenly in the plot to avoid shading. Light was provided by three neon lamps (21Watt each) above the plots conveniently screened with a plastic net (1mm mesh) to modulate the intensity. The irradiance at the replicates level was measured with a Li-Cor LI-192 quantum sensor. We imposed a 12:12 h light:dark cycle and excluded possible external light sources using black plastic foils to screen the shelves. Before starting the experiment, the setup was tested for few days to ensure that possible limited air circulation due to plastic foils screens and neon lamp heat did not cause an increase in the temperature. The experiment lasted for four weeks and the culture media were replaced once after 2 weeks.

Statistical analysis

We assessed, if regeneration occurred in each replicate explant, comparing photos taken at the beginning and at the end of the experiment and recorded the number of newly formed lateral branches per explant, if any. We tested the effects of experimental factors on regeneration by means of ANOVA and SNK post-hoc test using the package ‘GAD’ with R 2.15.0 software (Team 2012). Because ‘Plots’ effect was not significant under the full model ($F_{df\ 4,144}$= 0.34, P>0.05), we ran the analysis under a reduced model thus increasing the statistical power. Given the large sample size, we decided not to transform data as, under these circumstances, the F test is not influenced by the violation of the homogeneity of the variance (Underwood 1997). Additionally, we visually evaluated if culture sterility was maintained through the experiment by checking for presence/absence of sterility (e.g. transparency/opacity of the medium). We tested the effects of factors on culture sterility by applying a permutational ANOVA, with 9999 permutations on a similarity matrix, based on the simple matching method in PERMANOVA+ for PRIMER 6.0 software (Clarke and Gorley 2006).

Results and Discussion

Regeneration from fragmented thalli of *C. barbata*

The highest regeneration of explants occurred when they were sterilized using the repeated rinsing protocol, cultured at 25°C in seawater and at the high radiance (70-80 µmol $m^{-2}s^{-1}$). Under these conditions, we observed 3.4 ± 2.9 (mean ± SE) lateral branches per explant.

We found that regeneration was affected by interactions of multiple experimental factors (Tab. 1). In particular, there was a significant effect of the interaction between light, temperature and culture medium ($F_{df\ 1,168}$= 6,76; $P<0.05$). At 18°C, the light level did not significantly affect regeneration, whereas seawater performed better than Von Stosch (Grund) medium (Fig. 1). On the contrary, at 25°C, high irradiance determined the greatest regeneration in seawater while it was completely inhibited in Von Stosch (Grund) treatments. Low irradiance impaired the generation of lateral branches with both media. The three sterilization protocols differently affected the tissue regrowth depending on the culture medium used (Medium × Sterilization protocol, Fig. 2, Table 1). The regeneration of structures was equally poor for explants cultured in Von Stosch (Grund) medium independently from the sterilization protocol used. Conversely, regeneration increased in seawater with no significant differences between repeated rinsing protocol and the commercial ProClin® preservative. These two sterilization protocols were clearly different from ethylic alcohol that led to nearly no growth (Fig. 2). Similarly, little growth occurred, when the explants were exposed to low irradiance, independent of the sterilization procedure (Light × Sterilization protocol, Fig. 3, Table 1). However, at high irradiance, significantly different results were found amongst the three sterilization techniques. At high light intensity, the highest number of lateral structures was found in explants exposed to the repeated rinsing technique, followed by sterilization with ProClin®, and the lowest regrowth occurring in explants sterilized with ethylic alcohol. The use of ProClin® led to similar regrowth performance, irrespectively of light intensity (Fig. 3).

Table 1 Effect of abiotic and procedural factors on algal regeneration from fragmented adult thalli of *Cystoseira barbata*. Response variable: number of regenerated structures per explant. Factors are: Temperature, Te; Lights, Li; Sterilization protocol, St; Culture medium, Me. Data were analyzed by ANOVA. We used package 'GAD' with R software (Team 2012). Significant Responses are in bold.

Source	df	MS	*F*	P
Temperature	1	0.3333	0.22	0.6371
Light	1	8.3333	5.58	**0.0193**
Sterilization	2	11.1927	7.50	**0.0008**
Medium	1	27.0000	18.09	**0.0000**
Te × Li	1	6.7500	4.52	**0.0349**
Te × St	2	0.6927	0.46	0.6295
Te × Me	1	0.3333	0.22	0.6371
Li × St	2	5.5365	3.71	**0.0265**
Li × Me	1	6.7500	4.52	**0.0349**
St × Me	2	6.3906	4.28	**0.0154**
Te × Li × St	2	2.0156	1.35	0.2619
Te × Li × Me	1	10.0833	6.76	**0.0102**
Te × St × Me	2	1.2865	0.86	0.4242
Li × St × Me	2	3.4844	2.33	0.1000
Te × Li × St × Me	2	3.1927	2.14	0.1210
Res	168	1.4926		

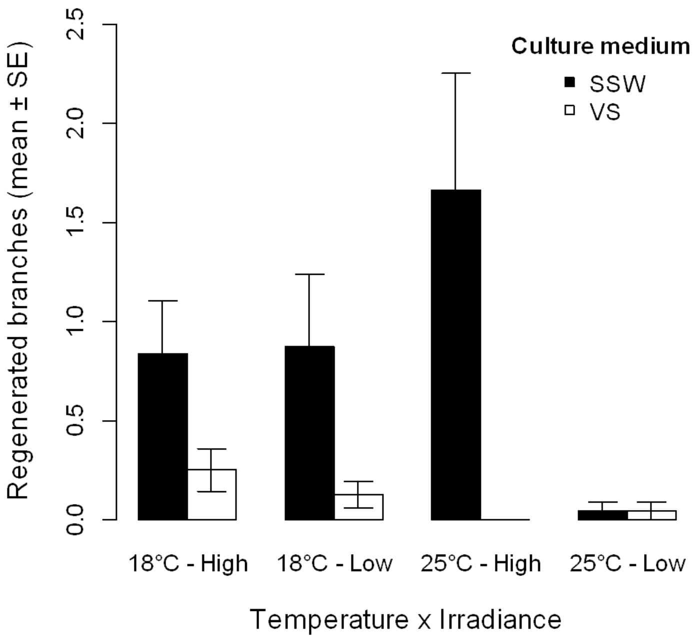

Figure1 Effects of temperature, light irradiance and culture media on regeneration of structures from fragmented thalli of *Cystoseira barbata*. Combinations of experimental levels of temperature (18°C *vs* 25 °C) and irradiance (High *vs* Low) are shown on the x-axis; culture media are sterilized seawater [SSW , black] and Von Stosch (Grund) [VS, white]; N=24. Mean number of regenerated lateral branches per explant is reported on the y-axis (mean ± Standard error).

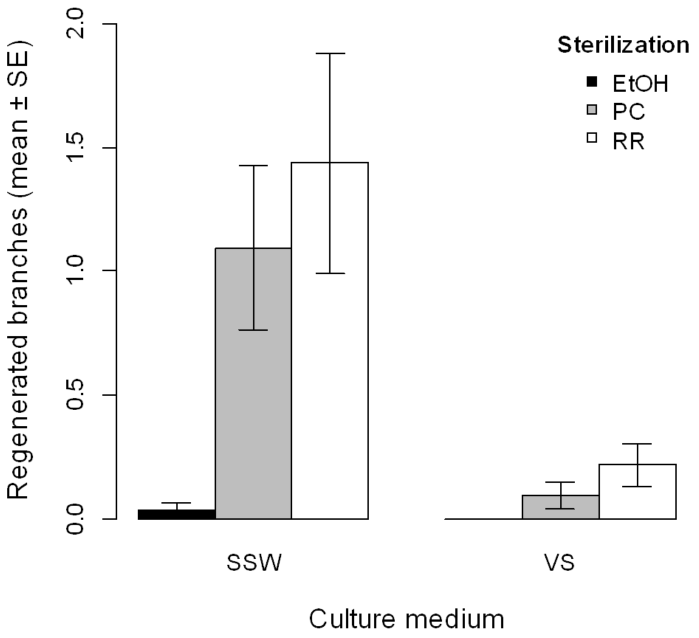

Figure 2 Effects of culture medium and sterilization protocol on regeneration of structures from fragmented thalli of *Cystoseira barbata*. Sterilization protocol: ethylic alcohol (EtOH, black), ProClin® preservative (PC, grey) and repeated rinsing in sterile seawater (RR, white); culture media are sterilized seawater [SSW] and Von Stosch (Grund) [VS]; N=32. Mean number of regenerated lateral branches per explant is reported on the y-axis (mean ± Standard error).

