



Status of vulnerable *Cystoseira* populations along the Italian infralittoral fringe, and relationships with environmental and anthropogenic variables

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ABSTRACT

We analyzed the occurrence and status of infralittoral fringe populations of *Cystoseira* spp. (Fucales) at thirteen rocky sites around the Italian coastline, and explored the relationships with relevant environmental and anthropogenic variables. We found *Cystoseira* populations at 11 sites: most were scattered and comprised mono-specific stands of *C. compressa*, and only 6 sites also supported sparse specimens of either *C. amentacea* var. *stricta* or *C. brachycarpa*. Coastal human population density, Chlorophyll *a* seawater concentrations, sea surface temperature, annual range of sea surface temperature and wave fetch explained most of the variation of the status of *C. compressa*. We hypothesize a generally unhealthy state of the Italian *Cystoseira* infralittoral fringe populations and identify multiple co-occurring anthropogenic stressors as the likely drivers of these poor conditions. Extensive baseline monitoring is needed to describe how *Cystoseira* populations are changing, and implement a management framework for the conservation of these valuable but vulnerable habitats.

1. Introduction

Shallow coastal areas comprise some of the most productive, diverse and at the same time threatened marine ecosystems (Harley et al., 2006; Airoidi and Beck, 2007). Pollution, overfishing, habitat destruction, coastal development, and the introduction of alien species have all severely affected shallow marine ecosystems (Airoidi and Beck, 2007; Crain et al., 2009; Claudet and Frascchetti, 2010; Coll et al., 2010). Fragmentation and loss are further exacerbated by global climatic changes, such as acidification, increased sea-surface temperatures and increased the frequency of extreme events (Micheli et al., 2013). These escalating impacts require identification of the factors enhancing or inhibiting the future persistence of coastal ecosystems (Brown et al., 2013, 2014; Giakoumi et al., 2015), so that adequate management can be put in place. Amount of remaining biogenic habitat, physical setting, and local-scale stressors are some of the factors most frequently identified as critical in promoting or preventing the capability of marine ecosystems to respond to increasing cumulative disturbances (O'Leary et al., 2017).

Canopy-forming algae form some of the most diverse, productive and valuable ecosystems along intertidal and shallow subtidal rocky coasts (Steneck et al., 2002). In the Mediterranean Sea, canopy-forming

algae are mainly comprised of species of the genus *Cystoseira* C. Agardh (Fucales, Phaeophyceae). Their distribution is controlled by several environmental variables including depth, water temperature, substratum characteristics, coastline geomorphology, wave exposure and nutrient concentrations (Giaccone and Bruni, 1973; Ballesteros, 1990; Falace et al., 2005; Ballesteros et al., 2007; Sales and Ballesteros, 2009; Nikolić et al., 2013; Lasinio et al., 2017). Further, human pressures are increasingly limiting their distribution (Chrysosvergis and Panayotidis, 1995; Rodríguez-Prieto and Polo, 1996; Soltan et al., 2001; Arevalo et al., 2007; Sales et al., 2011). During the last decades *Cystoseira* populations have retracted their ranges considerably particularly close to urban areas (Benedetti-Cecchi et al., 2001; Soltan et al., 2001; Thibaut et al., 2005, 2015; Ballesteros et al., 2007; Mangialajo et al., 2007, 2008; Perkol-Finkel and Airoidi, 2010), being replaced by structurally less complex communities dominated by turf-forming, or other ephemeral seaweeds, mussels (Benedetti-Cecchi et al., 2001; Connell et al., 2014; Strain et al., 2014) or sea urchin barrens (Agnetta et al., 2015). The sensitivity of *Cystoseira* populations and other canopy algae to a variety of anthropogenic stressors is increasingly well understood (Ballesteros et al., 2007; Mangialajo et al., 2007; Asnaghi et al., 2009; Sales et al., 2011), making these systems useful indicators of water and ecosystem quality according to the Water Framework Directive (2000/

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60/EC) (Commission, E., 2000). Nevertheless, the factors ultimately explaining their distribution and capability to persist have been harder to identify (Sales and Ballesteros, 2009; Perkol-Finkel and Airoldi, 2010; Strain et al., 2015; Buonomo et al., 2017b), probably involving many interacting environmental, biological and anthropogenic variables (Strain et al., 2014). Indeed, while many regions have experienced dramatic loss of these ecosystems (Airoldi et al., 2014 and references therein; Thibaut et al., 2015), in other regions losses have been limited to the most severely impacted sites and some populations have surprisingly persisted in a relatively healthy status (Thibaut et al., 2014). Understanding what factors or combinations of factors control the ultimate distribution and conditions of these ecosystems is a key priority to establish effective conservation measures.

Several species of *Cystoseira* typically contribute to form dense, narrow (about 20–30 cm in height) fringing belts along the microtidal Mediterranean rocky coastline. Lying between the littoral and the sublittoral zones, this infralittoral fringe is a particularly vulnerable area, being subject to a range of natural as well as anthropogenic disturbances originating from both the land and the sea (Thompson et al., 2002). Despite its recognized value and vulnerability, data on the distribution and status of this habitat are surprisingly limited. Descriptions are available for some areas or regions, but broader-scale ecological analyses are rare.

We analyzed the distribution and abundance of infralittoral fringe populations of *Cystoseira* at 13 rocky coast localities along the Italian coastline, covering a range of biogeographic location, environmental characteristics and levels of anthropogenic pressures. For the most common species, *C. compressa*, we described its ecological status as a combination of percentage cover, density, morphometric characteristics, and abundance of epiphytes. Thallus height and branches length are typically affected by a variety of factors including temperature, photoperiod, and wave exposure (Gómez-Garreta et al., 2002; Falace et al., 2005), thereby providing relevant ecological indications, and low cover, density or excess coverage by epibiota can be reflective of unhealthy conditions (Reference). We further tested whether any variation in these “ecological status” descriptors was related to environmental and anthropogenic factors potentially relevant for the growth and/or distribution of macroalgae in the infralittoral fringe, including wave exposure, photosynthetic active radiation, salinity, tidal range, seawater temperature, annual range of sea surface temperature, marine Chlorophyll *a*, nitrate and phosphate concentrations, distance from nearest urban centre and coastal human population density. Light conditions can influence the growth of *C. compressa*, and wave exposure can affect its morphology (Gómez-Garreta et al., 2002; Falace et al., 2005). Seawater temperature and its variations can have profound effects on seaweeds, affecting the growth, reproduction, survival and distribution of macroalgae (Graiff et al., 2015; Martínez et al., 2015). Salinity was reported to affect the phenotypic variability of *Fucus vesiculosus* (Ruuskanen and Bäck, 1999), while the morphology of the intertidal fucoid *Hormosira banksii* changed with tidal regime (Mueller et al., 2015). Rarefaction and/or disappearance of *Cystoseira* species (Mangialajo et al., 2008; Sales and Ballesteros, 2009) have been related to high anthropogenic pressures and concentrations of nutrients (Chlorophyll *a*, nitrate and phosphate). We discuss our results in light of previous findings of *Cystoseira* along the Italian coasts to explore ongoing trends and suggest priority areas of intervention.

2. Materials and methods

2.1. Study sites, species and environmental and anthropogenic factors

The Italian peninsula and its islands extend > 950 km from north to south into the central Mediterranean basin, with a coastline of approximately 7600 km. Flat sandy shores alternate with high rocky coasts along the peninsula that is surrounded by four different seas (Fig. 1). Despite the presence of several Marine Protected Areas (MPA),

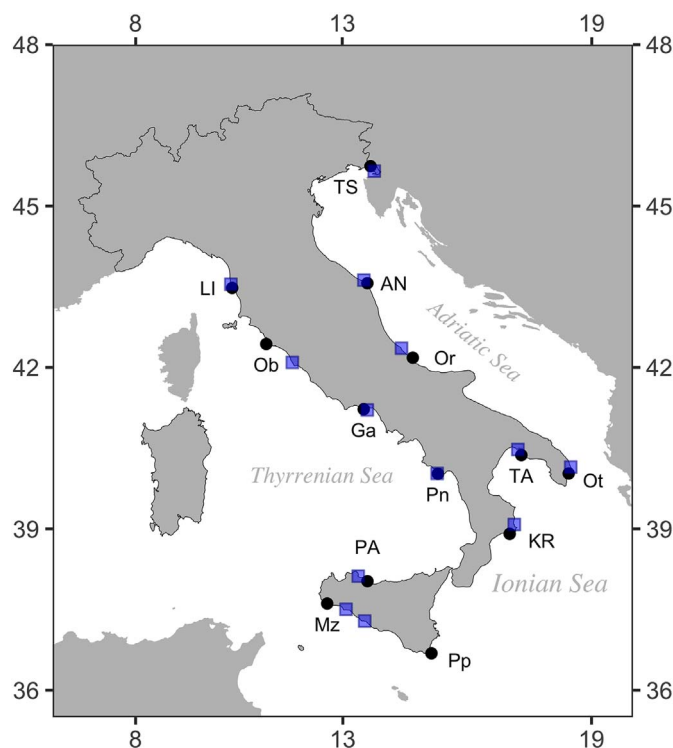


Fig. 1. Location of the 13 rocky study sites along the Italian coastline (black dots). TS: Trieste (Grignano), AN: Ancona (Portonovo), LI: Livorno (Calafuria), Ob: Orbetello (Santo Stefano), Or: Ortona (Punta Aderci), Ga: Gaeta (Torre San Vito), Pn: Palinuro (Faracchio), Ot: Otranto (Santa Cesarea Terme), TA: Taranto (Leporano Marina), KR: Crotona (Le Castella), PA: Palermo (Altavilla), Mz: Trapani (Mazara del Vallo), Pp: Siracusa (Portopalo di Capo Passero). The position of the ISPR buoys is indicated by the blue squares. Geographic coordinates of the sites and ISPR buoys are reported in Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the Italian coast is generally overexploited, as the long and narrow shape and the mountainous geography tend to concentrate the large population along the coasts.

