

Role of two co-occurring Mediterranean sea urchins in the formation of barren from-Cystoseira canopy

Questa è la versione Post print del seguente articolo:

Original

Role of two co-occurring Mediterranean sea urchins in the formation of barren from-Cystoseira canopy / Agnetta, D; Badalamenti, F; Ceccherelli, Giulia; Di Trapani, F; Bonaviri, C; Gianguzza, P.. - In: ESTUARINE, COASTAL AND SHELF SCIENCE. - ISSN 0272-7714. - 152:(2015), pp. 73-77. [10.1016/j.ecss.2014.11.023]

Availability:

This version is available at: 11388/45984 since: 2022-05-31T14:48:15Z

Publisher:

Published

DOI:10.1016/j.ecss.2014.11.023

Terms of use:

Chiunque può accedere liberamente al full text dei lavori resi disponibili come "Open Access".

Publisher copyright

note finali coverpage

(Article begins on next page)

Role of two co-occurring Mediterranean sea urchins in the formation of barren from *Cystoseira* canopy

D. Agnetta ^{*a}, F. Badalamenti ^a, G. Ceccherelli ^b, F. Di Trapani ^c, C. Bonaviri ^c, P. Gianguzza ^c

^a CNR-IAMC, Sede di Castellammare del Golfo, Via G. da Verrazzano 17, 91014 Castellammare del Golfo (TP), Italy

^b Dipartimento di Scienze della Natura e del Territorio (DIPNET), Università di Sassari, Via Piandanna, 4 – 07100 Sassari, Italy

^c Dipartimento di Scienze della Terra e del Mare (DiSTeM), Università di Palermo, Via Archirafi, 22 – 90123 Palermo, Italy

* Corresponding author: davide.agnetta@iamc.cnr.it, Tel.:+39092435013; fax: +39092435084

Key-words: *Paracentrotus lividus*; *Arbacia lixula*; feeding behaviour, barren formation; *Cystoseira* spp.

Abstract

In the Mediterranean Sea the co-occurring sea urchins *Paracentrotus lividus* and *Arbacia lixula* are usually considered to share the same ecological role in the formation of barren from *Cystoseira* canopy. However, their foraging ability may vary due to feeding behavior and species-specific morphological traits. The relative effects of *P. lividus* and *A. lixula* on *Cystoseira* canopy was tested experimentally both in the laboratory, at a density of about 20 ind./m², and in the field by gut content analysis. Results, both in the field and in the laboratory experiments, show that *A. lixula* is unable to affect *Cystoseira* spp. Furthermore, these results confirmed the great ability of *P. lividus* to consume *Cystoseira* canopy, thus supporting the evidence of the major role of this species in the creation of barren state.

1. Introduction

Canopy-forming brown algae are habitat formers able to locally modify physical and biological factors and understory assemblages (Ballesteros et al. 1998; Bulleri et al. 2002) leading to biological amelioration (*sensu* Moore et al. 2007). There is concern globally about their widespread loss across many parts of the world's rocky shores (e.g. Airoidi and Beck 2007). This is a result of their sensitivity to several direct and indirect human stressors (Perkol-Finkel and Airoidi 2010).

On Mediterranean rocky reefs, such habitat formers are well represented by the genus *Cystoseira* C. Agardh (Fucales, Phaeophyceae). These algae are distributed from the intertidal to the upper circalittoral and perform numerous ecosystem services as they provide high primary production and source of food, nutrient cycling, substrata for settlement, protection from predators and shelter from disturbance (Graham 2004; Ballesteros et al. 2009).

Over the last few decades most of the *Cystoseira* species have experienced severe decline in many Mediterranean regions (Thibaut et al. 2005; Mangialajo et al. 2008). Urbanisation is thought to have the most disrupting effects on *Cystoseira* canopy, particularly because it affects water clarity through eutrophication and alters sedimentation and water motion (Mangialajo et al. 2008). Furthermore, anthropogenic stressors such as global warming

1 and overfishing have also invoked this process. Overfishing of large sea urchin predator fish, especially *Diplodus* spp.,
2 can cause severe sea urchin outbreaks (*Paracentrotus lividus* and *Arbacia lixula*) and promote a shift in rocky benthic
3 community structure (Hereu et al. 2008; Sala et al. 2012, **Cardona et al. 2013**). The variation in sea urchin grazing
4 intensity may drive switches between one complex state, dominated by a stratified assemblage of several erect algae
5 including the *Cystoseira* genus, to a simpler one, dominated by few encrusting algae, the so-called 'barren ground'
6 (Shears and Babcock 2002; Estes et al. 2011).
7
8
9
10