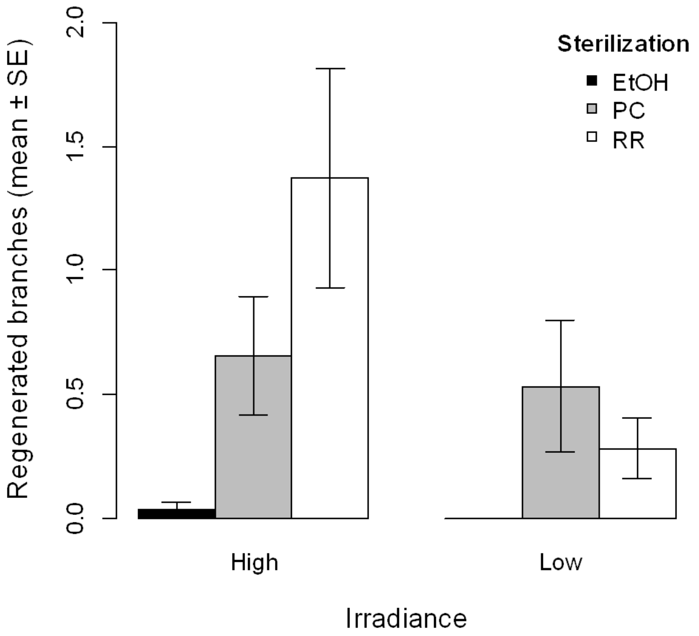

Figure 3 Effects of Light and sterilization protocol on regeneration of structures from fragmented thalli of *Cystoseira barbata*. Sterilization protocol: ethylic alcohol (EtOH, black), ProClin® preservative (PC, grey) and repeated rinsing in sterile seawater (RR, white); N=32. Mean number of regenerated lateral branches per explant is reported on the y-axis (mean ± Standard error).

Axenic culture condition achievement

Culture medium, temperature, and sterilization protocol were the factors that displayed he highest effect on the sterility of replicate cultures (Table 2). The effect of both temperature and sterilization protocol were highly dependent on the culture medium used. The proportion of axenic cultures was significantly higher at 18°C than at 25°C when using seawater as medium (0.52 ± 0.15 mean proportion of sterile culture ± SE at 18°C, Fig. 4). Whenever using Von Stosch (Grund) medium, sterility only occurred in 10% of replicates. When associated with this medium, the use of ethylic alcohol was the only effective sterilization protocol, resulting statistically different from both protocol using ProClin® and repeated rinsing in sterilized seawater (Fig. 5). Indeed, the latter two sterilization methods failed to preserve sterility, showing poor to nil effectiveness, when explant were cultured in Von Stosch (Grund) medium. Conversely, the use of seawater allowed achieving sterility in a higher proportion of cultures. Importantly, whichever was the sterilization techniques used, we obtained similar proportion of sterile cultures (Fig. 5).

Table 2 Effect of abiotic and procedural factors on cultures sterility. Factors are: Temperature, Te; Lights, Li; Sterilization protocol, St; Culture medium, Me. Response variable: presenc/absence of sterility in replicate cultures. Data were analyzed by permutational ANOVA with 9999 permutations on a similarity matrix, based on the simple matching method. We used the statistical package PERMANOVA+ for PRIMER 6.0 software. Significant responses are in bold.

Source	df	MS	Pseudo-F	P
Temperature	1	15052	11.177	**0.0010**
Light	1	52	0.039	0.8514
Sterilization	2	5365	3.983	**0.0206**
Medium	1	18802	13.961	**0.0004**
Te × Li	1	1302	0.967	0.3319
Te × St	2	990	0.735	0.4833
Te × Me	1	22969	17.055	**0.0001**
Li × St	2	2240	1.663	0.1896
Li × Me	1	469	0.348	0.5491
St × Me	2	6927	5.144	**0.0064**
Te × Li × St	2	990	0.735	0.481
Te × Li × Me	1	1302	0.967	0.3183
Te × St × Me	2	1094	0.812	0.4508
Li × St × Me	2	2969	2.204	0.1133
Te × Li × St × Me	2	3177	2.359	0.0933
Res	168	1347		

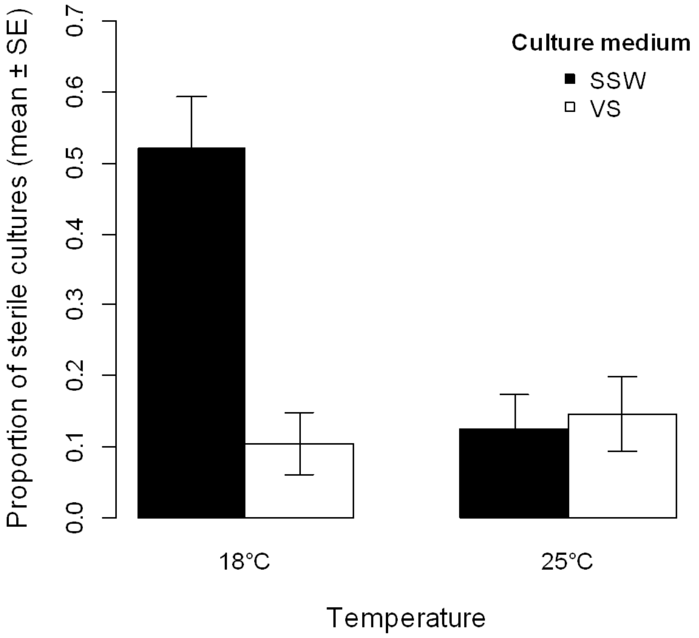

Figure 4 Effects of temperature and culture medium on culture sterility. Temperature (18°C vs 25 °C) is shown on the x-axis; culture media are sterilized seawater [SSW, black] and Von Stosch (Grund) [VS, white]; N=48. Mean proportion of cultures remaining sterile is reported on the y-axis (mean ± Standard error).

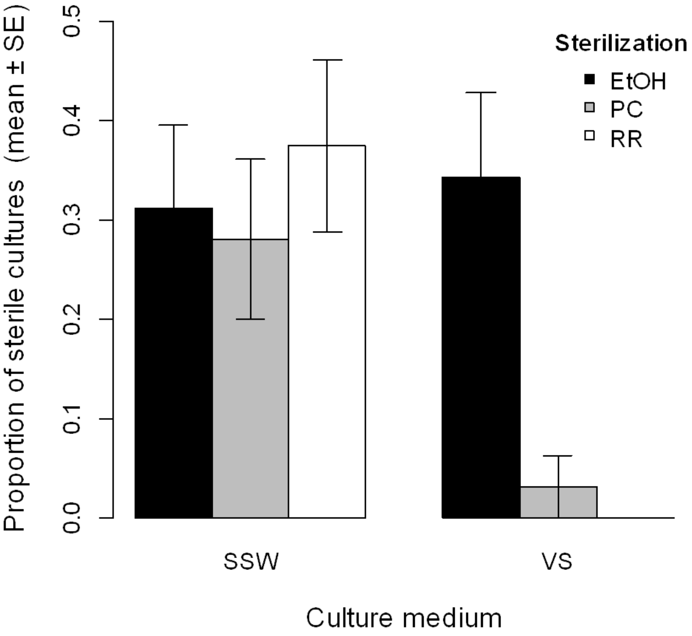

Figure 5 Effects culture medium and sterilization protocol on culture sterility. Sterilization protocol: ethylic alcohol (EtOH, black), ProClin® preservative (PC, grey) and repeated rinsing in sterile seawater (RR, white); culture media are sterilized seawater [SSW] and Von Stosch (Grund) [VS]; N=32. Mean proportion of sterile cultures is reported on the y-axis (mean ± Standard error).

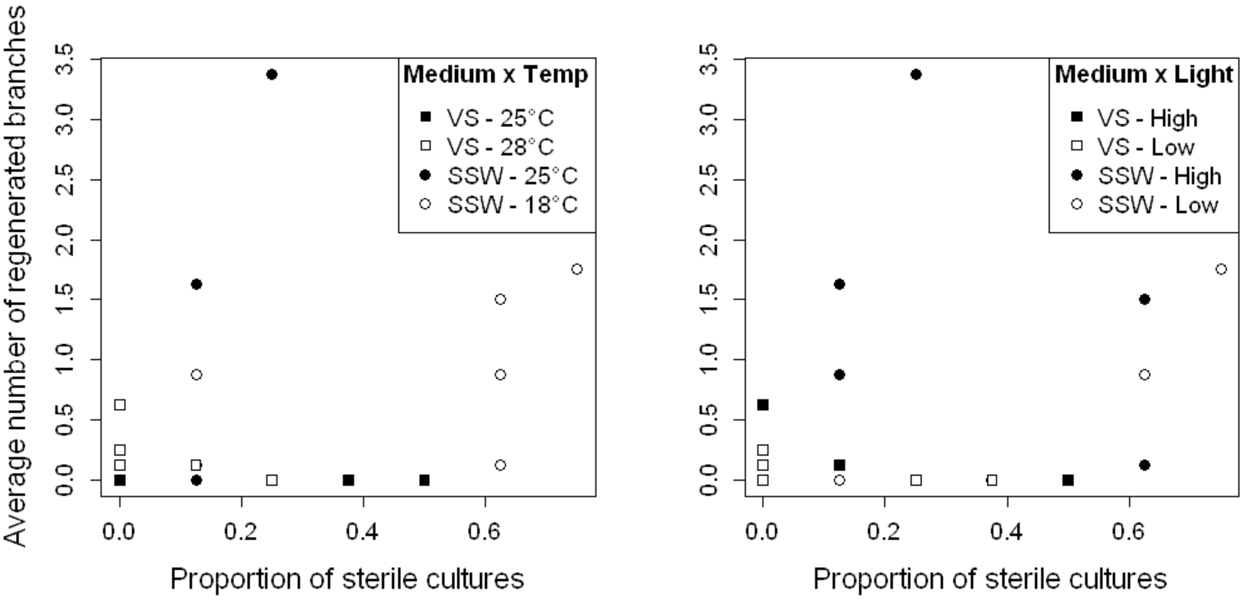

Figure 6 Relationship between regeneration and sterility. Symbols highlight combinations of culture medium with temperature (right panel, black=25°C, white= 18°C) and irradiance (left panel, black=High, white= Low). Squares indicate Von Stosch (Grund) [VS] medium, circle sterilized seawater [SSW].

