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Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea

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Summary

1. Artificial structures have become ubiquitous features of coastal landscapes. Although they provide novel habitats for the colonization of marine organisms, their role in facilitating biological invasions has been largely unexplored.
2. We investigated the distribution and dynamics of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, at a variety of spatial scales on breakwaters in the north Adriatic Sea, and analysed experimentally the mechanisms underlying its establishment. We assessed the provision of sheltered habitats by breakwaters, the role of disturbance (e.g. from recreational harvesting and storms) acting at different times of the year, and the interactions between *Codium* and the dominant native space-occupier, the mussel *Mytilus galloprovincialis*.
3. *Codium fragile* ssp. *tomentosoides* has established viable populations on artificial structures along the shores investigated. The density, cover and size (length, branching and weight) of annual erect thalli of *Codium* was enhanced in sheltered conditions, resulting in the monopolization of landward low-shore habitats of breakwaters.
4. On the landward sides of breakwaters, disturbance enhanced recruitment of *Codium*. The time when bare space was provided within mussels beds was crucial. Removal of mussels in April or January did not affect the recruitment of *Codium*, whereas harvest in August, shortly before *Codium* gamete release, doubled its success. On the seaward sides of breakwaters, the effects of disturbance were more complex because mussels both inhibited recruitment of *Codium* and provided shelter from wave action to adult thalli.
5. *Synthesis and applications*. Artificial structures can provide suitable habitats for non-indigenous marine species and function as corridors for their expansion. Physical (wave exposure) and biotic (resident assemblages) features of artificial habitats can be important determinants of their susceptibility to biological invasions. Alternative options in the design of artificial structures and effective management of native assemblages could minimize their role in biological invasions. In particular, increased water motion and retention of space by mussels in spring–summer would be effective in reducing the ability of *C. fragile* ssp. *tomentosoides* to persist on the breakwaters investigated in this study.

Key-words: biological invasions, *Codium fragile* ssp. *tomentosoides*, facilitation, hard coastal defence structures, recruitment, urbanization, wave exposure

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Introduction

Natural patterns of migration and dispersal of species are dramatically disrupted by human activities, so that the introduction of non-indigenous species into new regions, accidental or deliberate, has become a common

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occurrence. As a consequence, biological invasions are acknowledged to be among the most severe threats to terrestrial and marine biodiversity (Kareiva 1996; Williamson 1996; Vitousek *et al*. 1997; Grosholz 2002).

Although studies have assessed the changes caused by the introduction of non-indigenous species on native assemblages (Simberloff & Von Holle 1999; Grosholz 2002), less effort has been devoted to understanding the mechanisms by which these species succeed in getting established within a recipient assemblage. This issue is pivotal to improving our ability to predict pathways of invasion and susceptible locales (Mack *et al*. 2000) and thus prevent and manage invasions (Grosholz 2002; Levin *et al*. 2002). Life-history traits of the invader along with physical (Ceccherelli & Cinelli 1999; Byers 2002; Stachowicz *et al*. 2002) and biological attributes (Kennedy *et al*. 2002; Stachowicz *et al*. 2002; Meiners, Cadenasso & Pickett 2004) of invaded environments have been advocated as determinants of successful establishment in new regions.

Artificial habitats, such as breakwaters, jetties, seawalls, floating pontoons and pier pilings, have become common hard substrata along entire coastlines (Bacchiocchi & Airoldi 2003; Bulleri & Chapman 2004), bays (Sammarco, Atchison & Boland 2004) and estuaries (Connell & Glasby 1999; Chapman & Bulleri 2003). Although such structures often support non-indigenous species (Holloway & Keough 2002; Lambert & Lambert 2003; Thornber *et al*. 2004; Bulleri, Abbiati & Airoldi, in press), their susceptibility to biological invasions remains largely unexplored. However, artificial structures could not only provide suitable habitat for some invaders but also enhance their further spread, by functioning as corridors across areas of unsuitable habitat (e.g. across sandy or muddy areas). Under future global climate change scenarios, the intensity of storms and height of sea level are predicted to increase, augmenting the need for hard coastal defence structures (e.g. breakwaters and seawalls). Under these scenarios, a comprehensive understanding of patterns of biological invasion in coastal areas requires consideration of the role of artificial structures as suitable habitats for non-indigenous species.

Hard structures for coastal protection in the northern Adriatic Sea have been colonized by the introduced green alga *Codium fragile* (Sur.) Harriot ssp. *tomentosoides* (van Goor) Silva, hereafter referred to as *Codium* (Bulleri, Abbiati & Airoldi, in press). This alga, native to east Asia, has become an important component of low intertidal and shallow subtidal assemblages of many temperate rocky shores around the world (Trowbridge 1998), with dramatic ecological consequences on native assemblages (Carlton & Scanlon 1985; Scheibling & Anthony 2001; Chapman, Scheibling & Chapman 2002; Levin *et al*. 2002).