We sampled the infralittoral fringe, from mean sea level MSL to extreme low water of spring tides ELWS, ≈ -30 cm. Few species of *Cystoseira* can potentially colonize this zone along the Italian coasts: *C. amentacea* (*C. Agardh*) Bory and its variety *C. amentacea* var. *stricta* Montagne, *C. mediterranea* Sauvageau, *C. tamariscifolia* (Hudson) Papenfuss, *C. compressa* (Esper) Gerloff & Nizamuddin and more rarely *C. brachycarpa* J. Agardh and *C. humilis* Schousboe ex Kützting (Giaccone and Bruni, 1973; Ballesteros and Romero, 1988; Giaccone et al., 1992, 1993, 1994; Gómez-Garreta et al., 2002; Piazzini and Cinelli, 2002; Piazzini et al., 2009; Furnari et al., 2010). *C. amentacea*, *C. compressa*, *C. brachycarpa* and *C. humilis* can potentially occur in many regions around the Italian coasts, while *C. mediterranea* and *C. tamariscifolia* are limited to few areas (Furnari et al., 2010). *C. compressa* is the most common species, being relatively tolerant to some environmental and anthropogenic stressors compared to other species of *Cystoseira* (Thibaut et al., 2005; Mangialajo et al., 2008).

Sampling was carried out at 13 locations (hereafter referred to as sites; Fig. 1; Table S1), characterized by the presence of extensive rocky shores and accessible from the coast without using a boat. The sites were selected to represent a variety of different conditions along the Italian peninsula and to cover a wide latitudinal gradient. The final choice was also dictated by the proximity to oceanographic buoys, which were needed to access important environmental parameters. All sites presented naturally exposed, gently sloping to sub-vertical rocky platforms, typically favorable for the growth of *Cystoseira* spp. (Laminio et al., 2017). The main environmental and anthropogenic characteristics for each site are summarized in Table 1 and described as part of the results.

Table 1

Environmental and anthropogenic variables at the study sites. Chla = average annual value of Chlorophyll *a* seawater concentration; PAR = average annual value of Photosynthetic Active Radiation; SBOT = average annual value salinity; Fetch = wave fetch expressed as log₁₀ of numbers of cells of fetch values; SST = mean annual sea surface temperature; SST-range = annual range of sea surface temperature; Tide = average annual value tidal range; N = average annual value of nitrate seawater concentration; P = average annual value of phosphate seawater concentration; Dens.pop.10 km = coastal human population density expressed as the number of residents per km²; Dist.uc = distance in meter from the urban center. Site codes as in Fig. 1 and Table S1.

Site	Chla (mg/m ³)	PAR (E/m ² /day)	SBOT (psu)	SST (°C)	SST-range (°C)	Tide (cm)	Fetch (log ₁₀ (cells))	N (mmol/m ³)	P (mmol/m ³)	Dist.uc (m)	Dens.pop.10 km (n° ind/km ²)
TS	1.13	30.66	36.27	16.50	17.10	89.10	3.24	22.89	0.07	3716	803
AN	1.90	31.18	34.84	16.40	17.90	31.70	3.58	7.27	0.02	6050	70
LI	0.45	32.48	38.74	18.80	12.80	31.40	3.57	0.62	0.02	610	49
Ob	0.28	34.39	38.75	18.70	5.80	26.50	3.11	0.40	0.02	0	138
Or	1.28	32.76	36.90	17.50	18.50	36.00	3.58	0.53	0.02	4309	52
Ga	0.79	34.15	38.81	19.20	11.70	33.70	3.62	0.29	0.01	2617	402
TA	0.29	35.01	38.97	18.70	14.40	30.50	3.45	0.30	0.02	0	409
Ot	0.31	35.16	38.85	18.80	14.50	39.10	3.53	0.53	0.02	347	52
Ph	0.17	35.47	38.81	19.80	12.30	31.80	3.41	0.22	0.02	916	98
KR	0.28	34.95	39.11	19.10	14.30	24.40	3.50	0.24	0.02	0	67
PA	0.26	36.11	38.90	20.00	12.70	29.70	3.60	0.21	0.02	0	188
MZ	0.23	37.09	39.06	19.10	8.70	19.60	3.62	0.14	0.02	0	211
Pp	0.22	38.50	39.34	18.90	8.90	23.70	3.53	0.07	0.01	0	58

For each study site, we collected data relative to 9 environmental (mean sea surface temperature SST, annual range of sea surface temperature SST-range - calculated as difference between the mean temperatures of the warmest and coldest months of the year - tidal range, photosynthetic active radiation PAR, salinity, wave action, and seawater concentrations of Chlorophyll *a*, nitrate and phosphate) and 2 anthropogenic (population density and distance from nearest town) variables (Table 1) that could potentially affect *Cystoseira* populations. Whenever available, we retrieved data over at least 10 years. Estimates of SST, SST-range and tidal range were derived by the closest ISPRA (Istituto Superiore per la Protezione e Ricerca Ambientale, www.mareografico.it, temporal range 2000–2012) buoy to the site of interest (Fig. 1). The annual mean marine Chlorophyll *a* concentration, PAR and salinity at each site were obtained from the Environmental Marine Information System (EMIS, mcc.jrc.ec.europa.eu/emis/, temporal range 2003–2012, spatial resolution 4 km) using the “EMISR” R package (Dubroca, 2014). Annual means of nitrate and phosphate concentrations were obtained from the “biogeochemical model and data assimilation of surface Chlorophyll concentration” based on satellite data OPATM-BFM (Generated using CMEMS products, <http://marine.copernicus.eu/>, temporal range 2002–2012). Wave fetch was calculated as the sum of fetch values in the cells (200 m) defined by 16 angular sectors (22.5° each) and expressed as log₁₀ (Burrows et al., 2008). This method provides an objective measure of wave exposure and allows to separate the effects of wave exposure from the variation due to other factors (Burrows et al., 2008; Burrows, 2012). High wave exposure can increase density, cover, morphology of canopy-forming algae, also reducing epiphyte load and increase nutrient exchange (Pedersen et al., 2012; Smale and Moore, 2017). Coastal population density in a radius of 10 km from each site of interest was derived from ISTAT (Istituto Nazionale di Statistica, data series 2011). The distance along a straight line to the nearest urban center was calculated using a geographical information system (GIS) taking the distance from the site to the nearest “centro abitato” (meaning “urban center”) polygon, using the shapefile “Sezioni litoranee” provided by ISTAT.

2.2. Ecological status of *Cystoseira* populations

Sampling was carried out from 24 June to 23 July 2013, when the erect fronds of *Cystoseira* (a genus with vegetative seasonality) were still well present at all study sites where we could find the species. At each site, we visually explored an area encompassing about 50 m of rocky shore. If the species was not found, we further expanded the area to check for the species presence up to around 300 m of coast. At each site where we could find *Cystoseira*, we identified the species and estimated their percentage cover and density at low tide, using 6, randomly located quadrats (30 × 30 cm). Where we could not find *Cystoseira*, cover and density were set as zero. These values do not imply that the species is not present elsewhere in the region, but still suggest a limited occurrence and potentially depleted status. Cover was estimated as described by Dethier et al. (1993), using a frame divided into 25 equal squares: we attributed a cover score from 0 to 4 to each square, and then summed up scores where the taxon was present. Organisms filling < 1/4 square were given the value of 0.5. The density of each species of *Cystoseira* was estimated as the number of individuals per quadrat.

C. compressa was the only species common enough to test for possible relationships between its ecological status (described as a combination of percentage cover, density, morphometric characteristics, and abundance of epiphytes) and environmental/anthropogenic factors across sites. At each site, we randomly collected 10 thalli of this species, which were fixed in a 4% formalin seawater solution for subsequent laboratory morphometric measurements (Falace et al., 2005). These measures included: thallus height, from the basal disc to the tip of the frond; frond width, measured as major lateral distance of the thallus placed on a plane surface; average length and diameter of primary and

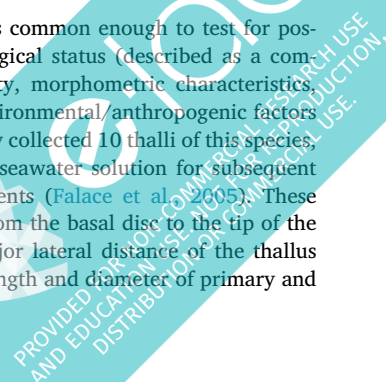


Table 2

Descriptors of the ecological status of *C. compressa*. Values are means \pm SD ($n = 6$ – 10). Cover = percentage cover of *C. compressa*; Density = density of *C. compressa*; AFDW = ash free dry weight; Th_h = thallus height; Fr_w = frond width; Bl_1 = first order branch length; Bl_2 = second order branch length; Bd_1 = first order branch diameter; Bd_2 = second order branch diameter; w_epi = total weight of epiphytes; n_epi = total number of epiphyte species. Site codes as in Fig. 1 and Table S1.