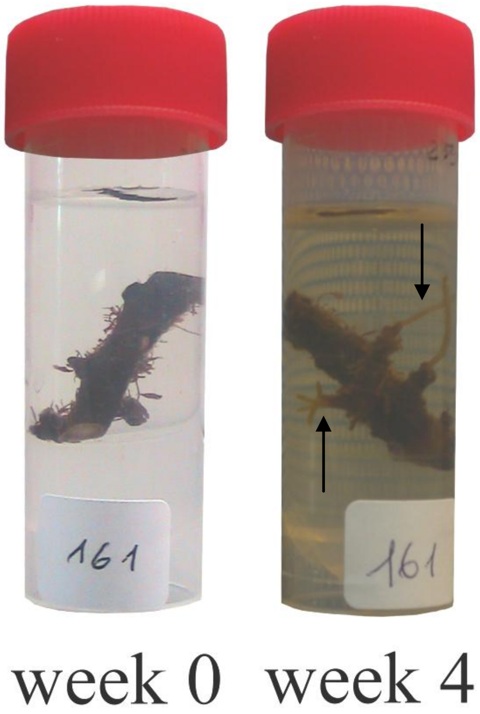

Figure 7 Regeneration potential of *Cystoseira barbata* from fragments of adult thalli. Here a fragment is shown at the beginning of the experiment and at the end, after 4 weeks. Black arrows indicate newly generated lateral branches.

Concluding remarks

Cystoseria barbata has the potential to generate new structures from fragmented thalli when cultured *in vitro*. The regrowth of lateral branches was promoted by a combination of high temperature and high irradiance levels. Previous studies showed that maximum net photosynthesis in *C. barbata* occurs at temperatures ranging from 20°C to 30°C and that a broad spectrum of light irradiance can be used by this algae (Baghdadli et al. 1990). Moreover, stronger intensities of light facilitated the growth of germlings (Irving et al. 2009). Therefore, the metabolism of explants could have increased at the higher temperature. At 25°C augmented demand of energy for regeneration could have made light a limiting factor, whereas energy supply was possibly enough at 18°C (just out of the optimal temperature range for *Cystoseira*). Moreover, higher temperature values could have also favored the development of microorganisms (White et al. 1991) thus compromising the sterility of the cultures that is a fundamental requisite for healthy algal growth (Baweja et al. 2009). However, the high irradiance values could have limited the production of contaminants by affecting either their viability or their detrimental effect (e.g. inhibiting secondary metabolites), influencing the relevant regeneration observed under high temperature and irradiance (Fig. 1) (Hernandez et al. 2007, Ruiz-Gonzalez et al. 2012).

Both, the culture medium and the sterilization protocol influenced sterility and consequently regrowth of algal structures. As Von Stosch (Grund) is rich in minerals and vitamins, the poor performance of this medium compared to that of simple seawater is likely due to the positive effect of its composition in promoting contaminants (Fig. 6). The use of ethylic alcohol was the most effective protocol among those tested, being the only one showing similar results independently of the medium used. However it also led to a significant reduction in regeneration, thus likely implying severe damage to the explants tissues. The combined use of the repeated rinsing sterilization protocol and sterilized seawater represented the optimal tradeoff between meeting sterility requirements and promoting the expression of *C. barbata* regeneration potential.

Overall we identified, a successful protocol for the regeneration in 4 weeks of new algal structures (i.e. lateral branches) from fragments of adult thalli (Fig.7). Further studies could help understanding the role of both, abiotic and procedural factors affecting the regeneration potential of *Cystoreira barbata*. These could help developing new conservation options and improve existing transplantations techniques by, for example, providing enough material to support large field experiments. Being able to create and maintain a stock of algal individuals could result in more cost-effective restoration projects and a lower detrimental impact on natural donor populations. In the present study, 192 explants were prepared from only 10 adult thalli, therefore indicating that with only minimal collection in the field, potentially large quantities of *C. barbata* may be regrown, once culture methods are established

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Supporting Information

Table S1 Composition of Von Stosch (Grund) medium (Harrison and Berges 2005).

	Stock solution (g/l of water)	Volume (ml)	Final concentration in culture media (M)
$Na_2\beta$glicerophosphate	5.36	10	2.48×10^{-4}
$NaNO_3$	42.52	10	5.00×10^{-3}
$FeSO_4 \cdot 7H_2O$	0.28	10	1.00×10^{-5}
$MnCl_2 \cdot 4H_2O$	1.96	10	1.00×10^{-4}
Na_2 EDTA$\cdot 2H_2O$	3.72	10	1.00×10^{-4}
Vitamins stock solution	Table S2	10	

Table S2 Composition of vitamin stock solution for Von Stosch (Grund) medium (Harrison and Berges 2005).

	1° Stock solution (g/l of water)	Quantity	Final concentration in culture media (M)
$Na_2\beta$-glicerophosphate	-	200 mg	5.93×10^{-6}
$NaNO_3$	0.1	10 ml	4.09×10^{-9}
$FeSO_4 \cdot 7H_2O$	0.2	10 ml	1.48×10^{-9}

Chapter 7: General conclusion

Globally, coastal areas are home to nearly two thirds of the world’s population (Creel 2003) and sustain the socio-economic development of their nations. The defense of the coasts is a pressing problem, as projected scenarios of increasing storminess and sea level rise (Lin et al. 2012, Stouffer 2012) will exacerbate coastal flooding and erosion (Knogge et al. 2004, Nicholls 2011). Policy makers and environmental managers have to act urgently and proactively to reduce the exposure of population to coastal hazard risks. This thesis has analyzed two ecological-based approaches to coastal defense: 1) the important role of coastal ecosystems in providing relevant services for coastal hazard risk reduction, which could be incorporated into adaptive coastal management; and 2) the possibility to enhance the ecological value of marine artificial structures (including coastal defence structures) as habitats for marine communities. It also highlighted some important factors controlling the ecological functioning of artificial structures and their contribution to the maintenance of biodiversity and flow of ecosystem services in coastal areas.

The first part of the thesis provided quantitative evidence, based on meta-analysis, of the wave attenuation service provided by coral reefs at a global scale. The results presented in chapter 2 clearly showed that reef systems provide substantial protection against natural hazards by effectively reducing both wave energy and wave height. Spatial analyses highlighted that almost 200 million people inhabiting at-risk areas potentially benefit of coral reef wave attenuation service. Results indicate that coral reefs can provide wave attenuation comparable to hard artificial defenses such as breakwaters. Moreover costs associated with coral reef protection and restoration are sensibly lower than those required to build and maintain gray infrastructure. The restoration and conservation of coral reefs thus should be considered an ecologically sustainable coastal defense strategy, alternative to investing solely in artificial structures. Indeed, numerous other benefits, including food security and livelihoods, will be provided. Other coastal systems, such as salt marshes and mangroves (Gedan et al. 2010), have already been shown to offer coastal protection. Therefore this study strengthens reliability of ecosystems as a key element of coastal hazard risk reduction by adding more evidence from the globally important coral reef ecosystem.

Where original natural ecosystems have been irreparably lost, where no trade-offs can be accepted, traditional coastal armoring may still represent the only viable option (Anthoff et al. 2010). Nowadays breakwaters, seawalls, groynes, jetties, dykes and other marine infrastructures, such as offshore installation, are abundant in marine coastal seascapes, and these structures are predicted to increase (Dugan et al. 2011). Although significant economical and even ecological benefits are often attributed to the construction of these artificial habitats, there are open questions about the ecological performance and value of marine infrastructures as habitat for marine fauna and flora. The second part of this thesis focused on assessing the ecological value of artificial substrata for marine epibenthos in comparison with natural substrata, and understanding the different ecological functioning of the two systems. In chapters 3 and 4 I documented the suitability of coastal artificial structures compared to natural rocky reefs to support native, ecologically relevant, habitat-forming canopy algae, and through experiments clarified the potential underlying drivers. I also evaluated the feasibility of enhancing the ecological value of artificial structures for coastal defense by promoting the growth of desired species, such as threatened, canopy-forming algae of the genus *Cystoseira*, which are amongst the most ecologically valuable, habitat forming species in Mediterranean rocky habitats.