The present study investigated the distribution and dynamics of *Codium* on breakwaters at a variety of spatial scales along the north-east coast of the Adriatic Sea, and identified some of the mechanisms underlying its successful establishment. First, we assessed the regional distribution of *Codium*, integrating the existing information with a field survey. Secondly, as colonization of *Codium* seems to be enhanced in wave-sheltered conditions (Trowbridge 1995, 1999; Bégin & Scheibling 2003), we compared the abundance and morphology of *Codium* between the landward and seaward sides of breakwaters, to test whether artificial, sheltered habitats offer particularly favourable conditions for this species. Thirdly, we investigated the role of disturbance in regulating the interaction between *Codium* and the main native space-occupier, the mussel *Mytilus galloprovincialis* Lamarck. Therefore, we experimentally disturbed mussel beds and tested whether the effects on recruitment of *Codium* varied between the landward and seaward sides of breakwaters and in relation to the time of the year at which the disturbance occurred. Finally, since stressful physical conditions tend to favour positive interactions among species (Bertness & Callaway 1994), we tested whether mussels could facilitate the survival of *Codium* in artificial, wave-exposed habitats on the seaward sides of breakwaters through stabilization of the thallus.

Study system

The north-east coast of the Adriatic Sea (Italy) is a flat, alluvional system that extends, almost uninterrupted, for more than 300 km. The area is moderately exposed to wave action and the few limestone rocky shores occurring in the region (at Gabicce and Ancona) generally offer few naturally sheltered habitats. The area is subject to a relatively large tidal excursion (about 80 cm) in comparison with other regions of the Mediterranean basin, and receives inputs of freshwater and nutrients from the Po River. Severe erosion, together with poor coastal defence policies, has led to the proliferation of hard structures over more than 60% of the shoreline (Cencini 1998). This has resulted in more than 190 km of breakwaters, groynes, seawalls and jetties (Bondesan, Calderoni & Dal Cin 1978). The construction of hard structures along the coast was particularly intensive during the 1970s and 1980s, but is still ongoing. Other characteristics of the region are described in Bacchiocchi & Airoldi (2003) and references therein.

The regional survey covered a variety of coastal structures at several locations, from Trieste to Porto Recanati, while local studies and experiments were done on breakwaters at Cesenatico (Table 1). Breakwaters built with large blocks of quarried rock (long axis ranging from 1 to 3 m) are deployed on shallow sediments at a distance of about 220 m from the shore, with an average length of 100 m, and are separated by gaps of about 20 m. Breakwaters extend about 2–3 m below and above the mean level of low water (MLLW), thus providing both subtidal and intertidal habitats for marine life (Bacchiocchi & Airoldi 2003).

The mussel *M. galloprovincialis* monopolizes low intertidal and shallow subtidal habitats of breakwaters, generally forming multilayered thick beds on the landward sides and thinner beds (one or two layers) on the

Table 1. Occurrence of *Codium fragile* ssp. *tomentosoides* on artificial (exposed and sheltered habitats) and natural (only exposed, because sheltered natural rocky habitats are not available in the region) substrata along the north-east coast of the Adriatic Sea. Latitude and longitude are reported for each of the study locations. The source of information is specified and includes: direct field sampling in July 2004 (locations in italics), information from the literature, personal communications and data from previous field observations (L Airoldi & F. Bulleri, unpublished data). When indicated, percentage covers represent average values from 30 replicates (10 quadrats on each of three breakwaters); +, *Codium* present; NA, type of habitat not available

			Type of substratum		
Location	Latitude (N)	Longitude (E)	Natural	Artificial sheltered	Artificial exposed
Trieste	45°39′	13°46′	+*	+†	Not found†‡
Lagoon of Venezia	45°26′	12°19′	+§	+§	+§
Lido delle Nazioni (LN)	44°44′	12°14′	NA	+	Not found
Casal Borsetti (CB)	44°33′	12°17′	NA	+	+
Lido Adriano (LA)	44°23′	12°19′	NA	13%	+
Cesenatico	44°11′	12°24′	NA	48%	6%
Gabicce (GB)	43°58′	12°46′	+	33%	+
Falconara (FL)	43°37′	13°24′	NA	29%	+
Monte Conero (MC)	43°32′	13°37′	+¶	Not found¶	Not found¶
Porto Recanati (PR)	43°25′	13°40′	NA	Not found	Not found

*Bressan, Trebbi & Babbini (2000).
†A. Falace, personal communication.
‡F. Bulleri & L. Airoldi, personal observations in September 2003 and June 2004.
§Sfriso (1987) and A. Sfriso personal communication.
¶F. Bulleri & L. Airoldi, personal observations in May 2003, March, June and August of 2004.

seaward sides. Other common sessile invertebrates include oysters (*Ostrea edulis* Linnaeus and, to a less extent, the introduced *Crassostrea gigas* Thunberg), barnacles and the limpet *Patella caerulea* Linnaeus. *Ulva intestinalis* Linnaeus and several filamentous forms (i.e. *Cladophora* spp., *Polysiphonia* spp. and *Ceramium* spp.) are common macroalgae on both primary and secondary substrata. Breakwaters also host dense stands of *Codium*. First sighted in 1950 in the north-west Mediterranean Sea, this alga attained peak densities in the 1960s but regressed afterwards (Boudouresque 1994). The ability of *Codium* to achieve a world-wide distribution has been attributed to its life-history traits (reviewed by Trowbridge 1998). In many regions, although macroscopic thalli generally disappear during winter months, holdfasts are perennial and can regenerate new plants when environmental conditions improve (Trowbridge 1995, 1996). Sexual reproduction has not been observed and the alga reproduces parthenogenetically, enhancing its ability to establish even when at low densities (Trowbridge 1998). It is also able to propagate vegetatively through fragments of the thallus, vegetative buds, single utricules and medullary filaments (Borden & Stein 1969). These are likely to play a key role in long-distance dispersal (Trowbridge 1998). Undifferentiated filaments, generally referred to as the vaucherioid stage, have been observed forming mats on a variety of hard surfaces, including rock, shells and floating debris (Trowbridge 1998 and references therein).