Site	Cover (%/30cm ²)	Density (n° ind/30cm ²)	AFDW (gr)	Th_h (mm)	Fr_w (mm)	Bl_1 (mm)	Bl_2 (mm)	Bd_1 (mm)	Bd_2 (mm)	w_epi (gr)	n_epi (n° ind)
TS	0	0	0	0	0	0	0	0	0	0	0
AN	25.0 \pm 20.0	3 \pm 2	0.72 \pm 0.2	92.9 \pm 22.8	28.2 \pm 7.1	53.7 \pm 17.7	28 \pm 3.4	1.7 \pm 0.2	0.9 \pm 0.1	8.02	2
LI	18.3 \pm 7.8	5 \pm 2	1.62 \pm 0.4	96.1 \pm 13.9	46.7 \pm 8.3	54.5 \pm 10	22.6 \pm 2.8	1.7 \pm 0.2	1.2 \pm 0.2	0.26	1
Ob	0.5 \pm 0.8	0 \pm 1	0.52 \pm 0	43.8 \pm 1.7	48 \pm 12.6	43 \pm 4.4	17.4 \pm 4.5	2.6 \pm 0.5	2 \pm 0	0	0
Or	23.0 \pm 11.4	3 \pm 0	3.43 \pm 1.9	222.3 \pm 7.8	43.2 \pm 7.1	81.1 \pm 24.7	37.1 \pm 7	1.6 \pm 0.1	1.2 \pm 0.2	3.79	2
Ga	15.5 \pm 18.0	2 \pm 2	1.23 \pm 0.6	95 \pm 15.6	37.8 \pm 12.9	61.8 \pm 16.9	23.4 \pm 2.1	1.6 \pm 0.1	1.1 \pm 0.1	4.02	2
TA	0	0	0	0	0	0	0	0	0	0	0
Ot	12.8 \pm 17.4	1 \pm 2	0.49 \pm 0.3	53.1 \pm 17.8	39.1 \pm 11.2	36.4 \pm 11	17.8 \pm 4.1	1.3 \pm 0.1	0.9 \pm 0.1	0	0
Pn	0.3 \pm 0.5	0 \pm 1	0.47 \pm 0.1	35.4 \pm 5.8	50.1 \pm 9	35.9 \pm 4.4	15.1 \pm 2.8	3 \pm 0.8	2.6 \pm 0.5	0	0
KR	37.7 \pm 22.3	5 \pm 3	1.67 \pm 0.9	147.6 \pm 33.4	57.6 \pm 13.2	76.5 \pm 15.8	24.5 \pm 5.9	1.3 \pm 0.2	0.8 \pm 0.1	0	0
PA	7.5 \pm 8.4	2 \pm 1	0.3 \pm 0.1	59 \pm 13	47.9 \pm 11.1	27.5 \pm 4.7	13.3 \pm 3.3	1 \pm 0.2	0.6 \pm 0.1	0.03	1
Mz	27.1 \pm 22.3	3 \pm 1	3.39 \pm 1.3	165.3 \pm 23.1	47.1 \pm 6.9	77.2 \pm 9.1	27.7 \pm 4.4	1.5 \pm 0.1	1.1 \pm 0.1	0.31	1
Pp	6.6 \pm 8.4	1 \pm 2	3.61 \pm 0.8	107.9 \pm 27.2	63 \pm 6.8	61.1 \pm 11.3	27.5 \pm 4.2	1.4 \pm 0.1	1 \pm 0.1	0.09	1

secondary branches ($n = 4$); and ash-free dry weight (AFDW), measured after immersing the thalli in a HCl solution (5%, v/v) for 24 h to remove possible calcareous epiphytes, drying them at 60 °C for 48 h and then placing them in a muffle furnace at 500 °C for 4 h (Stein-Taylor et al., 1985).

We also recorded the abundance and composition of the most common epibiota of *C. compressa*, which could directly or indirectly affect their hosts (see Discussion). For each thallus, epibiota were removed, weighed (wet weight) and identified to the lowest possible taxonomic level, compatibly with the small sizes and/or the absence of characters facilitating their identification (e.g. reproductive structures).

2.3. Data analyses

For each site, we calculated the average of percentage covers ($n = 6$), densities ($n = 6$), morphometric measures ($n = 10$) and amounts of epiphytes ($n = 10$) of *C. compressa* (Table 2). We then explored if there was any relationship between the set of “status” descriptors and the set of key local environmental and anthropogenic variables across sites. We used the “chart.Correlation” function in the “PerformanceAnalytics” R package (Peterson and Carl, 2014) to detect strong correlations between or possible skewness of environmental and anthropogenic variables. We corrected for right-skewness by applying a $\log(x + 1)$ transformation to nitrate, phosphate and Chlorophyll *a* concentrations, and a square root transformation of distance to the nearest urban center and coastal human population density. Due to the high correlation of phosphate concentration with tidal range ($\text{cor.} = 0.91$) we removed phosphate concentrations from the subsequent analyses (Fig. S2). Moreover, we removed salinity because highly correlated with Chlorophyll *a* concentration ($\text{cor.} = -0.92$) and sea surface temperature ($\text{cor.} = -0.91$), and Distance from urban center because highly related with Chlorophyll *a* concentration ($\text{cor.} = 0.92$) (Fig. S1). Similarly, we investigated possible skewness and/or strong correlation among pairs of descriptors of the ecological status of *C. compressa*. We applied a square-root transformation to AFDW, thallus height, weight of epiphytes, cover and density of *C. compressa* to correct for right-skewness (Fig. S1). We retained variables with a correlation below 0.90: AFDW, frond width, branches diameter of the second order, weight of epiphytes and density of *C. compressa* (Fig. S2). We normalized the set of descriptors of the ecological status of *C. compressa* as they were expressed in different scales, and we created a Euclidean distance matrix to test the relationships with the environmental and anthropogenic parameters using a DistLM analysis (Legendre and Anderson, 1999). We performed this analysis using PERMANOVA + (Anderson et al., 2008) in PRIMER v.6 (Clarke and Gorley, 2006). We used Best and Bayesian Information Criterion (BIC)

as selection procedure and selection criterion respectively (9999 permutations), to find a reduced model that retained only variables with good explanatory power. BIC includes a more severe penalty for the inclusion of extraneous prediction variables, compared to the other selection criterion (es. R^2 , adjusted R^2 , AIC and AICc), and was preferred due to the small number of data points relative to the number of variables of this study, a problem known as Freedman's paradox (Anderson et al., 2008; Lukacs et al., 2010). We used a distance-based redundancy analysis (db-RDA) to visualize the reduced model obtained. Moreover, we superimposed vectors of the variable of the ecological status of *C. compressa* showing highest correlation (Pearson correlation) with the set of environmental and anthropogenic factors selected (Anderson et al., 2008).

3. Results

3.1. Environmental and anthropogenic variables

All sites were moderately exposed to waves, with fetch values $> 3 \log_{10}$ (cells). For most sites, average annual tides were ≈ 20 – 30 cm, except TS with average tides of ≈ 90 cm. Annual average seawater salinities were around 39 psu, with values < 37 psu at two sites only (AN and TS). Two sites, TS and AN presented the highest concentrations of nitrate (22.89 mmol/m³ and 7.27 mmol/m³ respectively) and Chlorophyll *a* (1.13 mg/m³, 1.90 mg/m³ respectively), while Or presented a value of 1.28 mg/m³ of Chlorophyll *a*. At the other sites nitrate and Chlorophyll *a* concentrations were < 0.62 mmol/m³ and < 0.79 mg/m³, respectively, with the minimum values registered for nitrates at Pp (0.07 mmol/m³) and for Chlorophyll *a* at Pn (0.17 mg/m³). Phosphate concentration ranged from 0.01 mmol/m³ at Pp and Ga to 0.07 mmol/m³ at TS. PAR and mean SST decreased with latitude (Fig. S3 A–B), with PAR ranging between ≈ 39 E/m²/day and ≈ 31 E/m²/day and SST ranging between 20 °C and 16 °C. An opposite trend was observed for the SST-range, that increased at northern sites as opposed to southern locations (Fig. S3 C). Six sites, KR, Mz, Ob, PA, Pp, and TA, were within an urban center section, while AN was the most distant site ~ 6 km. The coastal human population densities within a radius of 10 km ranged from ≈ 50 n° ind/Km² at LI, Or and Ot to ≈ 800 n° ind/Km² at TS.

3.2. Cover, density morphology and epibiota of *Cystoseira* spp.

At the 13 study sites we found 3 species of *Cystoseira*: *C. amantacea* var. *stricta*, *C. compressa* and *C. brachycarpa*. The three species were never simultaneously observed at any sites. Seven sites (KR, Ga, LI, Ot, Pn, Pp and Mz) presented combinations of two species; four sites (AN,