Results showed that artificial structure do not function as rocky reefs, and their value as habitat for native habitat-forming species (such as canopy algae) can be very variable depending on local environmental and biological factors. Juveniles of *Cystoseira barbata* could be successfully transplanted at both natural and artificial habitats. Survival was not affected either by lack of surrounding adult algal individuals or by substratum orientation. *C. barbata* was also equally successful on substrata of different materials (e.g. cement, clay and limestone). This implies that, once reproductive individuals have grown on artificial structures, *C. barbata* recruits could potentially settle on breakwaters favoring the establishment of viable populations. However, transplantation success was consistently limited at artificial structures by biotic disturbance from a variety of small and large macrograzers. In chapter 5, RUV observation clearly indicated that these species, comprising both fishes and crabs of different sizes, were interacting (both via "consumptive" and "non-consumptive" interactions) with *Cystoseira* much more actively at the artificial habitats than at natural rocky reefs, effectively limiting the growth of a canopy. In chapter 6 I finally explored the regeneration potential of *Cystoseira barbata* fragments in relation to different temperature, light irradiance, sterilization protocol and culture medium. By using *in vitro* propagation techniques I showed that *Cystoseira barbata* has the potential for in vitro propagation with possible relevant application for restoration on both natural and artificial substrata.

Future work should explore the reasons behind the different ecological functioning of artificial and natural habitats and possibly unravel the factors and mechanisms that cause it. Indeed, the comprehension of the functioning of systems associated with artificial habitats is the key to allow environmental managers to identify proper mitigation options and to forecast the impact of alternative coastal development plans.

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Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures

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Summary

1. With nearly two-thirds of the human population concentrated along coastlines, coastal development and urbanized seascapes are inevitable. Proliferation of coastal and marine infrastructures, such as breakwaters, ports, seawalls and offshore installations, is associated with loss of natural habitats. This calls for new strategies aimed at elevating the ecological and biological value of coastal infrastructures, while minimizing their ecological footprint.

2. We explored the feasibility of using coastal defence structures as a scaffold for the conservation of threatened marine species. We experimented with fucoids, canopy-forming algae on Mediterranean coasts, in the light of their declared conservation priority. We transplanted juveniles of *Cystoseira barbata* to a number of breakwaters and natural sites along the Adriatic Sea (Italy) and tested which factors could facilitate or inhibit its successful establishment.

3. Survival of transplanted *C. barbata* was greater at most artificial and natural sites examined compared to the native sites where severe habitat loss was ongoing. Survival was greater at landward compared to seaward positions on the infrastructure, while no relevant effects of substratum characteristics (horizontal vs. vertical orientation, variable composition and increasing complexity) were observed. Lack of surrounding adult fronds did not impair the survival or growth of the transplants, suggesting a high transplantation potential also on novel infrastructures.

4. Success of transplantation in areas remote from the source population was limited by biotic disturbance, which was more intense on coastal infrastructures in sedimentary environments compared to natural rocky sites.

5. *Synthesis and applications*. Coastal and marine infrastructures can be harnessed to enhance desired species (such as threatened canopy-forming algae). A comprehensive understanding of the ecological functioning of these urban seascapes compared to natural habitats is required to minimize detrimental impacts, or potentially increase the ecological value, of coastal structures and efficiently incorporate such strategies into management and conservation actions. We investigated the influence of habitat type (including natural and artificial), surface complexity, herbivore exclusion, proximity to established populations and orientation on the transplantation success of threatened algae.

Key-words: canopy-forming algae, coastal infrastructures, conservation, *Cystoseira*, enhancement, management, transplantation, urban seascapes

Introduction

With nearly two-thirds of the world's population concentrated in coastal areas (Creel 2003), substantial coastal development is inevitable. The land–sea interface is exploited for various human uses including industry, transportation, energy and recreation (Airoldi & Beck 2007). These forms of coastal development are frequently associated with fragmentation and loss of natural habitats, damaged seascapes and reduced biodiversity (Airoldi & Beck 2007; Crain *et al.* 2009; Dugan *et al.* 2011).

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It is known that coastal infrastructures do not function as surrogates to natural habitats (Bulleri & Chapman 2004; Jackson, Chapman & Underwood 2008). Their vertical profile compresses the intertidal zones, and their homogenous surfaces combined with high frequency of disturbances tend to favour impoverished assemblages dominated by opportunistic and invasive species (Bulleri & Airoldi 2005; Chapman *et al.* 2009; Airoldi & Bulleri 2011).

As coastal infrastructures are expected to proliferate alongside with human population (UN 2008), efforts should be made not only to minimize their detrimental impacts, but also to elevate their possible ecological value. This requires understanding of the types of assemblages or ecosystem functions that are desirable and feasible in these habitats. Initial steps in this direction have been made in highly urbanized areas in both temperate (Airoldi *et al.* 2005b; Chapman & Blockley 2009; Browne & Chapman 2011) and tropical environments (Perkol-Finkel *et al.* 2006, 2008). Nonetheless, the notion of combining ecological principles to urban infrastructure is rather new (Mitsch 1996; Bergen, Bolton & Fridley 2001) and to date has been scarcely applied in marine environments.

We examined the feasibility of facilitating the growth of threatened fucoid macroalgae of the genus *Cystoseira* on coastal defence structures. Fucoids and kelps form diverse, structurally complex and highly productive canopy habitats along many temperate rocky coasts (Steneck *et al.* 2002). Canopies are suffering widespread habitat loss at global scales (Airoldi & Beck 2007; Connell *et al.* 2008; Mangialajo, Chiantore & Cattaneo-Vietti 2008). Decline in the Mediterranean Sea is well documented, and today six Mediterranean species of *Cystoseira* are listed as threatened in the Bern Convention and in the Mediterranean Action Plan. In the Mediterranean, the proximate cause for loss of *Cystoseira* is anthropogenic disturbance, largely in the form of urbanization (Benedetti-Cecchi *et al.* 2001). Recent experiments have shown the potential for recovery of canopy-forming macroalgae through various approaches, including transplanting or seeding macroalgae back to their original habitat (Correa *et al.* 2006; Susini *et al.* 2007; Perkol-Finkel & Airoldi 2010), and the use of artificial reef for algal restoration is increasing (Terawaki *et al.* 2003; Falace, Zanelli & Bressan 2006; Park & Lee 2010). Here, we explored the alternative possibility of using coastal infrastructures as gardens for these important habitat-formers, and deploying them for other societal needs. This approach would enhance the ecological value of these infrastructures, without compromising their original function.

Relatively, few studies have attempted to transplant canopy-forming macroalgae onto artificial substrata (Terawaki *et al.* 2003; Jonsson *et al.* 2006), and little is known about the factors enhancing the success of these interventions. We transplanted juveniles of *Cystoseira barbata* Stackhouse C. Agardh onto a number of breakwaters and natural sites along the Italian North Adriatic Sea (Italy). Marine infrastructures offer atypical substrates for benthic assemblages in terms of orientation, exposure, structure and surface texture (Vaselli, Bulleri & Benedetti-Cecchi 2008; Burt *et al.* 2009; Bulleri & Chapman 2010), all of which are known to affect the recruitment, survival and growth of fucoids and other macroalgae (Harlin & Lindbergh 1977; Wells, Moll & Bolton 1989; Airoldi 2001; Jonsson *et al.* 2006). We tested whether the survival and growth of transplants differed between natural and artificial habitats, horizontal vs. vertical substrata, between landward vs. seaward sides of the breakwaters, or among substrata of different composition and increasing surface complexity. We also analysed whether lack of naturally occurring surrounding adult canopies on such infrastructures, which normally facilitate natural recruitment of canopies (Connell 2005; Irving & Connell 2006), limits successful transplantation. Finally, we used caging experiments to test the possible role of grazing pressure on success of transplantation, as this factor has been previously described as limiting for growth of macroalgae on coastal defence structures (Jonsson *et al.* 2006) and because pilot tests suggested the importance of this factor in our study system.

Materials and methods

STUDY AREA AND SPECIES

The study was conducted at the Monte Conero promontory (43° 33′N, 13° 37′E) and the surrounding urbanized sandy coastline of the North Italian Adriatic Sea (Fig. 1). The rocky promontory hosts some of the last-remaining scattered populations of the threatened genus *Cystoseira* along the central-northern Italian Adriatic coast (Perkol-Finkel & Airoldi 2010). The fragmented state of these populations probably results from a synergistic effect of low substratum stability and competition with opportunistic species (Perkol-Finkel & Airoldi 2010). We sourced *Cystoseira* from two sites 'Due Sorelle' and 'La Vela'. The algal assemblages at these sites were composed mainly of the species *Cystoseira barbata* C. Agardh (Fucales: Sargassaceae) that was found in varying densities from *c.* 2 to 5 m depth. A detailed description of the study area, the biology of the species and historical changes in the distributions of macroalgal canopies can be found in Perkol-Finkel & Airoldi (2010).

Other rocky habitats in the area exist only in the form of detached breakwaters, two of which, at the localities named Urbani and Numana (Fig. 1), were used for the experiments. According to preliminary surveys, the natural bedrocks surrounding these breakwaters had a very sporadic appearance of naturally recruited *C. barbata.* We also transplanted juveniles onto breakwaters at the localities of Marotta, Lido Adriano and Punta Marina (*c.* 50, 140 and 150 km north of Monte Conero), where no *Cystoseira* naturally occurs.