Materials and methods

REGIONAL DISTRIBUTION OF *CODIUM*

The current distribution of *Codium* on hard human-made structures along the north-east coast of the Adriatic Sea was assessed by integrating information from recent studies available in the literature with data from previous field observations (L. Airoldi *et al*., unpublished data; F. Bulleri *et al*., unpublished data) and through an *ad hoc* field survey in July 2004 (Table 1). Because of the peak in abundance and size of *Codium* at this time of the year (Bulleri, Abbiati & Airoldi, in press), chances of discovering small populations were high. The occurrence of *Codium* on natural rocky shores was also assessed where these were present (i.e. at Trieste, Gabicce and Monte Conero). Whenever possible, observations were carried out in at least three independent structures or areas (Table 1), which were thoroughly searched to verify the presence of *Codium*. Where *Codium* was common, its percentage cover was quantified in 10 randomly placed 20 × 20-cm quadrats.

DISTRIBUTION, DYNAMICS AND MORPHOLOGY OF *CODIUM* ON BREAKWATERS

Between May 2003 and December 2004, the distribution, morphology and dynamics of *Codium* at low intertidal levels (0·2–0 m above the MLLW) were analysed at monthly intervals on three breakwaters (several hundred metres apart), selected at random among those available at Cesenatico. In order to test whether *Codium* would be favoured on the sheltered landward sides of breakwaters compared with the seaward exposed sides, the density and cover of the alga were quantified in five replicate 20 × 20-cm quadrats on each of three randomly identified blocks on each side of the breakwaters. The quadrats were sampled visually, using a plastic grid with 25 subquadrats. Percentage cover was estimated by giving a score from 0% to 4% to each subquadrat (Dethier *et al*. 1993), while density was estimated as the total number of thalli. Ten thalli were also collected at random from each block and brought back to the laboratory, where wet weight, length (as the maximum length of each frond) and degree of branching (as the maximum number of dichotomies) were measured according to Trowbridge (1996). Ten to 15 thalli among the 30 available for each side of the breakwaters were further examined under a dissecting microscope to assess the reproductive status of the alga. After each sample, the blocks were marked using epoxy putty (Veneziani Subcoat, Yacht Systems s.v.l., Trieste, Italy) to avoid resampling and guarantee independence of data through time (Underwood 1997).

The cover, density, length, degree of branching and weight of thalli of *Codium* were analysed by four-factor ANOVAs, including the factors time (random and crossed), breakwater (random and crossed), exposure (fixed and crossed) and block (random and nested within the interaction time × breakwater × exposure). Heterogeneity of variances was checked by means of Cochran's test and data were appropriately transformed when necessary (Underwood 1997). When homogeneity of variances could not be achieved by transformation, data were analysed nonetheless, as analysis of variance is robust for departure from this assumption when there are many independent replicates and sizes of samples are equal (Underwood 1997). Results were, however, interpreted with caution by judging significance more conservatively ($\alpha = 0{\cdot}01$). The SNK test was used for a posteriori comparison of the means (Winer, Brown & Michels 1991).

EFFECTS OF DISTURBANCE TO MUSSEL BEDS ON RECRUITMENT OF *CODIUM*

Although parthenogenic gametes of *Codium* (hereafter referred to as gametes) can settle and germinate on a variety of secondary substrata (e.g. shellfish, coralline algae, serpulid polychaetes and solitary tunicates; Trowbridge 1998), there is evidence that colonization of *Codium* can be enhanced in habitats with large amounts of unoccupied space (Trowbridge 1998). In the north Adriatic Sea, thalli of *Codium* are not perennial and are fertile in late summer–early autumn (Bulleri, Abbiati & Airoldi, in press). Further, the breakwaters are frequently disturbed by a variety of factors that remove mussels and open patches of unoccupied space, the most relevant of which include spring and autumn storms and recreational harvesting of mussels during summer (Bacchiocchi 2004; Airoldi *et al*. 2005). Therefore, the interaction between timing of disturbance and gamete release could be crucial in determining the recruitment success of *Codium*, as observed for other species (Sousa 1979; Reed, Laur & Ebeling 1988; Airoldi 2000; Benedetti-Cecchi 2000). This hypothesis was tested by experimentally disturbing mussels beds in spring, summer and autumn, respectively before, during and after the release of gametes of *Codium*.