11 In the Mediterranean Sea *P. lividus* and *A. lixula* are commonly found in both barren grounds and erected
12 macroalgae assemblages (Guidetti and Dulčić 2007; Agnetta et al. 2013) and traditionally they have been considered a
13 guild of herbivores (Bulleri et al. 1999, Bulleri et al. 2002). However recent investigations have distinguished the diets
14 and trophic positions of the two species showing that *A. lixula* is an omnivore tending to carnivory, while *P. lividus* is
15 basically a herbivore that can turn into an omnivore both on barren and vegetated rocky areas (Agnetta et al. 2013).
16 Recent evidence suggests that the roles of the two species in maintaining the extension of barrens overlaps (Bulleri et al.
17 1999; Bonaviri et al. 2011; Bulleri 2013).
18
19
20
21
22
23
24
25

26 Despite the fact that sea urchin grazing is generally accepted to be very important to habitat modifications on
27 Mediterranean rocky shores, comparisons of the **relative role** of *A. lixula* and *P. lividus* to **form barrens from**
28 *Cystoseira* **canopy** is largely overlooked and has not yet been studied in any great detail.
29
30
31

32 In order to fill this important ecological gap we performed a laboratory experiment to observe the feeding
33 behaviour of *A. lixula* and *P. lividus* and catch interspecific differences in their approach to *Cystoseira* spp. and to
34 assess their relative ability to consume **and dislodge** *Cystoseira* spp. (**i.e. barren formation**). We also studied the gut
35 content of these species in natural conditions with the aim of comparing the amount of *Cystoseira* consumed by the two
36 predators in the field. We predicted **that** 1) different ways of approaching the algae would be demonstrated by the two
37 species in the laboratory experiment 2) only *P. lividus* would be able to consume *Cystoseira* and 3) that *Cystoseira* spp.
38 play a greater role in *P. lividus* **diet rather** than in *A. lixula*.
39
40
41
42
43
44
45

46 **2. Material and Methods**

47 **2.1. Study area**

48 The study was performed in the upper infralittoral (3- 6 m) of the Ustica Island, located off the north coast of
49 Sicily (Western Mediterranean, 38°42'20"N -10°43'43" E), where crustose algae are interspersed with pools of
50 *Cystoseira* spp. patches (mainly *Cystoseira brachicarpa* var. *balearica* and *Cystoseira compressa*) forming a binary
51 patchy landscape (Gianguzza et al. 2010).
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 The sea urchins *P. lividus* and *A. lixula* co-occur in this system (annual mean density of adults $\times \text{m}^{-2} \pm \text{SE}$ was $2.70 \pm$
2 0.63 and 3.10 ± 0.72 , respectively $N = 160$ **individuals** \times species) providing an optimal opportunity to assess their
3 grazing on *Cystoseira* spp.
4

5 2.2. Laboratory trials

6 A laboratory experiment was done from May to July 2011 to evaluate the ability to consume *Cystoseira* canopy
7 by *P. lividus* and *A. lixula* (Fig. 1). The experiment was set up randomly collecting adult sea urchins (both *P. lividus* and
8 *A. lixula* 35–50 cm in test diameter without spines) and cobbles covered by *Cystoseira* spp. (external face from about
9 10×10 cm to 18×15 cm) from a small bay of Ustica Island. After field collection cobbles were placed in large sealed
10 plastic tanks containing oxygenated seawater for transportation to the laboratory. The sea urchins were brought to the
11 same laboratory packed in ice. Before starting the experiment *P. lividus* and *A. lixula* were starved for 2 weeks and kept
12 in separate tanks (300 L) to ensure that the two species had experienced similar conditions and to prevent changes in
13 natural feeding responses (Rochette et al. 1994). Sessile organisms on cobbles, or on *Cystoseira*, were removed.
14 *Cystoseira* were maintained in different storage tanks (300 L). All organisms were maintained with circulating natural
15 seawater, at ambient light (12 h light and 12 h darkness) and at a temperature of 20°C for the whole duration of the
16 experiment.
17