TRANSPLANTATION EXPERIMENTS

We transplanted juveniles (2–3 months old, 5 cm high) of *C. barbata* collected from loose boulders at Due Sorelle and La Vela in

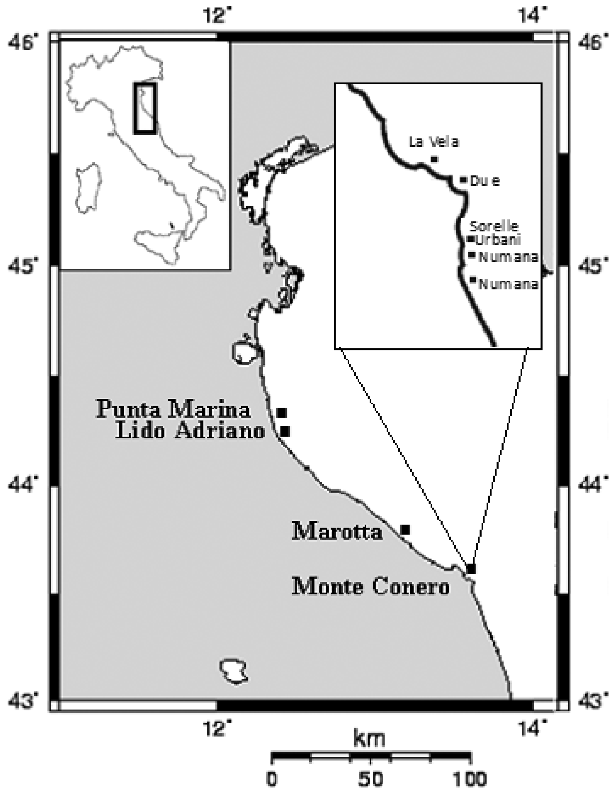

Fig. 1. Map of the study sites along the north Adriatic Sea, and insert map of locations at the Monte Conero promontory.

June 2008. Previous studies showed that recruits in these habitats have low survival probability because of severe substratum instability (Perkol-Finkel & Airoldi 2010). The boulders were broken into small fragments holding 1–2 individuals that were transplanted onto the substrate into the new habitats using epoxy putty (Subcoat S. Veneziani) to form experimental plots comprising five transplanted individuals.

Such plots were transplanted in four habitat types (hereafter 'Habitats'). These included (i) 'Native habitat', that is, the loose boulder fields where the few juveniles naturally occurring in the area are found and from which they were initially collected, and three additional habitats (hereafter 'Other Habitats') where natural recruitment of juveniles was not observed, including (ii) Natural bedrock habitat (i.e. stable bedrocks represented by boulders >10m^3 in size or eroded rocky platforms), (iii) Artificial habitat – seaward side, and (iv) Artificial habitat – landward side. For each habitat, two replicated areas (hereafter 'Areas') were established. For the Native and Natural habitats, one area was set at La Vela and another at Due Sorelle. For the artificial habitats, one area was set at Urbani and another at Numana. Within each area, four plots with transplants were created in each of the following positions (hereafter 'Positions'): (i) horizontally surrounded with naturally occurring adults (HA), (ii) horizontally without surrounding adults (HW) and (iii) vertically with no surrounding adults (V). Vertical positions with surrounding adults were not included because of the natural scarcity of adults on vertical surfaces. There were no comparable positions in the native habitat, which was represented by small, irregular, loose boulder fields with no consistent relief.

As the main goal of this experiment was to test the feasibility of enhancing fragmented communities of *C. barbata* by transplantation onto artificial structures and identify optimal conditions (i.e. position) for such transplantations, there was no need to include transplantation methodological controls (normally used when transplantation is used to explore aspects of the ecology of the species), as any effect of transplantation would be part of the hypothesis of interest. Transplantation into the original native habitat and into stable rocky bedrocks served as a comparison to understand how successful would be the transplantation in artificial conditions compared to more natural conditions at natural bedrocks.

The height of the juveniles was recorded at the time of transplantation, and growth was monitored along with survival rates in September and October 2008 and in February 2009. At each date, we also measured the size of unmanipulated *C. barbata* juveniles naturally occurring at La Vela and Due Sorelle to explore whether transplanted juveniles had different growth rates from unmanipulated ones. For this, all juveniles were carefully removed from one random 6 × 6 cm plot on each of three randomly selected boulders, for subsequent measurements in the laboratory. Survival of unmanipulated juveniles from native habitats was known to be virtually nil (Perkol-Finkel & Airoldi 2010), and no formal comparison was included.

Differences in the average survival and sizes of transplanted juveniles between habitats and positions were tested using asymmetrical permutational ANOVAs, including three factors: Habitat type (where the Native habitat was confronted with the three Other habitats: Natural bedrock, Artificial seaward and Artificial landward; fixed factor), Area (two areas, nested in each habitat; random factor) and Position [horizontal surrounded with adults (HA), horizontal without adults (HW) and vertical (V); fixed factor]. These asymmetrical analyses involved partitioning components of variation through two sub-analyses (see: Winer 1971). First, we ran two-way analyses testing for differences among the four habitats and areas, and contrasting the native habitat with the three other habitats irrespective of the possible different positions at the other habitats. Second, we ran three-way analyses, testing for effects of habitat, positions and areas at the other habitats only. We used the statistical package PERMANOVA+ for PRIMER (Anderson, Gorley & Clarke 2008) to partition the variability and obtain *F*-statistics on a matrix of Euclidean distances calculated from the original raw data and calculated all *P*-values using 9999 random permutations of the appropriate exchangeable units and Type III sums of squares to cope with the unbalanced design (Anderson, Gorley & Clarke 2008). We used PERMANOVA (as opposed to a classic ANOVA test) due to ease of use with complex unbalanced design and to avoid the usual normality assumptions. The analyses were performed on data retrieved in October 2008, as this was the last date for which all plots remained intact; after this date, some areas (one Natural bedrock and one Artificial seaward) were damaged by a storm in December 2008. Both survival and size data had homogeneous variances [Levenes' (1960) univariate test run using PERMISD (Anderson, Gorley & Clarke 2008)], and there was no need for transformation. The average size of all surviving transplants at the end of the experiment, in February 2009, was also compared to the average size of naturally occurring juveniles using a *t*-test.

To test whether the conditions identified as optimal for the growth of *Cystoseira* also applied to more remote coastal infrastructures in sedimentary environments, we ran two additional transplantation experiments. The first was set at the seaward and landward sides of two breakwaters located at Punta Marina and Lido Adriano, simultaneously with the experiment set in the Monte Conero promontory (Fig. 1). Juveniles were transported by car to these locations as quickly as possible in 100-L tanks. At each side of the breakwaters, four plots (with five individuals in each) were transplanted at each of the following positions: (i) Horizontally without surrounding adults (HW) and (ii) Vertically with no surrounding adults (V). Some individuals were kept in tanks on land for approximately the same time of transportation and transplanted back at the original source location at Due Sorelle as procedural controls. All juveniles transplanted to breakwaters showed 100% mortality within a week of transplantation, and no further sampling was performed.

Such a rapid loss of transplants was inconsistent with the results from the experiments carried out on breakwaters in the Monte Conero region, and not related to the transplantation procedure, therefore, the following year (June 2009) we ran a second experiment at the locality of Marotta (Fig. 1), which presented water conditions more similar to those at Monte Conero than the other two stations. Four small boulders (*c.* 0·1 × 0·1 m) holding numerous recruits of *C. barbata* were transplanted from Due Sorelle and established horizontally without surrounding adults (HW) at the landward sides of two replicated breakwaters. Here too, zero survival was recorded, as all transplants disappeared within 3 days.

CAGING EXPERIMENTS

We used caging experiments to explore whether the loss of transplants observed at artificial habitats set on sedimentary shorelines was related to environmental factors (e.g. lower water quality or excess sedimentation along a sedimentary shoreline), biotic factors (i.e. pressure from grazers or other sources of biological disturbance) or a combination of both. In June 2009, we collected 32 small boulders (*c.* 10 cm diameter) densely covered with naturally occurring juveniles of *C. barbata* from La Vela. The boulders were attached to the breakwaters, using epoxy putty, at each of two sites randomly selected at Due Sorelle (natural sites on a stable bedrock) and on two breakwaters at Marotta (artificial sites on a sandy bottom setting). We did not include a comparison with artificial habitats in a rocky setting as we had already demonstrated in the prior transplantation experiment that survival and growth of transplants in this habitat was similar to that of transplants on natural bedrocks. We predicted that if loss of transplants at artificial sandy sites was related to biotic factors, their survival would increase below cages, which limit access to potential grazers. Conversely, differences in survival between the study locations would persist below cages under the prevailing effects of different local environmental conditions.