In March 2003, 16 blocks more than 3 m apart were selected at random on each of three haphazardly chosen breakwaters (several hundred metres apart). Subsets of four blocks were randomly assigned to the control treatment (mussels left untouched) and to each of three different times of removal of mussels: April 2003 (before gamete release), August 2003 (during gamete release) and January 2004 (after gamete release). Because of logistic and time constraints, we did not provide an estimate of the potential variability of the effects of removals of mussels within each period and the results should be interpreted accordingly. The average covers of mussels on the landward and seaward sides of breakwaters were 81% and 87% in April 2003, 62% and 71% in August 2003 and 31% and 56% in January 2004. The manipulation was intended to simulate natural (storms) or human (harvesting) disturbances, which generally cause the removal of mussels from most of the surface of blocks (F. Bulleri, personal observation). Mussels were removed by means of paint-scrapers, paying attention not to alter the topography of the substratum through the production of crevices and cracks. Propagules of *Codium* are released in late summer–early autumn but recruits become macroscopic in the spring. Therefore, effects of treatments were evaluated in the following May (2004) when recruits of *Codium* became clearly visible. Because of the small size and high density of thalli, counts of individual recruits were difficult and recruitment of *Codium* was estimated as percentage cover in four replicate 20 × 20-cm quadrats for each block, as previously described. Percentage cover data were analysed by a four-way ANOVA, including the factors breakwater (random and crossed), exposure (fixed and crossed), treatment (fixed and crossed) and block (random and nested within the interaction breakwater × exposure × treatment).

A further study was designed to differentiate the relative contribution to *Codium* regeneration arising from the settlement and germination of new propagules from the water column and the vegetative regrowth of the remnants of perennial holdfasts, vaucherioid filaments or other resting stages on the rock beneath mussel beds. In June 2003, the density of thalli of *Codium* was quantified in four replicate quadrats on each of the blocks from which mussels had been removed in April 2003 or left untouched (control). As, presumably, no significant release of propagules occurred between April and June 2003 (because *Codium* is fertile at the end of the summer), differences between treatments should reflect the responses of resting vaucherioid filaments, holdfasts or propagules trapped beneath mussels. Covers of juvenile thalli of *Codium* were analysed by means of the same four-way ANOVA model used to analyse data in May 2004, but the factor treatment included only two levels (April removal and control).

EFFECTS OF MUSSELS ON THE SURVIVAL OF *CODIUM* IN WAVE-EXPOSED HABITATS

Following the observation that, on the seaward sides of breakwaters, a large proportion (> 92%) of thalli of

Codium was embedded within a tight matrix of mussels covering their stipes for most of the length, we hypothesized that survival of *Codium* in such wave-swept environments could be facilitated by stabilization of the holdfast and stipe by mussels (Benedetti-Cecchi, Nuti & Cinelli 1996). To test this hypothesis, in May 2003, six blocks were randomly selected on the seaward sides of three breakwaters, at low intertidal levels. On each block, the position of 10–12 thalli of *Codium*, randomly chosen, was recorded as the distance from two fixed screws for later identification. Three of the blocks were then left unmanipulated (control treatment), while on the other three, mussels packed around the stipes of *Codium* were removed within a radius of about 2 cm (removal treatment). Mussels were carefully removed with forceps, paying attention not to damage the plants. In order to control for potential artefacts of the manipulation, mussels adhering to thalli on control blocks were pulled gently with forceps to loosen their attachment, without provoking their dislodgement. After 2 days, these mussels had been able to re-attach firmly to the substratum (both thalli of *Codium* and adjacent mussels). The number of surviving thalli was recorded 10 days after the beginning of the experiment. The experiment was repeated on different blocks of the same breakwaters the following year, in May 2004 (surviving thalli were recorded after 8 days). Survival data (as percentage) were analysed by means of a three-way ANOVA, including the factors start (random and crossed), breakwater (random and crossed) and treatment (fixed and crossed).

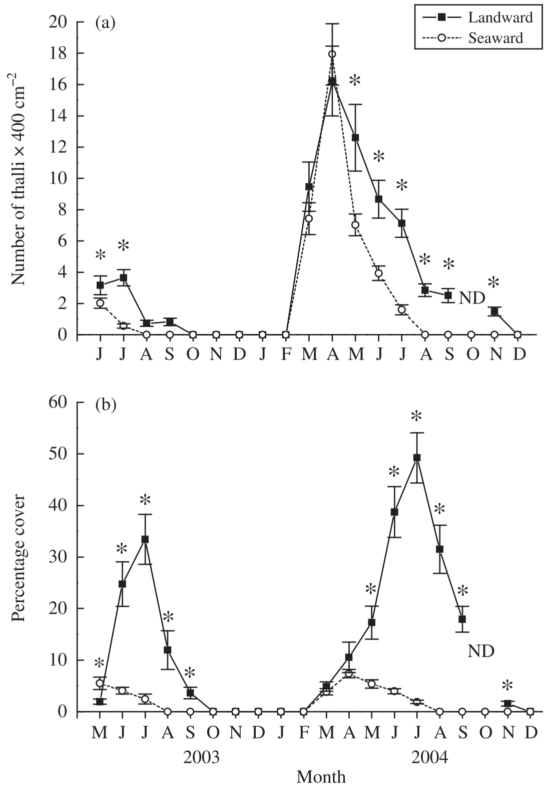

Fig. 1. Density of thalli (a) and percentage cover (b) of *Codium* on the landward and seaward sides of breakwaters in Cesenatico from May 2003 to December 2004. Data are averages (± 1 SE) from 45 independent replicates (five quadrats on each of three blocks on either landward or seaward sides of each of three breakwaters). ND, no data. Asterisks indicate significant differences between landward and seaward sides (SNK tests).