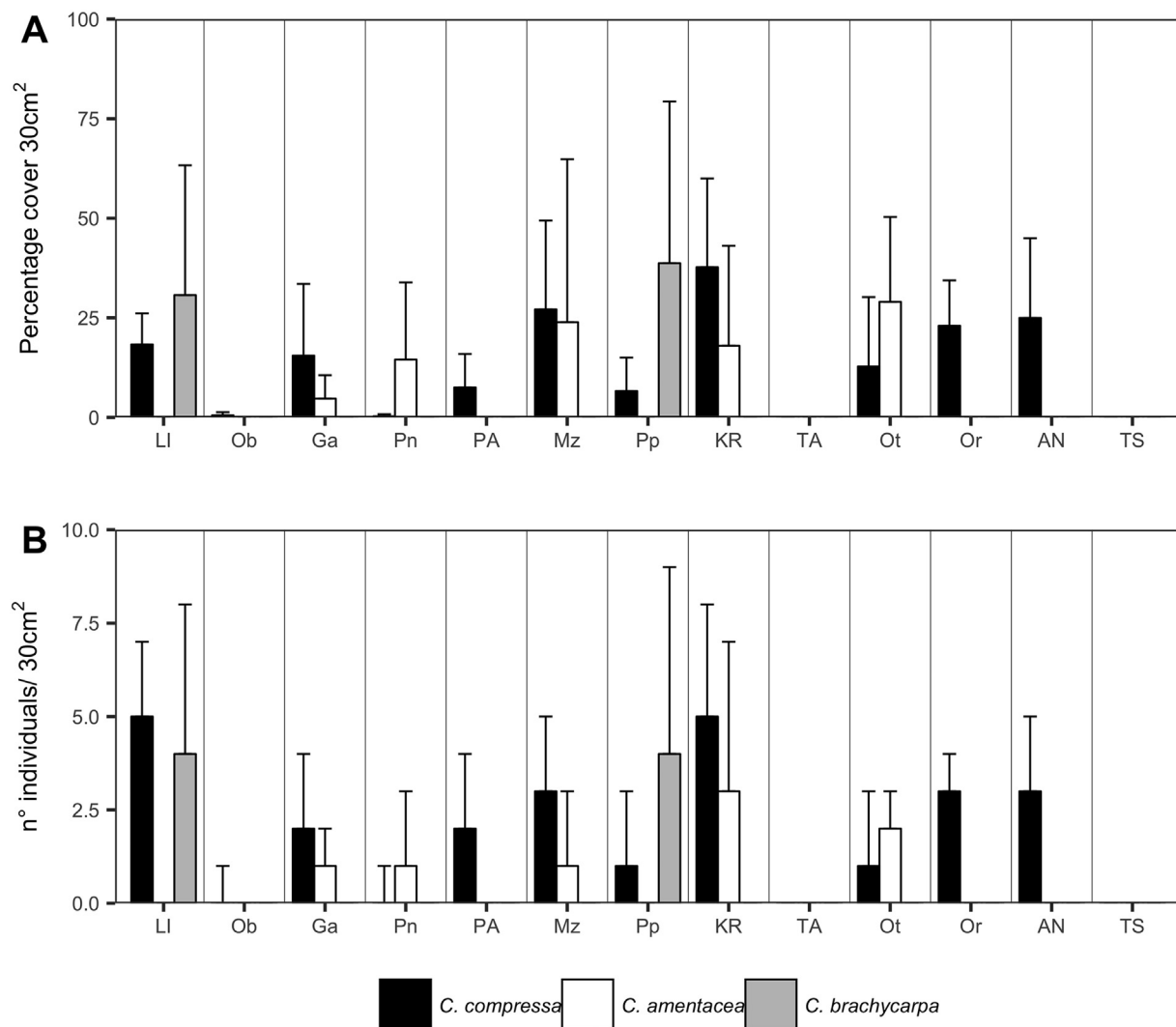


Fig. 2. Percentage cover (A) and density (B) of the 3 infralittoral fringe species of *Cystoseira* found at the 13 study sites. Data are averages \pm 1 SE ($n = 6$). Site codes as in Fig. 1 and Table S1.

Or, Ob and PA) presented one species only, while at two sites (TA and TS) we did not find any *Cystoseira*. Percentage cover and density differed largely both among and within sites (Fig. 2A and B). *C. amentacea* was found at 5 sites, with average percentage cover ranging from 5% at Ga to 24% at Mz. *C. brachycarpa* was found at 2 sites with an average cover of 30–38%. *C. compressa* was the most widespread species, occurring at 11 sites, but average percentage cover was always $< 38\%$ (Fig. 2A). The maximal average density was 5 individuals per plot (900 cm^2), reached by *C. compressa* at two sites, KR and LI, followed by *C. brachycarpa* with 4 individuals at Pp and LI, while *C. amentacea* reached 3 individuals only at KR (Fig. 2B).

The morphometric measures of *C. compressa* differed among sites (Table 2). For example, thallus length (Th_h) ranged from $35.4 \pm 5.8 \text{ mm}$ to $222.3 \pm 7.8 \text{ mm}$ at Pn and Or, respectively. Length of first-order branches (Bl₁) ranged from 27.5 ± 4.7 at PA to 81.1 ± 24.7 at Or, while the length of second-order branches (Bl₂) ranged from 13.3 ± 3.3 at PA to 37.1 ± 7 at Or. Only two sites, Ob and Pn, presented individuals of *C. compressa* with branch diameter (Bd₁, Bd₂) $> 2 \text{ mm}$, while little variation was found among the other sites, with average values about 1.5 mm. Biomasses (AFDW) were highest at Pp, Mz and Or, with $3.61 \pm 0.8 \text{ g}$, $3.43 \pm 1.9 \text{ g}$ and $3.39 \pm 1.3 \text{ g}$ respectively, and lowest at Ot, Pn and PA, with $0.49 \pm 0.3 \text{ g}$, 0.47 ± 0.1 and $0.3 \pm 0.1 \text{ g}$ respectively.

In total 22 epibiont taxa were identified on *C. compressa* (Table S2).

They mostly comprised filamentous red algae (Rhodophyta). Animal epibionts mostly comprised mussels (*Mytilus galloprovincialis*) and were present only in a few locations (LI, AN, GA and Or). AN, GA and Or presented higher weights of epibiota (Table S2).

3.3. Relationship between the ecological status of *C. compressa* and environmental and anthropogenic variables

Density of coastal human population, wave fetch, tidal range, and nitrate seawater concentration significantly explained 29%, 23%, 21% and 18% of the variability in the set of descriptors of the ecological status of *C. compressa*, respectively, while other factors did not show significant relationships when tested individually (Table 3A). When Best selection was used, the best single variable for modelling the ecological status of *C. compressa* remained coastal human density (Table 3B), while the combination of environmental and anthropogenic parameters best explaining overall variation included 5 variables: Chlorophyll *a*, wave fetch, SST, SST-range and coastal human population density (Table 3C). The first two axes of the dbrDA ordination triplot cumulatively explained 87% of the fitted and 68% of the total variation in the ecological status of *C. compressa* populations (Fig. 3). The variable contributing most to the first dbrDA axis was coastal human population density (+0.718), while Chlorophyll *a* seawater concentration was the variable most related to the second axis

Table 3

Results of DistLM analysis of the status of *C. compressa*: (A) Marginal tests, (B) Best result for each number of variables, (C) Overall best solutions. SS (trace) = portion of sum of squares related to the analyzed predictor variable; Pseudo-F = F value by permutation; P = Significant (pperm < 0.05) predictor variables are in bold; Prop = the proportion of the status of *C. compressa* explained by each environmental and anthropogenic parameters; BIC = Bayesian Information Criterion; RSS = residual sum of squares; No.Vars = number of variables; Selection = variables selected. Variable: 1 = log.Chla, log of Chlorophyll *a* seawater concentration; 2 = PAR, Photosynthetic Active Radiation; 3 = Fetch, wave fetch; 4 = SST, mean sea surface temperature; 5 = SST-range, average annual range of sea surface temperature; 6 = Tide, tidal range; 7 = log.N, log of nitrate seawater concentration; 8 = sqrt.Dens.pop.10 km, square-root of coastal human population density within 10 km of the site.

(A) Marginal test				
Variable	SS (trace)	Pseudo-F	P	Prop.
log.Chla	11.181	2.5194	0.056	0.18635
PAR	8.289	1.7632	0.1561	0.13815
Fetch	13.588	3.2206	0.0231	0.22647
SST	8.6944	1.8641	0.1273	0.14491
SST.range	8.4109	1.7934	0.1549	0.14018
Tide	12.862	3.0015	0.0369	0.21437
log.N	10.614	2.3641	0.0468	0.1769
sqrt.Dens.pop.10 km	17.332	4.4683	0.0092	0.28887

(B) Best solution for each number of variables				
BIC	R ²	RSS	No.Vars	Selections
20.58	0.28887	42.668	1	8
19.301	0.47092	31.745	2	1,8
18.188	0.60131	23.921	3	1,3,8
16.917	0.70316	17.81	4	1,3,5,8
16.55	0.76311	14.214	5	1,3–5,8
17.663	0.78814	12.712	6	1–5,8
18.815	0.80996	11.403	7	1–6,8
19.964	0.82958	10.225	8	All

(C) Overall best solutions				
BIC	R ²	RSS	No.Vars	Selections
16.55	0.76311	14.214	5	1,3–5,8
16.917	0.70316	17.81	4	1,3,5,8
17.663	0.78814	12.712	6	1–5,8
17.933	0.67903	19.258	4	1,3,4,8
17.985	0.78282	13.031	6	1,3–6,8
18.009	0.78243	13.054	6	1,3–5,7,8
18.188	0.60131	23.921	3	1,3,8
18.252	0.72996	16.202	5	1–4,8
18.306	0.72884	16.27	5	1–3,5,8
18.657	0.72141	16.715	5	1,3,5,6,8

(– 0.512). Wave fetch and SST-range were related with both first and second axes (Fig. 3, Table S3), while SST was more related (+ 0.491) with the second dbrDA axis (Fig. 3, Table S3). All descriptors of the ecological status of *C. compressa* were negatively related to the first axis of dbrDA. Therefore, they showed a negative relationship with coastal human population and SST-range (Fig. 3, Table S4). The abundance of epiphytes was positively related to Chlorophyll *a* concentration, while the density of *C. compressa* was positively related to increasing wave fetch (Fig. 3, Table S4).

4. Discussion

Although limited in spatial extent (small stretches of coast at 13 sites) and temporal coverage (one snapshot sampling), our assessment sets a starting baseline of the current condition of infralittoral fringe populations of *Cystoseira* along the Italian coasts and identifies some of the most

likely underlying factors. We found only three species of *Cystoseira* (*C. amentacea*, *C. compressa* and *C. brachycarpa*) out of the six potentially belonging to the species pool of the study sites (Furnari et al., 2010, Table S1). *C. compressa* was the most common species, being found at eleven sites, but hardly with covers above 25%. Coastal human population density, used as a proxy of urbanization, explained most of the variation in the ecological status of *C. compressa*, followed by wave fetch, SST, SST-range and Chlorophyll *a* seawater concentration.