18 The experiment was aimed at assessing both the feeding behaviour and the relative ability of sea urchins to
19 consume *Cystoseira* and consisted of a treatment with three levels of urchin presence carried out in replicated ($n= 3$)
20 aquaria: 1) only *A. lixula* present, 2) only *P. lividus* present and 3) no urchins (controls) present. Each **aquarium** was 90
21 $\times 50 \times 50$ cm in size (ca. 200 L of sea water). In each aquarium a cobble covered with *Cystoseira* spp. was positioned.
22 Twenty individuals of one sea urchin species (a density of about 20 ind./m²) were then supplied where needed
23 according to the experiment protocol. Controls were considered in order to assess the performance of *Cystoseira* (i.e.
24 weight loss) in the absence of sea urchins. The cobbles with *Cystoseira* were weighed before being introduced in the
25 aquarium, then sea urchins were allowed to forage until either the canopy disappeared, or a maximum of thirty days,
26 whichever occurred first. When *Cystoseira* disappeared, we **recorded** the number of days spent for total consumption.
27 Moreover, in order to estimate consumption of *Cystoseira* (g), cobbles were re-weighed when the canopy disappeared,
28 or at the end time of the experiment. To ensure the independence of data each pool of sea urchins was used only once
29 (Underwood 1997). **A total of 18 hours was spent** observing the feeding behaviour of the sea urchins. Observation
30 times were equally distributed between the morning and afternoon for each of the first 3 days of the experiment. Each
31 observation was ten minutes in duration and dedicated to each aquarium where sea urchins were present.
32

33 2.3. *Cystoseira* spp. gut contents

1 The sea urchins were collected over four seasons: summer and autumn 2007, winter and spring 2008. For each
2 season collection took place on two random dates. Each time two sites, 400 m apart with similar orientation and
3 hydrodynamic conditions, were randomly selected on the western side of Ustica Island (as in Gianguzza et al. 2013). In
4 order to analyse sea urchin gut contents we collected six adult individuals of both species (> 35 mm test diameter) at
5 each site and time, **at 3-6 m of depth**. Sea urchins were dissected as soon as possible in order to avoid gut evacuation.
6 After dissection gut contents were immediately frozen. We later took at random two equal volumes of gut contents from
7 each sample and placed them on a 2.5 × 2.5 cm grid in a Petri dish under a 40 × microscope in order to discern the gut
8 items ingested and to evaluate the percentage of *Cystoseira* spp. out of the whole content.
9

10 2.4 Data analysis

11 Differences in percent *Cystoseira* wet weight from the beginning to the end of the laboratory experiments were
12 analysed using a 2 - way ANOVA with “Urchin” (Ur; three levels: *P. lividus*, *A. lixula* and no urchins) treated as a fixed
13 factor, and “Aquarium” (Aq; three levels) as a random and nested factor (n = 3).
14

15 Variability in *Cystoseira* spp. gut content between the two sea urchins was evaluated performing a 4 - way
16 ANOVA including the factors: “Species” (Sp; two levels: *P. lividus*, *A. lixula*) treated as a fixed factor, “Season” (Se;
17 four levels: Summer, Autumn, Winter, and Spring) as a fixed and orthogonal factor, “Time” (Ti; two levels) as a
18 random factor nested in “Se”, and “Site” (Si; two levels) as a random factor nested in Ti (n = 6). ANOVAs were
19 calculated after checking for homogeneity of variances (Cochran’s C test) **and fourth root transformation was**
20 **performed for the two ANOVAs**. Student-Newman-Keuls (SNK) tests (at $\alpha=0.05$) were used, where appropriate, for *a*
21 *posteriori* comparisons of the means (Winer et al. 1991; Underwood 1997).
22

23 3. Results

24 In the laboratory experiments, *P. lividus* consumed 100% of *Cystoseira* (30–35 g) within three days. On the
25 contrary, the algae remained untouched by *A. lixula* over a 30 day period. The consumption of *Cystoseira* spp. was
26 vastly different between sea urchin species (ANOVA, Tab. 1 and Fig. 1). Also, the general behaviour exhibited in the
27 aquaria by the two species was completely different. For example, *P. lividus* was able to rise up and climb on
28 arborescent *Cystoseira* spp., flexing down the fronds whilst trying to anchor them to the substrate by its tubular feet.
29 This afforded *P. lividus* better handling of its prey, from the fronds to the holdfast. Contrarily, *A. lixula* exhibited a
30 scraping behaviour all around the thalli base of *Cystoseira*, possibly looking for other prey on the cobbles.
31

32 The average percent cover of *Cystoseira* spp. in the gut content of sea urchins varied significantly between the
33 two species (ANOVA, $F_{1,160} = 151.92$, $P = 0.0002$). Overall, mean (\pm SE) percent cover of *Cystoseira* spp. in the gut
34 content was 2.16 ± 0.46 for *A. lixula* and 26.47 ± 2.07 for *P. lividus* suggesting higher grazing by **the latter species**.
35 This result was consistent through seasons and times (Fig. 2).
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4. Discussion