Results

REGIONAL DISTRIBUTION OF *CODIUM*

In the north Adriatic Sea, *Codium* is an important component of low-shore assemblages on the sheltered, landward sides of breakwaters and other human-made structures at most locations from Trieste in the north, to Monte Conero in the south, reaching peak covers at Cesenatico (Table 1). *Codium* has also been reported as an abundant species on both artificial substrata and natural consolidated sediments in the sheltered lagoon of Venezia (Table 1). Conversely, *Codium* was sparse on both natural and artificial exposed substrata. Although present at most locations, populations at exposed habitats generally consisted of few, small, scattered individuals, reaching measurable cover only at Cesenatico. *Codium* was not found on breakwaters in Porto Recanati, the southernmost location included in this study.

DISTRIBUTION, DYNAMICS AND MORPHOLOGY OF *CODIUM* ON BREAKWATERS

Densities and covers of *Codium* were generally greater on landward than seaward sides of breakwaters (Fig. 1 and Table 2). Despite the variation between years and breakwaters (Table 2), a consistent trend was evident, with *Codium* colonizing the landward and seaward sides of the structures to a similar extent in spring and early summer. With the progression of the summer, densities and covers of *Codium* quickly declined on the seaward sides, to virtually disappear in August in both 2003 and 2004. Conversely, *Codium* persisted longer on the landward sides, some thalli surviving until September–November (Fig. 1a). In contrast to the few small thalli remaining on the seaward sides of breakwaters, thalli on the landward sides attained significantly greater sizes (≫14 cm in length), degree of branching and weight (Fig. 2 and Table 2), resulting in average peak covers of about 32% and 48% in July 2003 and 2004, respectively (Fig. 1b).

EFFECTS OF DISTURBANCE TO MUSSEL BEDS ON RECRUITMENT OF *CODIUM*

In May 2004, the percentage cover of *Codium* was significantly larger on blocks where mussels had been removed in August 2003, compared with the other treatments. Effects were consistent between the landward and seaward sides of breakwaters and were detected despite the large variation among breakwaters and blocks (Fig. 3 and Table 3a).

There was a significant effect of removing mussels in spring (April 2003) on the percentage cover of *Codium* in early summer (June 2003), although its direction

Table 2. ANOVAs of the effects of time, breakwater, exposure and block on density, percentage cover, maximum length, degree of branching and wet weight of thalli of *Codium* in Cesenatico. Whenever the analysis showed a significant interaction, the *F*-ratio for the main effect and lower order interactions of relevant factors are not reported, as these are not logically interpretable (Underwood 1997). †Degrees of freedom for the analyses of density of thalli; ‡degrees of freedom for the analysis of percentage cover; §degrees of freedom for the analyses of length, branching and weight. $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$

Source of variation	d.f.	Density of thalli MS	Density of thalli *F*	Percentage cover MS	Percentage cover *F*	Length MS	Length *F*	No. branching MS	No. branching *F*	Wet weight MS	Wet weight *F*
Time (T)	11†, 12‡, 6§	52·11		39·04		1997·58		1888·50		71 405·44	
Breakwater (B)	2	2·47		0·86	0·41	8·99	0·51	1·52	0·13	316·98	
Exposure (E)	1	67·66		395·68		2494·30		1069·78		234 677·10	
T × B	22†, 24‡, 12§	2·24	2·41**	2·09	1·56	17·78	1·94	11·42	2·10	4 664·91	
T × E	11†, 12‡, 6§	6·73	6·44***	29·14	16·37***	421·30	22·35***	211·65	19·44***	48 437·11	
B × E	2	1·12	1·07	0·02	0·01	9·11	0·48	9·65	0·89	271·92	0·08
T × B × E	22†, 24‡, 12§	1·05	1·13	1·78	1·32	18·85	2·06	10·89	2·00	3 290·51	4·92***
Block (B × E × T)	144†, 156‡, 84§	0·93	2·08***	1·34	1·40**	9·15	2·70***	5·44	2·16***	668·29	1·06
Residual	864†, 936‡, 1134§	0·45		0·96		3·39		2·52		630·76	
Cochran's test		$P > 0{\cdot}05$		$P > 0{\cdot}05$		$P < 0{\cdot}01$		$P < 0{\cdot}01$		$P < 0{\cdot}01$	
Transformation		$\ln(x + 1)$		$\ln(x + 1)$		None		None		None	