Although populations of *Cystoseira* persist along some of the Mediterranean coastline (Thibaut et al., 2014; Berov et al., 2015), remarkable declines of these species have been reported both in subtidal and intertidal areas (Airoldi et al., 2014). Along the Italian coasts, there are few data on the past distribution of *Cystoseira* populations, and most are from qualitative floristic studies, which hampers quantitative analyses of historical changes and losses. Available records show that diverse species of *Cystoseira* used to flourish in the upper subtidal/

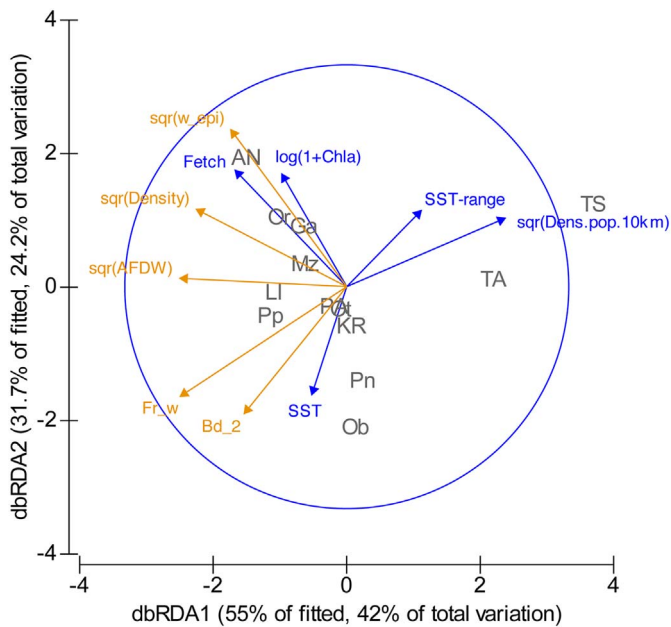


Fig. 3. Distance-based redundancy analysis (dbRDA) triplot showing relationships between the descriptors of the status of *C. compressa* (orange lines) and the environmental and anthropogenic variables (blue lines) selected by the DistLM model. $\log(1 + \text{Chla})$ = log of Chlorophyll *a* seawater concentration; Fetch = wave fetch; SST = mean sea surface temperature; SST-range = average annual range of sea surface temperature; $\text{sqr}(\text{Dens.pop.10 km})$ = square-root of coastal human population density within 10 km of site; $\text{sqr}(\text{Density})$ = square-root of density of *C. compressa*; $\text{sqr}(\text{AFDW})$ = square-root of ash-free dry weight; Fr_w = frond width; Bd_2 = second order branch diameter; $\text{sqr}(w_{\text{epi}})$ = square-root of total weight of epiphytes. Site codes as in Fig. 1 and Table S1. Correlation circle (Pearson correlation) is indicated in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

infralittoral fringe (Pignatti and Giaccone, 1967; Cinelli, 1969; Giaccone, 1969; Cinelli et al., 1976; Giaccone et al., 1985), while nowadays remaining populations are sparse (Benedetti-Cecchi et al., 2001; Serio et al., 2006; Mangialajo et al., 2008; Falace et al., 2010; Perkol-Finkel and Airoidi, 2010; Frascchetti et al., 2012). At TS, for example, in the 1960's, two species of *Cystoseira* were reported on the infralittoral fringe, *C. amantacea* var. *stricta* (as *C. spicata*) and *C. compressa* (as *C. abrotanifolia*) (Pignatti and Giaccone, 1967). In 2007 only *C. compressa* was recorded, while in the present study we could not find any *Cystoseira*, even if we cannot exclude its occurrence at other sites in the region. At AN, in the 1940–1960's, five species of *Cystoseira* were recorded, one from the infralittoral fringe, *C. compressa*, and four from the upper subtidal zone, *C. barbata*, *C. crinita*, *C. foeniculacea* (as *C. discors*), and *C. elegans* (Romagnoli and Solazzi, 2003). Since the 1990's, only two species, *C. compressa* and *C. barbata*, were found in the region (Perkol-Finkel and Airoidi, 2010). Currently, *C. barbata* has severely retracted, and in our study we only reported *C. compressa*. Further, in the following year 2014 we could not find any species left at the same study site (Mancuso pers. obs). At Pp, Giaccone et al. (1992) reported dense patches of three species: *C. compressa*, *C. brachycarpa* and *C. humilis*. In contrast, during our survey, we found only *C. compressa* and *C. brachycarpa* and recorded a notable decrease in the cover of *C. compressa* (from 20% to 7%) compared to past data. At LI, Piazzini et al. (2009) reported four infralittoral fringe/shallow subtidal species, comprising *C. compressa*, *C. brachycarpa*, *C. humilis* and *C. crinita*, already suggesting the loss of *C. amantacea* var. *stricta* reported from the past (Cinelli, 1969). In our study, we only found two species, *C. compressa* and *C. brachycarpa*. Providing an assessment of the extinction risk of these populations was beyond the scopes of the current work and would require different tools and far more extensive samplings (e.g. Buonomo et al., 2017 submitted). However, these data suggest a

concerning trend for these populations, motivating urgent monitoring and analyses.

All the Mediterranean species of the genus *Cystoseira* are included in the list of endangered or threatened species of the Annex II (recently amended by the decision IG.21/09, UNEP/MAP, 2013) of the Barcelona Convention (UNEP/MAP, 1995), except for *C. compressa*, which is considered relatively tolerant to human pressures compared to other species of *Cystoseira* (Thibaut et al., 2005; Mangialajo et al., 2008). Indeed, *C. compressa* was the only species relatively common, occurring at 11 out of 13 study sites. However, the coverage of this species was generally sparse and depleted compared to past conditions, wherever these were known. Further, its ecological status was strongly related to human pressures, including coastal human population density and Chlorophyll *a*. At most sites, *C. compressa* was the only canopy-forming species found, with a concerning erosion of the resilience potential at the ecosystem level. If *C. compressa* is also locally lost, there will be limited possibilities for functional replacement by other canopy-forming algae. This suggests the need for immediate effective protection to all species of *Cystoseira*, including *C. compressa*.

Several factors have been suggested to drive the loss of *Cystoseira* spp., including urbanization and eutrophication (Thibaut et al., 2005; Mangialajo et al., 2008; Sales and Ballesteros, 2009; Mineur et al., 2015), increase in water turbidity and sedimentation (Airoidi, 2003; Perkol-Finkel and Airoidi, 2010; Frascchetti et al., 2011; Strain et al., 2015), over-grazing (Agnetta et al., 2015), climate change related effects (Asnaghi et al., 2013), and likely combinations of multiple stressors in the most impacted regions (Claudet and Frascchetti, 2010; Strain et al., 2014). Our results suggest a suboptimal ecological status of infralittoral fringe *Cystoseira* populations and identify multiple stressors in urbanized marine areas as likely drivers of those poor conditions. For instance, coastal human population density, used as a proxy for urbanization, was the most important factor explaining the current status of *Cystoseira* populations along the Italian coasts. This variable was related to the greater biomass of *C. compressa* epiphytes, which in turn could affect the survival and growth of the host seaweed (Russell et al., 2005). At lower densities epiphytes could be beneficial to intertidal seaweeds by limiting grazing by herbivores (Harlin, 1975), reducing desiccation stress at low tide (Stewart, 1982) or reducing photo-inhibition at high light levels by providing shade (Wiencke and Davenport, 1988). However, at higher densities epiphytes can negatively affect seaweeds due to competition for light and nutrients (Berger et al., 2003), and to increased attraction of herbivores (Wahl and Hay, 1995; Karez et al., 2000). In the most extreme scenarios, the epiphytes can enhance the drag of the fronds and cause the loss of stipe and/or the blades in wave exposed areas (Buschmann and Gómez, 1993). Algae of the genus *Cystoseira* can host conspicuous epiphytic assemblages (Belegreati et al., 1999; Faucci and Boero, 2000), and the potential effects of changes in these associations as a consequence of natural or human-induced stressors deserve further attention (Mancuso et al., 2016).

SST and SST-range were also related to the status of *C. compressa*, suggesting a relevant effect of sea surface temperature variations. *C. compressa* decreased at the northern sites characterized by a larger variance of seawater temperature, while it was more abundant at the southern sites marked by more stable temperatures. The explanation of these dependencies could be related to the effect of temperature on functional and life history traits of the organisms, as observed for other intertidal rocky shore species (Sara et al., 2013; Gioini et al., 2016). For example, body temperature in mussels can be affected by both average

and extreme SST that in turn exert an influence on their survival (Montalto et al., 2016), reproductive success and failure (Sarà et al., 2011), behaviour and lastly distribution of organisms (Helmuth et al., 2014). Other indirect effects (sensu Connell and Ghedini, 2015) could include those mediated by biotic interactions (e.g. changes in species ranges, increased incidence of parasites, altered holobiont communities or modified abundance of predators). Friedland and Hare (2007), showed that the annual ranges in SST had changed dramatically during the last century, as a consequence of spring warming and fall cooling rates caused by climate change. Yu and Boer (2006) suggested that these changes can be spatially variable and that annual SST variability could increase more at mid than at southern latitudes. Present results showed that the likelihood to have the most depleted assemblages was at those localities characterized by co-occurring effects due to high local urbanization and high temperatures. This would suggest a potential role of multiple stressors in shaping canopy-forming seaweed status and increasing the vulnerability to stressful conditions, which is consistent with results from previous work (Strain et al., 2015; Perkol-Finkel and Airoldi, 2010). While there is an increasing understanding of the interactive effects of multiple stressors on marine ecosystems, we still know little about how to optimise their management. Strain et al. (2015), demonstrated experimentally that the mitigation of nutrient and sediment enrichment in urbanized marine coastal areas could enhance the resilience of canopy algae to projected global climate scenarios, increasing our ability to handle the challenges and consequences posed by the cost and delays of mitigation.

Overall, the picture emerging from this baseline assessment is a concerning one, where generally unhealthy assemblages of *Cystoseira* are at high risk from further coastal development and degradation as well as from climatic stressors. We urge for the establishment and implementation of an effective conservation plan for these valuable habitat-forming species. This is not a trivial task and requires identifying the ecological and evolutionary processes that can help maintaining these increasingly fragmented populations in the face of a changing environment (O'Leary et al., 2017). Recent work has contributed knowledge of several mechanisms that could help developing and applying appropriate conservation targets for these species. Reducing local anthropogenic stressors (such as excess nutrient or sediment loads) is an essential step to halt the severe and ongoing loss of these marine habitats (Sales and Ballesteros, 2009; Sales et al., 2011) and increase their resilience to future climatic stressors (Strain et al., 2014, 2015). This requires adopting clear objectives and mechanisms for reducing these stressors to levels compatible with the future persistence of these habitats, together with monitoring and adaptive management. Restoration of *Cystoseira* forests on both natural and artificial substrata is an additional management strategy that can be applied to counteract their local declines (Falace et al., 2006; Susini et al., 2007; Perkol-Finkel et al., 2012; Gianni et al., 2013), provided that the main drivers of loss are removed, that the right levels of connectivity are maintained for the restoration targets to be met (Buonomo et al., 2017b), and that the excess biotic pressures that often limit restoration interventions are controlled (Gianni et al., 2013; Ferrario et al., 2016). *Cystoseira* populations generate valuable ecosystems which maintain high levels of habitat complexity and biodiversity and sustain essential functions such as the creation of nursery areas (Cheminée et al., 2013; Mineur et al., 2015). It is fundamental that these services are quantified, and their economic value is estimated, to highlight the economic benefits of their conservation.