To unravel the two mechanisms, four boulders selected at random in each area were protected by 40 × 15x15 cm plastic mesh cages (hole size 1 × 1 cm) which excluded possible macrograzers (i.e. fish and sea-urchins), while the remaining four were left uncaged as controls. Because all transplants (both caged and non-caged) in Marotta were lost within 48 h, the experiment was repeated using 1 × 1 mm mesh cages, to exclude both macro and mesograzers, while control plots were left uncaged. We did not include a partial caging control as we did not know the nature of eventual grazers (see Discussion). However, to minimize possible environmental alterations by the cages (e.g. sedimentation or wave action), we conducted the experiment under calm sea conditions. In this experiment, the transplanted units were marble plates (10 × 10 × 2 cm) densely covered with *C. barbata* juveniles. The plates had been placed at La Vela in March 2009, at the start of the reproductive season, to measure patterns of recruitment and had not been manipulated in any way before this experiment. The density and cover of juveniles were measured for each plate prior to transplantation, and subsequent changes were monitored 4 and 8 days after transplantation. This short interval was sufficient to detect a clear response while limiting possible longer-term artefacts related to the use of fine mesh cages. Differences between treatments were analysed by permutational ANOVA (using the statistical package PERMANOVA as illustrated previously) on data from day 8. The model included the factors: Biotic pressures (caged vs. un-caged, fixed factor), Local Environment (Natural bedrock vs. artificial sandy, fixed factor) and Site (random factor nested within Local Environment).

RECRUITMENT EXPERIMENTS

As the feasibility of successfully rearing *C. barbata* on coastal infrastructures will ultimately depend on its ability to proliferate and recruit onto the artificial substrata following active transplantation, we analysed the effects of small scale complexity on settlement of *C. barbata* using clay settlement plates (10 × 10 × 2 cm). Six plates were prepared for each of three levels of complexity: low (smooth surface), medium (surface with crevices 1–2 mm deep) and high (surface with crevices *c.* 5 mm deep), and set randomly at La Vela in March 2009. Complexity was imprinted onto the moist clay using pieces of natural rock, to mimic natural features. Plates were attached to natural substratum close to adult fronds of *C. barbata* at La Vela during March 2009, at about 3 m depth, using epoxy putty. Recruits of *C. barbata* were counted at the end of June and August 2009. Differences between levels of complexity (fixed factor) were tested separately for each time by permutational ANOVA (Anderson, Gorley & Clarke 2008).

We also analysed the effects of different materials often used for the construction of marine infrastructures, that is, limestone (marble), concrete and clay. Six replicated plates (10 × 10 × 2 cm) of each material were set randomly at La Vela in March 2009. Recruits of *C. barbata* were counted at the end of June 2009. No further sampling was possible as these plates were lost during a storm. Effect of material (fixed factor) was tested by permutational ANOVA (Anderson, Gorley & Clarke 2008).

Results

TRANSPLANTATION EXPERIMENTS

Juveniles of *C. barbata* transplanted onto both natural bedrocks and artificial habitats had significantly greater survival relative to those transplanted back to their native (source) habitat (Fig. 2 and Table 1a, contrast Native vs. Other Habitats). While virtually no transplants survived after October 2008 in the native habitat (because of boulder overturning and disturbance), many transplants in the other habitats survived until February 2009. Survival was highest in landward artificial habitats, with average survival >30%, in comparison with *c.* 20% in the natural bedrock habitats and 9% in the seaward artificial habitats

(Fig. 2). Nonetheless, differences among these other habitats were not significant (Table 1). Variability among individual replicated plots was high, and some plots had 100% survival throughout the experiment, while others had no surviving transplants. There were no consistent detectable effects in relation to position in any of the three other habitats where it was tested (Fig. 2 and Table 1, effects of Position within Other Habitats contrasts).

No significant differences in the size of transplanted juveniles were found between native and other habitats (Fig. 3 and Table 1b, contrast Native vs. Other Habitats). However, all transplanted juveniles that survived were larger on average than naturally unmanipulated juveniles in the study region. These differences were significant (*t*-test, $P < 0{\cdot}01$) at the last monitoring date (February 2009) when transplanted juveniles had an average size of 10·79 ± 6·08 cm (mean ± 1 SD, $n = 83$), while natural unmanipulated juveniles were only 8·27 ± 3·88 cm (mean ± 1 SD, $n = 49$). Moreover, some transplanted thalli that survived to the following spring (2009) both in natural bedrocks and in artificial habitats were observed to have grown to adult size and hold reproductive structures. In fact, during the summer, first generation recruits were observed in close proximity to these transplants. While at the natural sites, it is possible that these new recruits originated from other adults in the area, and this was unlikely at the artificial sites where very few adults occurred naturally.

None of the juveniles transplanted onto breakwaters at Punta Marina, Lido Adriano or Marotta survived longer than 2–3 days. During these experiments, the sea was calm, leading to exclude a possible dislodgment by waves, and there were no signs of vandalism.

CAGING EXPERIMENTS

At the natural bedrock sites, caging did not influence the survival or the cover of juveniles, and all transplants remained equally intact both inside and outside of the cages (Fig. 4a,b). At the artificial sites in Marotta, uncaged transplants showed severe decline, with nearly 80% of the coverage lost within 8 days. These losses persisted when large mesh cages were used. Conversely, both survival and cover of transplanted juveniles at the artificial sites significantly increased when fine mesh cages were used (Table 2a,b, PERMANOVA, significant Treatment × Habitat interaction, $F_{(\mathrm{d.f.}\ =\ 1,18)} = 5{\cdot}8739$ $P < 0{\cdot}05$ for cover and $F_{(\mathrm{d.f.}\ =\ 1,18)} = 47{\cdot}459$ $P < 0{\cdot}05$ for survival). In these treatments, after 8 days, both cover and survival matched the values measured at the natural bedrock sites (Fig. 4 a,b).

RECRUITMENT EXPERIMENTS

By the end of the reproductive season (June 2009), all settlement plates had some *C. barbata* juveniles. The density of recruits was highly variable among individual plates, ranging from 6 to 64 individuals. Initially, complexity appeared to have a significant influence on settlement (PERMANOVA: $F_{(\mathrm{d.f.}\ =\ 2,14)} = 3{\cdot}893$, $P < 0{\cdot}05$), and densities of settlers on plates with medium complexity were on average almost double than those with low and high com-

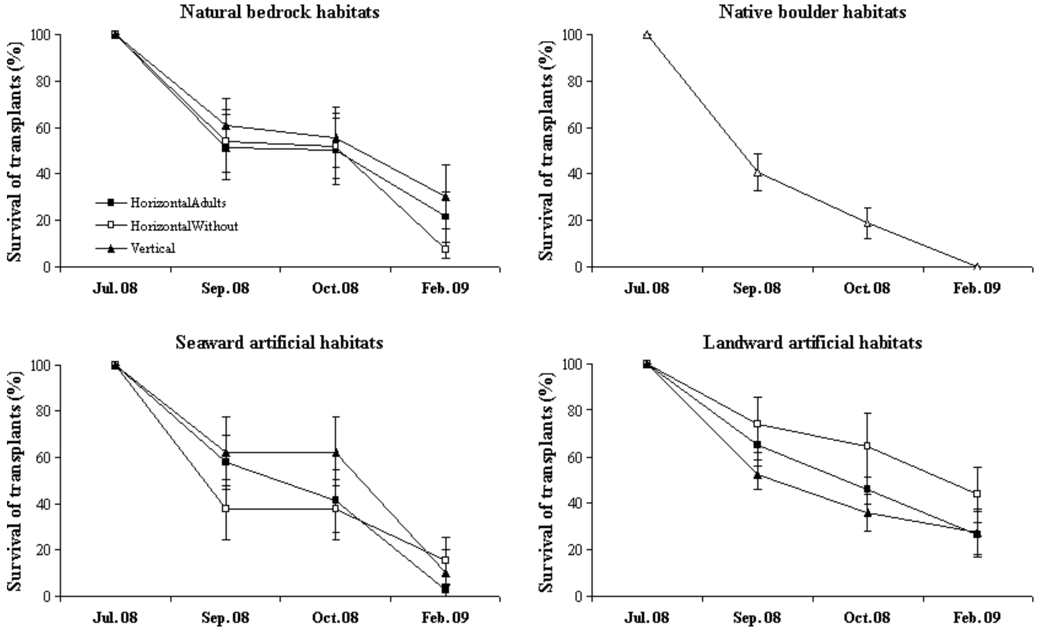

Fig. 2. Percentage (mean ± 1SE, $n = 8$, i.e. four plots for each of two areas) of recruits that survived out of those transplanted (five per plot) in July 2008 into four habitats (Natural bedrock, Seaward artificial, Landward artificial and Native boulder) at three positions [horizontal with surrounding adults (■), horizontal without surrounding adults (□), vertical (▲)] over the study period. Native habitat (△) had no comparable positions (see text for further explanation). Natural habitat data have been presented in part in Perkol-Finkel & Airoldi (2010).