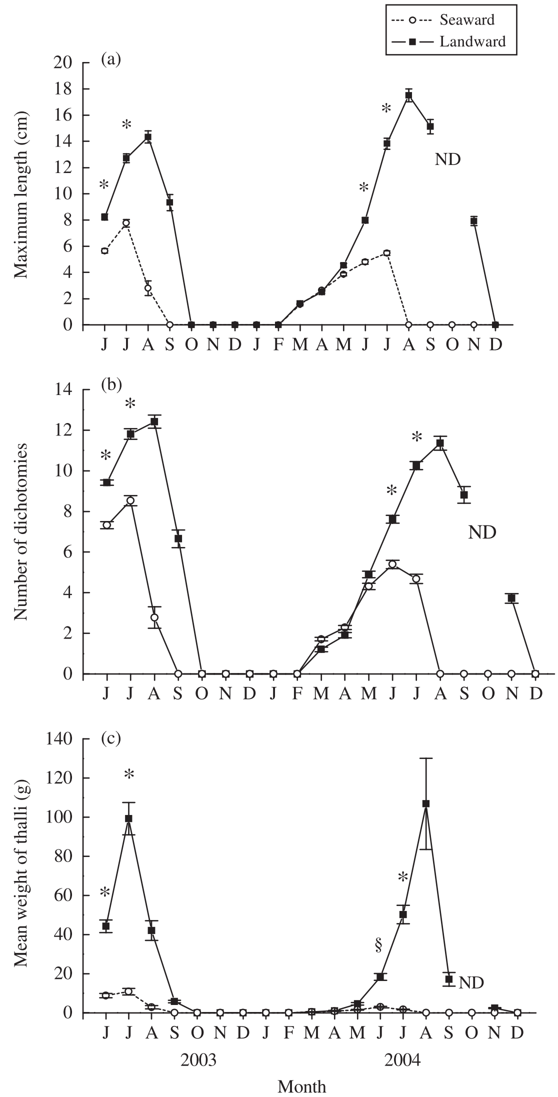

Fig. 2. Maximum length of fronds (a), degree of branching (b) and weight of thalli (c) of *Codium* on the landward and seaward sides of breakwaters in Cesenatico. Data are averages (± 1 SE) from 90 replicate thalli (10 thalli for each of three replicate blocks for each of three breakwaters); ND, no data. Asterisks indicate significant differences between the landward and seaward sides (SNK tests); § in (c) indicates that differences were significant on two of the three breakwaters. August 2003 was not included in the analyses because only 16 thalli could be found on blocks at the seaward sides of breakwaters.

varied between the landward and seaward sides of the breakwaters (Fig. 4 and Table 3b). The removal of mussels led to an increase in the percentage cover of *Codium* in landward habitats, while it caused a decrease in seaward habitats. These effects were consistent among breakwaters but not among blocks (Table 3b).

EFFECTS OF MUSSELS ON THE SURVIVAL OF *CODIUM* IN WAVE-EXPOSED HABITATS

The removal of mussels around the holdfast of thalli of *Codium* on blocks on the seaward sides of the breakwaters significantly decreased the survival of thalli after 8–10 days from the beginning of the experiment (Fig. 5 and Table 4).

Table 3. (a) ANOVA of the effects of breakwater, exposure, treatment (removal of mussels in April 2003 vs. August 2003 vs. January 2004 vs. control) and block on the percentage cover of *Codium* in May 2004; (b) ANOVA of the effects of breakwater, exposure, treatment (removal of mussels in April 2003 vs. control) and block on the percentage cover of *Codium* in June 2003. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Source of variation	(a)	d.f.	MS	*F*	(b)	d.f.	MS	*F*
Breakwater (B)		2	17·32	14·32***		2	1·75	0·65
Exposure (E)		1	9·30	2·50		1	1·77	
Treatment (T)		3	13·50	19·65**		1	0·00	
B × E		2	3·71	3·07		2	0·68	0·25
B × T		6	0·69	0·57		2	0·77	0·28
E × T		3	1·58	2·29		1	23·78	42·78*
B × E × T		6	0·69	0·57		2	0·56	0·21
Block (B × E × T)		72	1·21	2·95***		36	2·71	2·50***
Residual		288	0·41			144	1·08	
Cochran's test	*P* > 0·05				*P* > 0·05			
Transformation	ln(*x* + 1)				ln(*x* + 1)			
SNK tests	Treatment				Exposure × treatment			
	Aug03 > Control = Jan04 = Apr03				Landward: removal > control			
					Seaward: control > removal			

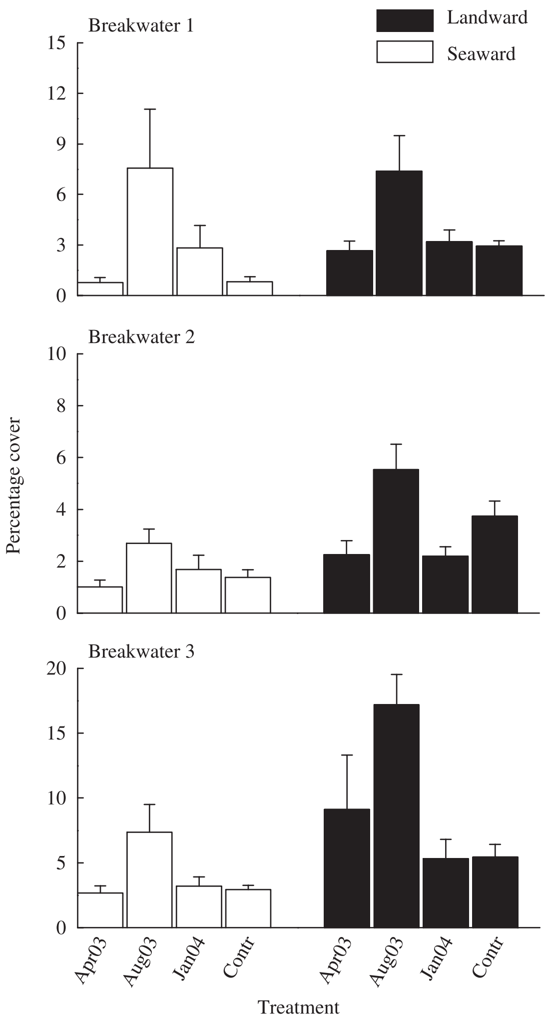

Fig. 3. Effects of the removal of mussels at different times of the year (April 2003, August 2003, January 2004 vs. control; Apr03, Aug03, Jan04, Contr, respectively) on the percentage cover of *Codium* in May 2004 on the landward and seaward sides of each of three breakwaters. Data are averages (+ 1 SE) from 16 replicate quadrats (four quadrats on each of four blocks). Note different *y*-axis scales.