In conclusion, the status of *Cystoseira* infralittoral fringe populations seems to be threatened by co-occurring stressors, including coastal human population density, Chlorophyll *a* seawater concentrations, and climate-related factors, as suggested by the relationships with sea surface temperature, annual range of sea surface temperature and wave fetch. Where available, comparison with historical data revealed a generally unhealthy state of *Cystoseira* infralittoral populations with high risk from further coastal development and degradation as well as

from climate change. There is a need for an extensive baseline monitoring to describe how these populations are changing over time, and implement a management framework for the conservation of these valuable, but vulnerable habitats.

5. Data availability and reproducible research

The repository with all the data and the scripts used to reproduce the research in this paper are available at <https://doi.org/10.17632/5y2rbwvbk.1> (Mancuso, 2017).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2017.10.068>.

References

- Agnetta, D., Badalamenti, F., Ceccherelli, G., Di Trapani, F., Bonaviri, C., Gianguzza, P., 2015. Role of two co-occurring Mediterranean sea urchins in the formation of barren from *Cystoseira* canopy. *Estuar. Coast. Shelf Sci.* 152, 73–77. <http://dx.doi.org/10.1016/j.ecss.2014.11.023>.
- Airoldi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanogr. Mar. Biol. Annu. Rev.* 41, 161–236. <http://dx.doi.org/10.1201/9780203180570.ch4>.
- Airoldi, L., Ballesteros, E., Buonomo, R., Van Belzen, J., Bouma, T.J., Cebrian, E., De Clerck, O., Engelen, A.H., Ferrario, F., Frascchetti, S., Gianni, F., Guidetti, P., Ivesa, L., Mancuso, F.P., Micheli, F., Perkol-Finkel, S., Serrão, E.A., Strain, E.M.A., Mangialajo, L., 2014. Marine forests at risk: solutions to halt the loss and promote the recovery of Mediterranean canopy-forming seaweeds. In: 28–33. *Proceedings of the 5th Mediterranean Symposium on Marine Vegetation. Regional Activity Centre for Specially Protected Areas (RAC/SPA)*.
- Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. In: *Oceanography and Marine Biology: An Annual Review*, pp. 345–405. <http://dx.doi.org/10.1201/9781420050943>.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods, 2008. PRIMER-E, Plymouth.
- Arevalo, R., Pinedo, S., Ballesteros, E., 2007. Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: descriptive study and test of proposed methods to assess water quality regarding macroalgae. *Mar. Pollut. Bull.* 55, 104–113. <http://dx.doi.org/10.1016/j.marpolbul.2006.08.023>.
- Asnaghi, V., Chiantore, M., Bertolotto, R.M., Parravicini, V., Cattaneo-Vietti, R., Gaino, F., Moretto, P., Privitera, D., Mangialajo, L., 2009. Implementation of the European water framework directive: natural variability associated with the CARLIT method on the rocky shores of the Ligurian Sea (Italy). *Mar. Ecol.* 30, 505–513. <http://dx.doi.org/10.1111/j.1439-0485.2009.00346.x>.
- Asnaghi, V., Chiantore, M., Mangialajo, L., Gazeau, F., Francour, P., Alliouane, S., Gattuso, J.P., 2013. Cascading effects of ocean acidification in a rocky subtidal community. *PLoS One* 8, e61978. <http://dx.doi.org/10.1371/journal.pone.0061978>.
- Ballesteros, E., 1990. Structure and dynamics of the community of *Cystoseira zosteroides* (Turner) C. Agardh (Fucales, Phaeophyceae) in the Northwestern Mediterranean. *Sci. Mar.* 54, 217–229.
- Ballesteros, E., Romero, J., 1988. Zonation patterns in tideless environments (Northwestern Mediterranean): looking for discontinuities in species distributions. *Investig. Pesq.* 52 (4), 595–616.
- Ballesteros, E., Torres, X., Pinedo, S., García, M., Mangialajo, L., de Torres, M., 2007. A new methodology based on littoral community cartography dominated by macroalgae for the implementation of the European Water Framework Directive. *Mar. Pollut. Bull.* 55, 172–180. <http://dx.doi.org/10.1016/j.marpolbul.2006.09.036>.
- Beleggras, M.R., Economou-Amilli, A., Ott, J.A., Bitis, I., 1999. Epiphytic patterns of macroalgal assemblages on *Cystoseira* species (Fucales, Phaeophyceae) in the east coast of Attica (Aegean Sea, Greece). *Hydrobiologia* 412, 67–80.
- Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-