Table 1. Asymmetrical analysis of the effects of habitat type and position on (a) percentage survival and (b) size of transplanted *Cystoseira barbata* recruits in October 2008. Factors are the following: habitat type (Native boulder was compared with three Other habitats: Natural bedrocks, Artificial seaward, Artificial landward, all fixed factors), area (two random areas, nested in habitat type) and position [horizontal surrounded with adults (HA), horizontal without adults (HW), and vertical (V), fixed factor] orthogonal to the Other habitats only. The analysis consists of two parts, one (upper) contrasting Native vs. Other habitats and the other (lower) examining survival within Other habitats in relation to the different positions. We used the statistical package PERMANOVA to partition the variability and obtain *F*-statistics on a matrix of Euclidean distances from the original raw data, and calculated all *P*-values using 9999 random permutations of the appropriate exchangeable units (Anderson, Gorley & Clarke 2008)

Source of variation	d.f.	MS	*F*
(a)			
Habitat	3		
Native vs. other habitats	1	6796·35	7·77*
Area (habitat)	4	874·35	0·73
Residual	72	1189·5	
Among other habitats			
Other habitats	2	190·3935	0·20
Area (other habitats)	3	961·6329	0·84
Position	2	271·8759	0·11
Position × other habitats	4	1496·8456	0·59
Position × area (other Ha)	6	2547·6733	2·22
Residual	54		
(b)			
Habitat	3		
Native vs. other habitats	1	1·1544	0·007
Area (habitat)	4	161·19	14·34
Residual	180	11·24	
Among other habitats			
Other habitats	2	72·72	0·55
Area (other habitats)	3	190·31	18·78*
Position	2	37·865	0·8322
Position × other habitats	4	48·315	3·4807
Position × area (other Ha)	6	13·921	1·373
Residual	162		

$^*P < 0{\cdot}05$.

plexities (Fig. 5). Two months later, average densities was still highest on plates with medium complexity, but differences between complexities were no longer significant (PERMANOVA: $F_{(\mathrm{d.f.}\ =\ 2,14)} = 2{\cdot}72$, $P > 0{\cdot}05$). The density of recruits was lower on concrete than on limestone and clay (Fig. 6), but there was a large variability among plates, and substratum composition did not appear to significantly affect settlement of *C. barbata* (PERMANOVA: $F_{(\mathrm{d.f.}\ =\ 2,13)} = 1{\cdot}684$, $P > 0{\cdot}05$).

Discussion

Transplanting *C. barbata* juveniles proved technically feasible on both natural bedrocks and man-made habitats in the area of Monte Conero, indicating the potential of coastal infrastructures to provide a suitable habitat for the growth of this threatened species. Overall, landward, sheltered rocky artificial habitats seemed most successful, regardless the presence of surrounding adults. Furthermore, the chances for survival and growth of transplanted individuals in the study area were greater than those measured in the native habitats, where this species is threatened because of long-term recruitment failure related to increasing instability of the substrata (Perkol-Finkel & Airoldi 2010). Assisted re-introduction or translocation can facilitate recovery of damaged populations (Lotze *et al.* 2011). Therefore, developing simple techniques to grow *C. barbata* on suitable habitats, either natural or artificial, could enhance the recovery potential of locally endangered populations of this species.

Transplanted juveniles showed no consistent survival patterns that relate to substratum orientation. This suggests that coastal infrastructures such as seawalls, breakwaters and pilings could provide potentially adequate habitats despite the greater proportion of inclined surfaces compared to natural habitats (Bulleri, Chapman & Underwood 2005; Chapman & Blockley 2009). Moreover, the survival of transplants was not impaired by lack of surrounding adults, suggesting that this would not be a limiting factor when managing assemblages on newly built man-made infrastructures that would obviously lack adult canopies.

Transplantation success was greater on landward, sheltered sides compared to exposed seaward sides of the breakwaters. This is in agreement with findings from Jonsson *et al.* (2006) who demonstrated that the higher flow speed on seaward compared to landward sides of breakwaters induced greater dislodgment of fucoid macroalgae. Indeed, the different sides of marine infrastructures provide distinct habitats for the growth of a variety of macroalgae and invertebrate species (e.g. Bacchiocchi & Airoldi 2003; Bulleri & Airoldi 2005; Burt *et al.* 2009). This ecological characteristic of many coastal infrastructures must be considered if we are to design and manage these structures for achieving desired secondary management goals and for enhancing their contribution to local biodiversity and ecosystem functions.

While several transplants survived and reproduced for over a year post-transplantation, we did not establish a substantial self-sustaining population (which was beyond the scope of the current research). Nonetheless, as most of the receiving habitats had relatively high levels of survivals several months after deployment, much of the mortality can be attributed to rough sea conditions and not as an immediate reaction to the transplantation procedure. Moreover, our transplantation efforts were limited in scale and only small sized recruits were transplanted. Future work should explore whether a larger-scale transplantation effort onto sheltered portions of coastal infrastructures would be self-sustaining and whether using larger transplants would increase their survival and thus facilitate establishment of viable populations.

While transplantation of *C. barbata* proved successful onto coastal infrastructures along a rocky coastline, sur-

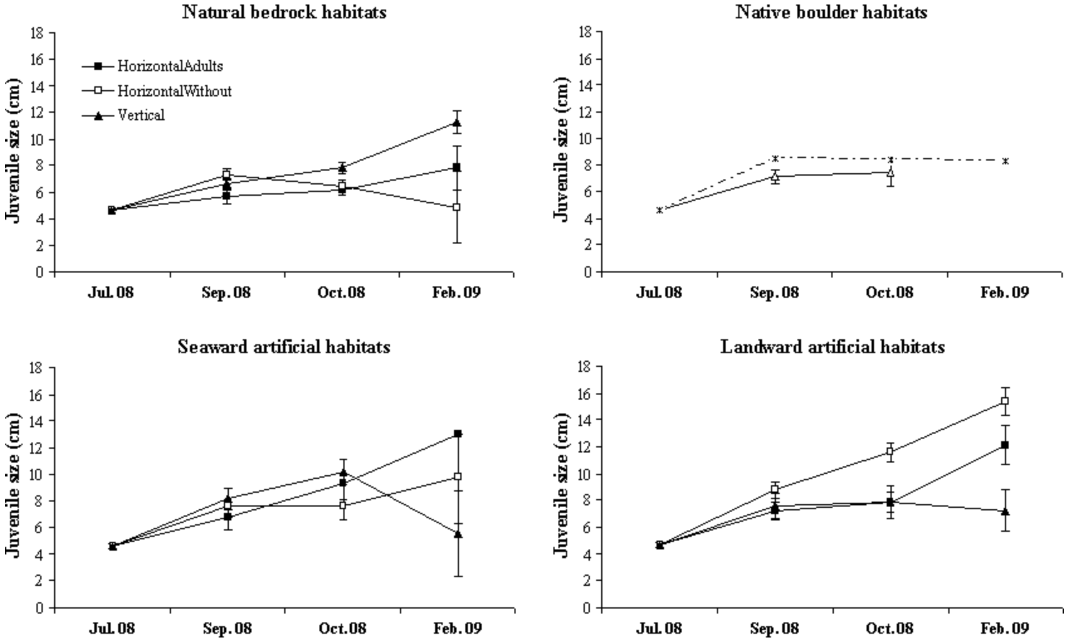

Fig. 3. Size of transplanted recruits at four habitats (Natural bedrock, Seaward artificial, Landward artificial and Native boulders) and three positions [horizontal with surrounding adults (■), horizontal without surrounding adults (□), vertical (▲)]. Native habitat (△) had no comparable positions (see text for further explanation). Size of natural, un-manipulated recruits in the study areas is also plotted. Data points show the mean (±1SE, n = 8, i.e. four plots for each of two areas) size of survived thalli of transplanted recruits within each plot (no measures were available for February 2009 for control habitats because no transplants remained). Data for natural un-manipulated recruits (*) are the mean (±1ES) of 80 recruits from three different boulders sampled from natural habitats at each time point. Natural habitat data have been presented in part in Perkol-Finkel & Airoldi (2010).

vival was not as promising when the structures were located along sedimentary coastlines, a typical setting of many coastal defence infrastructures (Airoldi *et al.* 2005b). The results of the caging experiment suggested that lack of survival of *C. barbata* transplants along sedimentary coastlines was not related to environmental factors (e.g. reduced water quality or excess sedimentation). Instead biotic disturbance was a determining factor limiting the survival of *C. barbata* in these habitats. Our tests with cages of different mesh sizes initially suggested that such biotic disturbance could be related mainly to the activity of small organisms (0·1–1 cm). However, preliminary results of ongoing experimental work by our group (aiming at clarifying the nature, distribution and generality of such biotic disturbance with the aid of underwater video cameras) suggest that loss of *Cystoseira* at some structures is related to a complex of both consumptive and non-consumptive disturbance by a variety of organisms of different sizes, ranging from small crabs to mullets (F. Ferrario, L. Ivesa, S. Perkol-Finkel, A. Jacklin & L. Airoldi, unpublished data). Some of these organisms are also present at natural rocky sites, but at lower densities and they do not show the same degree of interaction with the *Cystoseira*. Coastal infrastructures set on sedimentary shorelines represent 'oasis' of hard bottoms in a soft bottom environment (Airoldi *et al.* 2005a). As such, they might attract a greater abundance of predators compared to nearby natural habitats, similarly to what is thought to occur in other oasis systems such as seamounts (Rowden *et al.* 2010a,b). This unexplored aspect of the ecology of marine infrastructures deserves further attention.