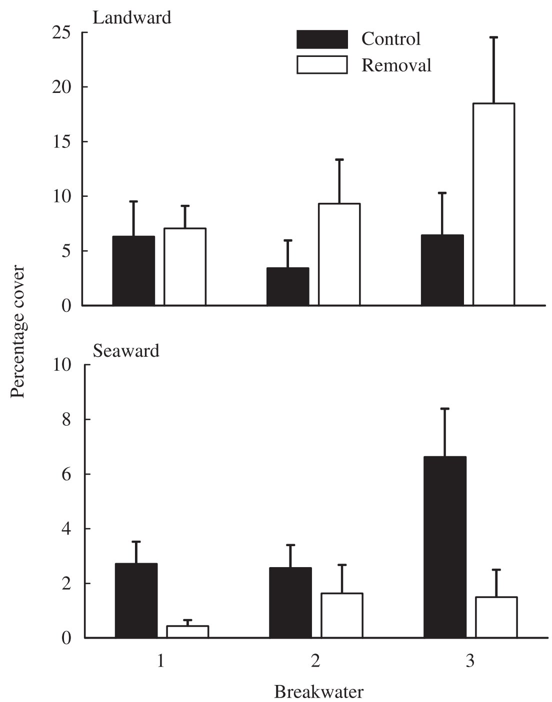

Fig. 4. Effects of the removal of mussels in April 2003 on the regeneration of macroscopic thalli of *Codium* (in June 2003), separately for the landward and the seaward sides of each of three breakwaters. Data are averages (+ 1 SE) from 16 replicate quadrats (four quadrats for each of four blocks). Note different *y*-axis scales.

The effects of the manipulation of mussels were consistent among breakwaters and between the two starts of the experiment, May 2003 and 2004 (Fig. 5 and Table 4).

Discussion

Codium has successfully established on coastal defence structures along the north-east coast of the Adriatic Sea, attaining covers comparable with those observed in the north-west Atlantic, where this species is spreading

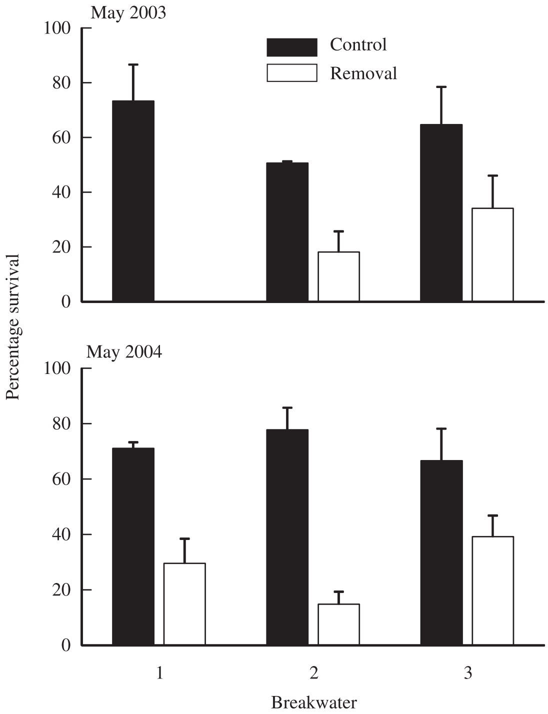

Fig. 5. Effects of the removal of mussels from thallus holdfasts on the survival of *Codium* on the seaward sides of each of three breakwaters, separately for the experiments started in May 2003 and May 2004. Survival (%) was calculated after 10 and 8 days, respectively, for May 2003 and 2004, on an initial number of 10–12 thalli. Data are averages (+ 1 SE) from three replicate blocks.

rapidly (Chapman, Scheibling & Chapman 2002; Levin *et al*. 2002; Bégin & Scheibling 2003). *Codium* was not previously reported among the components of marine flora along the coast included in our survey (Furnari *et al*. 2003), suggesting that the colonization of artificial habitats is recent and that this population is rapidly expanding. This is in contrast with trends of regression of *Codium* documented in other regions of the Mediterranean (Boudouresque 1994).

The north-eastern Adriatic has environmental characteristics that make it particularly susceptible to invasion (Occhipinti-Ambrogi 2001), including the presence of many potential sources (ports and aquaculture), a large variation in salinity and temperature and enrichment in nutrients. At the same time, the small availability of natural hard substrata suitable for the colonization of *Codium* in the region should have represented a natural barrier to its spread. The proliferation of defence structures has undeniably played a key role in the establishment and spread of *Codium* along the coasts of the north Adriatic Sea by providing suitable habitat for its settlement.