- scale effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* 214, 137–150. <http://dx.doi.org/10.3354/meps214137>.
- Berger, R., Henriksson, E., Kautsky, L., Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquat. Ecol.* 37, 1–11. <http://dx.doi.org/10.1023/A:1022136900630>.
- Berov, D., Ballesteros, E., Sales, M., Verlaque, M., 2015. Reinstatement of species rank for *Cystoseira bosporica* Sauvageau (Sargassaceae, Phaeophyceae). *Cryptogam. Algal.* 36, 65–80. <http://dx.doi.org/10.7872/crya.v36.iss1.2015.65>.
- Brown, C.J., Saunders, M.L., Possingham, H.P., Richardson, A.J., 2013. Managing for interactions between local and global stressors of ecosystems. *PLoS One* 8, e65765. <http://dx.doi.org/10.1371/journal.pone.0065765>.
- Brown, C.J., Saunders, M.L., Possingham, H.P., Richardson, A.J., 2014. Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Divers. Distrib.* 20, 538–546. <http://dx.doi.org/10.1111/ddi.12159>.
- Buonomo, R., Assis, J., Fernandes, F., Engelen, A.H., Airoldi, L., Serrão, E.A., 2017b. Habitat continuity and stepping-stone oceanographic distances explain population genetic connectivity of the brown alga *Cystoseira amentacea*. *Mol. Ecol.* 26, 766–780. <http://dx.doi.org/10.1111/mec.13960>.
- Buonomo, R., Chefaoui, R., Bermejo, R., Engelen, A., Serrão, E., Airoldi, L., 2017a. Predicted extinction of unique genetic diversity in marine forests of *Cystoseira* spp. *Glob. Chang. Biol.* (n.d.).
- Burrows, M., 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. *Mar. Ecol. Prog. Ser.* 445, 193–207. <http://dx.doi.org/10.3354/meps09422>.
- Burrows, M., Harvey, R., Robb, L., 2008. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Mar. Ecol. Prog. Ser.* 353, 1–12. <http://dx.doi.org/10.3354/meps07284>.
- Buschmann, A.H., Gómez, P., 1993. Interaction mechanisms between *Gracilaria chilensis* (Rhodophyta) and epiphytes. *Hydrobiologia* 260–261, 345–351. <http://dx.doi.org/10.1007/BF00049039>.
- Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., Cottalorda, J.M., Francour, P., 2013. Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes. *J. Exp. Mar. Biol. Ecol.* 442, 70–79. <http://dx.doi.org/10.1016/j.jembe.2013.02.003>.
- Chrysosvergis, F., Panayotidis, P., 1995. Communities of macrophytobenthos along an eutrophication gradient (Maliakos Gulf, Egean Sea, Greece). *Oceanol. Acta* 18, 649–658.
- Cinelli, F., 1969. Primo contributo alla conoscenza della vegetazione algale bentonica del litorale di Livorno. *Pubbl. Staz. zool. Napoli* 37, 545–566.
- Cinelli, F., Drago, D., Furnari, G., Giaccone, G., Scammacca, B., Solazzi, A., Sortino, M., Tolomio, C., 1976. Flora marina dell'isola di Linosa (Arcipelago delle Pelagie). *Mem. Biol. Mar. Oceanogr.* 6, 141–172.
- Clarke, K.R., Gorley, R., 2006. *Primer V6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Claudet, J., Fraschetti, S., 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biol. Conserv.* 143, 2195–2206. <http://dx.doi.org/10.1016/j.biocon.2010.06.004>.
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froggia, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.S., Koukouras, A., Lampadariou, N., Laxamana, E., de la Cuadra, C.M.L.F., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., Vicente, C.S., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Vouliastadou, E., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS One* 5, e11842. <http://dx.doi.org/10.1371/journal.pone.0011842>.
- Commission, E., 2000. *Water Framework Directive (2000/60/EC)*, Official Journal of the European Communities. (doi:2004R0726 - v.7 of 05.06.2013).
- Connell, S., Foster, M., Airoldi, L., 2014. What are algal turfs? Towards a better description of turfs. *Mar. Ecol. Prog. Ser.* 495, 299–307. <http://dx.doi.org/10.3354/meps10513>.
- Connell, S.D., Ghedini, G., 2015. Resisting regime-shifts: the stabilising effect of compensatory processes. *Trends Ecol. Evol.* 30, 513–515. <http://dx.doi.org/10.1016/j.tree.2015.06.014>.
- Crain, C.M., Halpern, B.S., Beck, M.W., Kappel, C.V., 2009. Understanding and managing human threats to the coastal marine environment. *Ann. N. Y. Acad. Sci.* 1162, 39–62. <http://dx.doi.org/10.1111/j.1749-6632.2009.04496.x>.
- Dethier, M., Graham, E., Cohen, S., Tear, L., 1993. Visual versus random-point percent cover estimations: “objective” is not always better. *Mar. Ecol. Prog. Ser.* 96, 93–100. <http://dx.doi.org/10.3354/meps096093>.
- Dubroca, L., 2014. EMISR: EMIS and GMIS Data Extraction and Analyses.
- Falace, A., Alongi, G., Cormaci, M., Furnari, G., Curiel, D., Cecere, E., Petrocelli, A., 2010. Changes in the benthic algae along the Adriatic Sea in the last three decades. *Chem. Ecol.* 26, 77–90. <http://dx.doi.org/10.1080/02757541003689837>.
- Falace, A., Zanelli, E., Bressan, G., 2005. Morphological and reproductive phenology of *Cystoseira compressa* (Esper) Gerloff & Nizamuddin (Fucales, Fucophyceae) in the Gulf of Trieste (North Adriatic). *Ann. Ser. Hist. Nat.* 15, 71–78.
- Falace, A., Zanelli, E., Bressan, G., 2006. Algal transplantation as a potential tool for artificial reef management and environmental mitigation. *Bull. Mar. Sci.* 78, 161–166.
- Fauci, A., Boero, F., 2000. Structure of an epiphytic hydroid community on *Cystoseira* at two sites of different wave exposure. *Sci. Mar.* 64, 255–264. <http://dx.doi.org/10.3989/scimar.2000.64s1255>.
- Ferrario, F., Ivesa, L., Jaklin, A., Perkol-Finkel, S., Airoldi, L., 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. *J. Appl. Ecol.* 53, 16–24. <http://dx.doi.org/10.1111/1365-2664.12533>.
- Fraschetti, S., Bevilacqua, S., Guarnieri, G., Terlizzi, A.M., 2012. Idiosyncratic effects of protection in a remote marine reserve. *Mar. Ecol. Prog. Ser.* 466, 21–34. <http://dx.doi.org/10.3354/meps09937>.
- Fraschetti, S., Terlizzi, A., Guarnieri, G., Pizzolante, F., D'Ambrosio, P., Maiorano, P., Beqiraj, S., Boero, F., 2011. Effects of unplanned development on marine biodiversity: a lesson from Albania (Central Mediterranean Sea). *J. Coast. Res.* 270, 106–115. http://dx.doi.org/10.2112/SI_58_10.
- Friedland, K.D., Hare, J.A., 2007. Long-term trends and regime shifts in sea surface temperature on the continental shelf of the northeast United States. *Cont. Shelf Res.* 27, 2313–2328. <http://dx.doi.org/10.1016/j.csr.2007.06.001>.
- Furnari, G., Giaccone, G., Cormaci, M., Alongi, G., Catra, M., Nisi, A., Serio, D., 2010. Macrophytobenthos. *Biol. Mar. Medit.* 17, 801–828.
- Giaccone, G., 1969. Raccolte di fitobenthos sulla banchina continentale Italiana. *G. Bot. Ital.* 103, 485–514.
- Giaccone, G., Alongi, G., Cossu, A., Di Geronimo, R.E., Serio, D., 1993. La vegetazione marina bentonica del Mediterraneo: 1. Sopralitorale e mesolitorale. *Boll. dell'Accademia Gioenia di Sci. Nat.* 26, 245–291.
- Giaccone, G., Alongi, G., Pizzuto, F., Cossu, A.V.L., 1994. La Vegetazione marina bentonica fotofila del Mediterraneo: 2. Infralitorale e Circolitorale: proposte di aggiornamento. *Boll. dell'Accademia Gioenia di Sci. Nat.* 27, 111–157.
- Giaccone, G., Bruni, A., 1973. Le Cistoseire la Vegetazione Sommersa del Mediterraneo. *Atti dell'Istituto Veneto di Sci. Lett. ed arti CXXXI*. pp. 59–103.
- Giaccone, G., Colonna, P., Graziano, C., Mannino, A.M., Tornatore, E., Cormaci, M., Furnari, G., Scammacca, B., 1985. Revisione della flora marina di Sicilia e isole minori. *Boll. dell'Accademia Gioenia di Sci. Nat.* 18, 537–781.
- Giaccone, G., Pizzuto, F., Serio, D., 1992. Aspetti della vegetazione sommersa in fondali della Sicilia sud-orientale (Sicura). *Boll. dell'Accademia Gioenia di Sci. Nat.* 25, 35–54.
- Giakoumi, S., Brown, C.J., Katsanevakis, S., Saunders, M.I., Possingham, H.P., 2015. Using threat maps for cost-effective prioritization of actions to conserve coastal habitats. *Mar. Policy* 61, 95–102. <http://dx.doi.org/10.1016/j.marpol.2015.07.004>.
- Gianni, F., Bartolini, F., Airoldi, L., Ballesteros, E., Francour, P., Guidetti, P., Meinesz, A., Thibaut, T., Mangialajo, L., 2013. Conservation and restoration of marine forests in the Mediterranean Sea and the potential role of marine protected areas. *Adv. Oceanogr. Limnol.* 4, 83–101. <http://dx.doi.org/10.1080/19475721.2013.845604>.
- Giomì, F., Mandaglio, C., Ganmanee, M., Han, G., Dong, Y., Williams, G.A., Sara, G., 2016. The Importance of Thermal History: Costs and Benefits of Heat Exposure in a Tropical, Rocky Shore Oyster. pp. 686–694. <http://dx.doi.org/10.1242/jeb.128892>.
- Gómez-Garreta, A., Barceló, M., Gallardo, T., Pérez-Ruzafa, I., Ribera, M.A., Rull, J., 2002. *Flora Phycologica Iberica*. Vol. 1 Fucales, Universida, ed. Murcia.
- Graiff, A., Liesner, D., Karsten, U., Bartsch, I., 2015. Temperature tolerance of western Baltic Sea *Fucus vesiculosus* – growth, photosynthesis and survival. *J. Exp. Mar. Biol. Ecol.* 471, 8–16. <http://dx.doi.org/10.1016/j.jembe.2015.05.009>.
- Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* 9, 228–241. <http://dx.doi.org/10.1111/j.1461-0248.2005.00871.x>.
- Harlin, M.M., 1975. Epiphyte-host relations in seagrass communities. *Aquat. Bot.* 1, 125–131. [http://dx.doi.org/10.1016/0304-3770\(75\)90017-0](http://dx.doi.org/10.1016/0304-3770(75)90017-0).
- Helmuth, B., Russell, B.D., Connell, S.D., Dong, Y., Harley, C.D., Lima, F.P., Sará, G., Williams, G.A., Mieszkowska, N., 2014. Beyond long-term averages: making biological sense of a rapidly changing world. *Clim. Chang. Responses* 1, 6. <http://dx.doi.org/10.1186/s40665-014-0006-0>.
- Karez, R., Engelbert, S., Sommer, U., 2000. Co-consumption and protective coating: two new proposed effects of epiphytes on their macroalgal hosts in mesograzed-epiphyte-host interactions. *Mar. Ecol. Prog. Ser.* 205, 85–93. <http://dx.doi.org/10.3354/meps205085>.
- Lasinio, G.J., Tullio, M.A., Ventura, D., Ardizzone, G., Abdelahad, N., 2017. Statistical analysis of the distribution of infralittoral *Cystoseira* populations on pristine coasts of four Tyrrhenian islands: proposed adjustment to the CARLIT index. *Ecol. Indic.* 73, 293–301. <http://dx.doi.org/10.1016/j.ecolind.2016.09.038>.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: Testing multi-species responses in multifactorial ecological experiments. *Ecol. Monogr.* 69, 1–24. <http://dx.doi.org/10.2307/2657192>.
- Lukacs, P.M., Burnham, K.P., Anderson, D.R., 2010. Model selection bias and Freedman's paradox. *Ann. Inst. Stat. Math.* 62, 117–125. <http://dx.doi.org/10.1007/s10463-009-0234-4>.
- Mancuso, F.P., D'Hondt, S., Willems, A., Airoldi, L., De Clerck, O., 2016. Diversity and temporal dynamics of the epiphytic bacterial communities associated with the canopy-forming seaweed *Cystoseira compressa* (Esper) Gerloff and Nizamuddin. *Front. Microbiol.* 7, 476. <http://dx.doi.org/10.3389/fmicb.2016.00476>.
- Mancuso, Francesco Paolo, 2017. “Status of vulnerable *Cystoseira* populations along the Italian infralittoral fringe, and relationships with environmental and anthropogenic variables - data and scripts”, Mendeley Data. Vol. 1. <https://doi.org/10.17632/5y2rbwbvbk.1>.
- Mangialajo, L., Chiantore, M., Cattaneo-Vietti, R., 2008. Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Mar. Ecol. Prog. Ser.* 358, 63–74. <http://dx.doi.org/10.3354/meps07400>.
- Mangialajo, L., Ruggieri, N., Asnaghi, V., Chiantore, M., Povero, P., Cattaneo-Vietti, R., 2007. Ecological status in the Ligurian Sea: the effect of coastline urbanisation and the importance of proper reference sites. *Mar. Pollut. Bull.* 55, 30–41. <http://dx.doi.org/10.1016/j.marpolbul.2006.08.022>.
- Martínez, B., Arenas, F., Trilla, A., Viejo, R.M., Carreño, F., 2015. Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. *Glob. Chang. Biol.* 21, 1422–1433. <http://dx.doi.org/10.1111/gcb.12889>.