Substratum composition and complexity have a strong influence on settlement, recruitment and survival of benthic fauna and flora in both natural (Harlin & Lindbergh 1977; Wells, Moll & Bolton 1989; Johnson & Brawley 1998; Guarnieri *et al.* 2009) and artificial substrata (Spieler, Gilliam & Sherman 2001; Chapman 2003; Burt *et al.* 2009). Coastal infrastructures such as seawalls, breakwaters and jetties may be constructed of stone, concrete, wood, steel or geotextiles (Dugan *et al.* 2011) and may be designed to incorporate greater habitat complexity (Moreira, Chapman & Underwood 2007; Chapman & Blockley 2009). For example, subtle change in infrastructure complexity, at small scale (e.g. addition of pits to a seawall as in Martins *et al.* (2010) or medium scale (e.g. addition of holes to concrete wave energy foundations as in Langhamer & Wilhelmsson (2009) can significantly increase the ability of the infrastructure to sustain greater abundance of organisms. Our tests with concrete and limestone (the most common materials in our study region) and clay (a potentially practical substratum for transplantation) showed similarly high levels of recruitment. Settlement was initially double on surfaces with medium complexity in comparison with simple or highly complex ones, yet this facilitation was apparently transient, probably due to post-settlement processes related to natural self-thinning

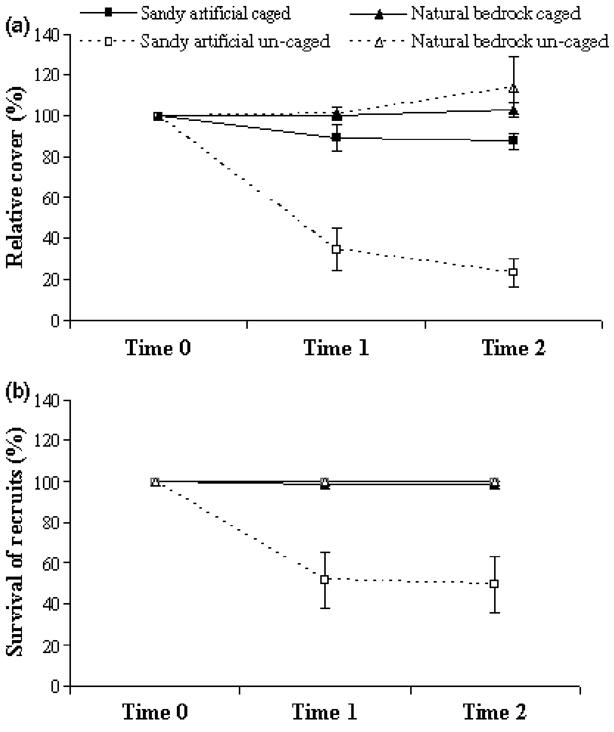

Fig. 4. (a) Relative cover and (b) percentage survival (in relation to initial cover and/or count, respectively, mean ± 1 SE) of caged (1 mm mesh size cage, full symbols) and un-caged (open symbols) recruits transplanted onto two breakwaters at Marotta [Sandy artificial (■)] vs. two natural bedrock areas in La Vela [natural bedrock (▲)]. Four plates covered with *Cystoseira barbata* recruits per treatment and site within each habitat. Values are presented as 100% when transplanted (Time 0) and then 4 and 8 days following transplantation (Time 1, Time 2, respectively).

Table 2. Results of tests for (a) Relative cover and (b) Percentage survival (in relation to initial cover and/or count respectively) of caged (1 mm mesh size cage) and uncaged recruits transplanted onto two breakwaters at two Sandy Artificial sites vs. two Natural bedrock sites. Factors are the following: treatment (Cages vs. Un-caged), habitat (Artificial Sandy vs. Natural Bedrock), site (nested in habitat: two breakwaters at Marotta and two areas in La Vela). Four plates covered with *Cystoseira barbata* recruits per treatment and site within each habitat. The tests were carried out 4 days following transplantation. We used the statistical package PERMANOVA to partition the variability and obtain *F*-statistics on a matrix of Euclidean distances from the original raw data and calculated all *P*-values using 9999 random permutations of the appropriate exchangeable units (Anderson, Gorley & Clarke 2008)

Source of variation	d.f.	MS	*F*
(a)			
Caging	1	3327·5	5·8739*
Habitat	1	3869·1	4·7762
Site (habitat)	2	812·3	2·5831
Caging × habitat	1	3327·5	5·8739*
Caging × site (habitat)	2	567·62	1·805
Residual	18	314·46	
(b)			
Caging	1	4494	24·604*
Habitat	1	17626	17·181
Site (habitat)	2	2057·4	2·6137
Caging × habitat	1	8670·5	47·459*
Caging × Site (habitat)	2	363·51	0·4618
Residual	18	7084·3	

*$P < 0·05$.

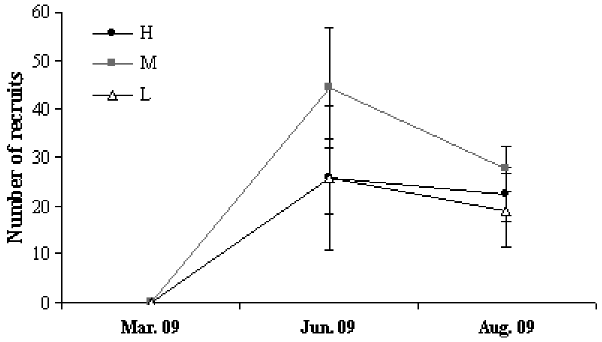

Fig. 5. Number of *Cystoseira barbata* recruits (mean ± 1SE, $n = 6$) on clay plates of different complexity levels: L = low, M = medium, H = high. Plates were set on March 2009 and counted in June and August 2009. Superimposed circles represent significant differences by Student–Newman–Keuls (SNK) test (M > H = L, $P < 0·05$).

(Reed 1990; Kendrick & Walker 1995; Johnson & Brawley 1998). Moreover, it is possible that engineering species like *Cystoseira* (Sala & Ballesteros 2012) modify their immediate environment once established in terms of, for example, hydrodynamic and/or sedimentation patterns, thus masking further effect of complexity. This suggests that the artificial substrata in the study area provide potentially suitable substrata for this canopy-forming alga and that other biological or ecological factors (such as those suggested by the caging experiment) limit its natural recruitment on the infrastructures.

Understanding how man-made habitats function in urbanized seascapes is fundamental if we are to design and manage these habitats in a way that enhances their contribution to marine biodiversity and flow of ecosystem services (Airoldi *et al.* 2005a; Chapman & Blockley 2009; Bulleri & Chapman 2010). We demonstrate that managing assemblages on marine infrastructures for desirable secondary management goals can be feasible, but requires a good understanding of the different ecology of these artificial systems. This is in agreement with Moschella *et al.* (2005) concluding that infrastructures can be modified to influence the abundance and species composition of epibiota to achieve desired management goals such as controlling growth of nuisance algae or promoting diversity of habitats and species for recreational activities. This emerging approach complements the evolving paradigm of ecological engineering (Mitsch 1996), aimed at integrating ecological, economic and social needs into the design of man-made ecosystems.

In conclusion, the current study contributes to bridging the gap between growing societal needs of coastal development and the need for conserving the marine environment (Mitsch 1996; Chapman & Blockley 2009; Inger

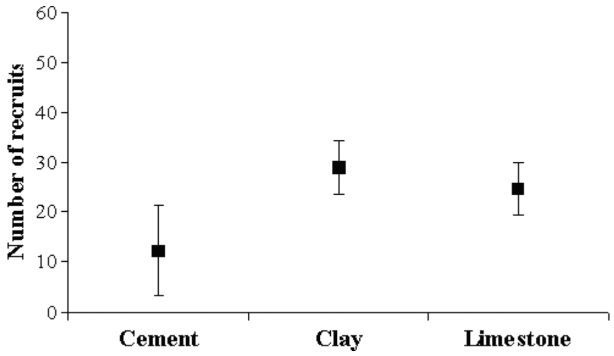

Fig. 6. Number of *Cystoseira barbata* recruits (mean ± 1SE, *n* = 6) on plates of different composition: concrete, clay and limestone. Plates were set on March 2009 and counted in June 2009.

et al. 2009; Bulleri & Chapman 2010). The ability to utilize coastal infrastructures as scaffolds for recovery of threatened species or for enhancement of desirable species has important applications for the conservation of biodiversity in globally expanding coastal urban environments. For example, current restoration or enhancement efforts based on the construction of artificial reefs (Reed *et al.* 2006; Schmidt *et al.* 2007; Dupont 2008) could be best replaced by utilizing existing infrastructures. This approach could be more sustainable in the long term, and be efficiently incorporated into marine spatial planning.

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