The sheltered, landward sides of breakwaters represent far better habitat for *Codium* than the seaward, exposed sides, in agreement with previous studies indicating that the colonization of this weed is enhanced in sheltered conditions, such as embayments and harbours (Trowbridge 1995, 1998; Trowbridge & Farnham 2004). In early spring, when the new generation of macroscopic thalli grows back, the density, percentage cover and

Table 4. Analysis of the effects of the removal of mussels on the percentage survival of *Codium* on the seaward sides of breakwaters, in May 2003 (Start 1) and May 2004 (Start 2). Pooling procedures were used according to Winer, Brown & Michels (1991); terms were eliminated when not significant at $P = 0{\cdot}25$. $^*P < 0{\cdot}05$

Source of variation	d.f.	MS	*F*
Start (S)	1	845·84	9·52
Breakwater (B)	2	371·14	4·18
Treatment (T)	1	18010·53†	28·87*
S × B	2	88·87	0·38
S × T	1	5·06	Eliminated
B × T	2	623·83	0·86
S × B × T	2	727·85	3·12
Residual	24	233·26	
Cochran's test	*P* > 0·05		
Transformation	None		

†Tested against the interaction breakwater × treatment.

morphology of *Codium* did not differ between the landward and seaward sides of breakwaters. Over the summer, however, more thalli persisted on landward than seaward sides and these could grow longer and more branched, forming dense canopies. Despite their small size, which should have reduced the probability of dislodgement (Blanchette 1997), only few scattered thalli of *Codium* survived in exposed habitats. After the peak of growth in July–August, the abundance and size of *Codium* also decreased in sheltered habitats, but sufficient thalli survived long enough to develop gametangia. The landward sides of breakwaters are therefore crucial for the persistence of *Codium* along the north-east coast of the Adriatic Sea, where sheltered hard substrata are naturally scarce.

The effects of local regime of disturbance on resident mussel beds also facilitated the persistence of *Codium* in sheltered habitats. Although *Codium* is able to settle on a variety of substrata, most adult thalli were directly attached to the rock. Juvenile thalli of *Codium* attached to mussels were found occasionally on the landward sides of breakwaters in the spring, but these were generally torn off the substratum as *Codium* reached a larger size (F. Bulleri *et al*., unpublished data). The availability of bare space is therefore a limiting resource for *Codium* in these habitats, as also observed elsewhere (Trowbridge 1995; Trowbridge & Todd 1999; Levin *et al*. 2002). Because *Codium* releases gametes over a relatively narrow temporal window at the end of the summer (F. Bulleri *et al*., unpublished data), the time at which patches of bare space were opened within mussel beds was crucial. Disturbance in April and January did not affect recruitment of *Codium*, but removal of mussels in August, shortly before gamete release, was effective in enhancing recruitment on both sides of breakwaters. In the study area, mortality of mussels on the landward sides of breakwaters is considerable over the summer because of a combination of illegal recreational harvesting of mussels, heat stress and wave effects (Airoldi *et al*. 2005). Such a regime of disturbance provides bare space for *Codium* at the right time of the year.

The effect of disturbance in regulating the interaction between mussels and *Codium* was more complex on the seaward sides of breakwaters. Although removal of mussels in August also had positive effects on recruitment of *Codium* at these exposed habitats, the subsequent survival of thalli was clearly dependent on facilitative effects of mussels. Under harsh physical conditions found on the seaward sides of breakwaters, facilitation tends to override competition (Bertness & Callaway 1994). Thus, overall effects of disturbance to mussel beds on *Codium* are probably negative and this could explain the poor performance of this weed in exposed habitats.

Codium rapidly responded to removal of mussels between April and June 2003. As presumably no significant release of propagules occurred at this time of the year, differences between treatments were attributed to resting vaucherioid filaments, holdfasts or propagules responding to the removal of the above matrix of mussels. Such responses were positive in sheltered habitats but negative in exposed habitats and may reflect the different structure of mussel beds. Mussels at the landward sides achieved larger sizes and formed thick beds that could prevent the regeneration of underneath resting stages of *Codium*. In contrast, mussels at the seaward sides were smaller and formed thinner beds that probably did not completely prevent the regrowth of thalli. Although resting stages can contribute over the short-term to the adult population of *Codium*, their contribution from one year to the next was negligible compared with that of propagules, as suggested by the lack of significant effects of April removals in the following May 2004.

Regardless of their invasibility in comparison with natural habitats, proliferation of artificial structures in the study area has created corridors for the dispersal of non-indigenous species across areas of unsuitable habitat. Under these circumstances, increasing our understanding of the role played by artificial structures in patterns of biological invasions is pivotal for predicting pathways and locales susceptible to invasions, according to the relevant life-history traits of potential invaders. Alternative management at regional and local levels could effectively minimize their importance as habitats for non-indigenous species. For example, the positioning of artificial structures along sandy or muddy coasts could be planned at a regional scale taking into account the dispersal ability of potential invaders (Airoldi *et al*. in press). A minimum distance between contiguous schemes of artificial structures greater than the maximum distance over which propagules of potential invaders can disperse would prevent artificial structures functioning as stepping stones. At local scales, alternative designs of artificial structures (e.g. type of substratum, complexity and heterogeneity) could enable compromises between the need to fulfil the primary economic and social goals for which they are built and environmental requirements. Chemical and physical attributes of artificial structures could be successfully controlled in order to decrease their suitability to potential invaders or promote the establishment of native assemblages more resistant to invasion. Finally, human usage of artificial habitats should be regulated according to similar principles driving protection and conservation of natural habitats (Airoldi *et al*. 2005); in the study area, preventing the harvesting of mussels from breakwaters during the summer could alone be effective at preserving the integrity of mussel beds and, hence, sensibly reducing recruitment of *Codium*.

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