- doi.org/10.1111/gcb.12655.
- Micheli, F., Halpern, B.S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Lewison, R., Nykjaer, L., Rosenberg, A.A., 2013. Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PLoS One* 8, e79889. <http://dx.doi.org/10.1371/journal.pone.0079889>.
- Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E., Thibaut, T., Van Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E.a., De Clerck, O., 2015. European seaweeds under pressure: consequences for communities and ecosystem functioning. *J. Sea Res.* 98, 91–108. <http://dx.doi.org/10.1016/j.seares.2014.11.004>.
- Montalto, V., Helmuth, B., Ruti, P.M., Dell'Aquila, A., Rinaldi, A., Sarà, G., 2016. A mechanistic approach reveals non-linear effects of climate warming on mussels throughout the Mediterranean sea. *Clim. Chang.* 139. <http://dx.doi.org/10.1007/s10584-016-1780-4>.
- Mueller, R., Fischer, A.M., Bolch, C.J.S., Wright, J.T., 2015. Environmental correlates of phenotypic variation: do variable tidal regimes influence morphology in intertidal seaweeds? *J. Phycol.* 51, 859–871. <http://dx.doi.org/10.1111/jpy.12329>.
- Nikolić, V., Žuljević, A., Mangialajo, L., Antolić, B., Kušpilić, G., Ballesteros, E., 2013. Cartography of littoral rocky-shore communities (CARLIT) as a tool for ecological quality assessment of coastal waters in the Eastern Adriatic Sea. *Ecol. Indic.* 34, 87–93. <http://dx.doi.org/10.1016/j.ecolind.2013.04.021>.
- O'Leary, J.K., Micheli, F., Airoldi, L., Boch, C., De Leo, G., Elahi, R., Ferretti, F., Graham, N.A.J., Litvin, S.Y., Low, N.H., Lummis, S., Nickols, K.J., Wong, J., 2017. The resilience of marine ecosystems to climatic disturbances. *Bioscience* 67, 208–220. <http://dx.doi.org/10.1093/biosci/biw161>.
- Pedersen, M., Nejrup, L., Fredriksen, S., Christie, H., Norderhaug, K., 2012. Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea*. *Mar. Ecol. Prog. Ser.* 451, 45–60. <http://dx.doi.org/10.3354/meps09594>.
- Perkol-Finkel, S., Airoldi, L., 2010. Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. *PLoS One* 5, e10791. <http://dx.doi.org/10.1371/journal.pone.0010791>.
- Perkol-Finkel, S., Ferrario, F., Nicotera, V., Airoldi, L., 2012. Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures. *J. Appl. Ecol.* 49, 1457–1466. <http://dx.doi.org/10.1111/j.1365-2664.2012.02204.x>.
- Peterson, B.G., Carl, P., 2014. PerformanceAnalytics: Econometric Tools for Performance and Risk Analysis.
- Piazzi, L., Cecchi, E., Pardi, G., Cinelli, F., 2009. I Popolamenti Macroalgali Di Calafuria (Livorno). *Atti Soc. toscana di Sci. Nat.* 116, 81–90.
- Piazzi, L., Cinelli, F., 2002. Contributo alla conoscenza dei popolamenti macroalgali dell'Isola di Giannutri (Arcipelago Toscano). *Inf. Bot. Ital.* 34, 79–86.
- Pignatti, S., Giaccone, G., 1967. Studi sulla produttività primaria del fitobenthos nel Golfo di Trieste. I. Flora sommersa del Golfo di Trieste. *Nuova Thalass.* 3, 1–17.
- Rodríguez-Prieto, C., Polo, L., 1996. Effects of sewage pollution in the structure and dynamics of the community of *Cystoseira mediterranea* (Fuciales, Phaeophyceae). *Sci. Mar.* 60, 263.
- Romagnoli, T., Solazzi, A., 2003. Evoluzione dei popolamenti fitobentonici lungo la Riviera del Conero dal 1941 al 2000. *Quad. Ist. Ric. Pesca Marittima* 1, 63–84.
- Russell, B.D., Elsdon, T.S., Gillanders, B.M., Connell, S.D., 2005. Nutrients increase epiphyte loads: broad-scale observations and an experimental assessment. *Mar. Biol.* 147, 551–558. <http://dx.doi.org/10.1007/s00227-005-1571-3>.
- Ruuskanen, A., Bäck, S., 1999. Morphological variation of northern Baltic Sea *Fucus vesiculosus* L. *Ophelia* 50, 43–59. <http://dx.doi.org/10.1080/00785326.1999.10409388>.
- Sales, M., Ballesteros, E., 2009. Shallow *Cystoseira* (Fuciales: Ochrophyta) assemblages thriving in sheltered areas from Menorca (NW Mediterranean): relationships with environmental factors and anthropogenic pressures. *Estuar. Coast. Shelf Sci.* 84, 476–482. <http://dx.doi.org/10.1016/j.ecss.2009.07.013>.
- Sales, M., Cebrían, E., Tomas, F., Ballesteros, E., 2011. Pollution impacts and recovery potential in three species of the genus *Cystoseira* (Fuciales, Heterokontophyta). *Estuar. Coast. Shelf Sci.* 92, 347–357. <http://dx.doi.org/10.1016/j.ecss.2011.01.008>.
- Sarà, G., Kearney, M., Helmuth, B., 2011. Combining heat-transfer and energy budget models to predict thermal stress in Mediterranean intertidal mussels. *Chem. Ecol.* 27, 135–145. <http://dx.doi.org/10.1080/02757540.2011.552227>.
- Sarà, G., Palmeri, V., Montalto, V., Rinaldi, A., Widdows, J., 2013. Parameterisation of bivalve functional traits for mechanistic eco-physiological dynamic energy budget (DEB) models. *Mar. Ecol. Prog. Ser.* 480, 99–117. <http://dx.doi.org/10.3354/meps10195>.
- Serio, D., Alongi, G., Catra, M., Cormaci, M., Furnari, G., 2006. Changes in the benthic algal flora of Linosa Island (Straits of Sicily, Mediterranean Sea). *Bot. Mar.* 49, 135–144. <http://dx.doi.org/10.1515/BOT.2006.018>.
- Smale, D.A., Moore, P.J., 2017. Variability in kelp forest structure along a latitudinal gradient in ocean temperature. *J. Exp. Mar. Biol. Ecol.* 486, 255–264. <http://dx.doi.org/10.1016/j.jembe.2016.10.023>.
- Soltan, D., Verlaque, M., François Boudouresque, C., Francour, P., 2001. Changes in macroalgal communities in the vicinity of a Mediterranean sewage outfall after the setting up of a treatment plant. *Mar. Pollut. Bull.* 42, 59–70. [http://dx.doi.org/10.1016/S0025-326X\(00\)00116-8](http://dx.doi.org/10.1016/S0025-326X(00)00116-8).
- Stein-Taylor, J.R., Littler, M.M., Littler, D.S., America, P.S. of, 1985. *Handbook of physiological methods. In: Ecological Field Methods: Macroalgae.* Vol. 4 Cambridge University Press.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.a., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29, 436–459. <http://dx.doi.org/10.1017/S0376892902000322>.
- Stewart, J.G., 1982. Anghor species and epiphytes in intertidal algal turf. *Pac. Sci.* 36, 45–59.
- Strain, E.M.A., Thomson, R.J., Micheli, F., Mancuso, F.P., Airoldi, L., 2014. Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Glob. Chang. Biol.* 20, 3300–3312. <http://dx.doi.org/10.1111/gcb.12619>.
- Strain, E.M.A., van Belzen, J., van Dalen, J., Bouma, T.J., Airoldi, L., 2015. Management of local stressors can improve the resilience of marine canopy algae to global stressors. *PLoS One* 10, e0120837. <http://dx.doi.org/10.1371/journal.pone.0120837>.
- Susini, M.L., Mangialajo, L., Thibaut, T., Meinesz, A., 2007. Development of a transplantation technique of *Cystoseira amentacea* var. *stricta* and *Cystoseira compressa*. *Hydrobiologia* 580, 241–244. <http://dx.doi.org/10.1007/s10750-006-0449-9>.
- Thibaut, T., Blanfune, A., Boudouresque, C.F., Verlaque, M., 2015. Decline and local extinction of Fuciales in French Riviera: the harbinger of future extinctions? *Mediterr. Mar. Sci.* 16, 206–224. <http://dx.doi.org/10.12681/mms.1032>.
- Thibaut, T., Blanfuné, A., Markovic, L., Verlaque, M., Boudouresque, C.F., Perret-Boudouresque, M., Mačić, V., Bottin, L., 2014. Unexpected abundance and long-term relative stability of the brown alga *Cystoseira amentacea*, hitherto regarded as a threatened species, in the north-western Mediterranean Sea. *Mar. Pollut. Bull.* 89, 305–323. <http://dx.doi.org/10.1016/j.marpolbul.2014.09.043>.
- Thibaut, T., Pinedo, S., Torras, X., Ballesteros, E., 2005. Long-term decline of the populations of Fuciales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Mar. Pollut. Bull.* 50, 1472–1489. <http://dx.doi.org/10.1016/j.marpolbul.2005.06.014>.
- Thompson, R.C., Crowe, T.P., Hawkins, S.J., 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environ. Conserv.* 29, 168–191. <http://dx.doi.org/10.1017/S0376892902000115>.
- UNEP/MAP, 1995. *Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean [Barcelona Convention 1995].* UNEP/MAP, Athens.
- UNEP/MAP, 2013. *Mediterranean Action Plan: Report of the 18th Ordinary Meeting of the Contracting Parties to the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean and its Protocols.* UNEP (DEPI)/MED IG.21/09 [id 6191], Athens.
- Wahl, M., Hay, M.E., 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia* 102, 329–340. <http://dx.doi.org/10.1007/BF00329800>.
- Wiencke, C., Davenport, J., 1988. Respiration and photosynthesis in the intertidal alga *Cladophora rupestris* (L.) Kütz. under fluctuating salinity regimes. *J. Exp. Mar. Biol. Ecol.* 114, 183–197. [http://dx.doi.org/10.1016/0022-0981\(88\)90137-2](http://dx.doi.org/10.1016/0022-0981(88)90137-2).
- Yu, B., Boer, G.J., 2006. The variance of sea surface temperature and projected changes with global warming. *Clim. Dyn.* 26, 801–821. <http://dx.doi.org/10.1007/s00382-006-0117-9>.