1 Factors affecting the feeding biology of echinoids have long been a subject of interest in marine ecological
2 literature. This is due to the fact that sea urchin grazing is frequently responsible for the destruction of canopy-forming
3 algae and the formation of barrens in shallow marine ecosystems (Lawrence 2013 and references therein).
4

5
6
7 Several studies have indicated a spatio-temporal variability of feeding behaviors (Konar and Estes 2003, **Flukes et al.**
8
9
10 **2012**) and there is evidence that this may depend on local threshold density (Bulleri 2013).

11
12 As expected, field and laboratory results have consistently shown that *P. lividus* is more efficient in consuming
13 *Cystoseira* spp. than *A. lixula*. Although gut content analysis creates uncertainty, due to possibly confounding effects
14 (density, food selection, etc.), a significant difference in the ingested *Cystoseira* was found between the two sea urchins.
15
16 In the laboratory, *A. lixula* at density of 20 ind./m² was unable to consume *Cystoseira* even though starved for 2 weeks
17 and maintained for 30 days in the presence of the alga. Conversely *P. lividus* was able to consume *Cystoseira* within 3
18 days. Whether this is a consequence of a greater ability of *P. lividus* to feed on *Cystoseira* algae or a much greater
19 palatability of the alga for *P. lividus* is **still to be evaluated**. As regards feeding choice, it is widely acknowledged that
20 many sea urchins strongly display selection **for** some seaweed species over others, and this has been linked to nutritive
21 value and physical – **chemical** properties of food (Frantzis and Gremare 1992). Furthermore, it is well known that
22 food manipulation by the different feeding traits (Aristotle's lantern and tube feet) is an important step in the echinoid
23 feeding process and algae species that are easily caught and transferred to the mouth would be favored (Lawrence
24 2013). Moreover, three basic feeding behaviors have been documented for sea urchins (1) **capture** of sediment or -
25 dissolved organic material, particularly in term of amino acids, with their sulcated spines and aboral tube feet and
26 adsorbed by dermal-skeleton, (2) removal of erect algae thalli and/or sessile invertebrates from hard substrate by means
27 of the powerful teeth of the Aristotle's lantern and (3) capture of drift algae, "drift-trapping behaviour", by the
28 ambulacral tube feet and spines and the subsequent transport of this material to the mouth (Conteras and Castilla 1987;
29 Lawrence 2013). Regarding this, the two urchin species differ morphologically: *P. lividus* has shorter and denser spines,
30 more extendible aboral tube feet and a weaker Aristotle's lantern than *A. lixula* and it is likely that such differences
31 affect their feeding behaviors (Santos and Flammang **2005; 2007**).
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49

50 The results clearly confirmed that *P. lividus* feeds mainly by gentler "grazing" and by "drift-trapping" *Cystoseira*
51 algae with its aboral tube feet. *A. lixula*, owning a strong Aristotle's lantern and tube feet exclusively on the oral side,
52 adopted a scraping behaviour (Privitera et al. 2008) all around the thalli of *Cystoseira*, possibly looking for sessile prey
53 on the cobble. Interestingly, results indicated a deep difference in *Cystoseira*, handling and dislodging ability between
54 the two sea urchins, probably affected not only by differences in feeding traits themselves but also by movement ability.
55
56
57
58
59
60
61
62
63
64
65

As observed, these features make *P. lividus* better adapted to penetrate, climb and knock down the erect thalli of *Cystoseira* as a result of its superior mobility (Agnetta et al. 2013).

The findings evidenced that **the ability to consume and dislodge *Cystoseira* spp. belongs merely to *P. lividus***. The fact that *Cystoseira* **remained intact**, notwithstanding the high *A. lixula* density in aquarium (20 urchins/m²), is worthy of consideration and in contrast with previous manipulative studies that had indicated a redundant role of the two sea urchins in controlling this algae (Bulleri et al. 1999; Bonaviri et al. 2011). Such inconsistency might depend on the initial conditions of the studied habitat: in our case *Cystoseira*-barren mosaic in the field, and cobbles covered by *Cystoseira* spp. in the aquaria, whereas in the other two studies the habitat was a barren dominated by turf and corallines respectively (Bulleri et al. 1999; Bonaviri et al., 2011).

From an ecological point of view, **the** results suggest that the likelihood of initial **barren** patch formation could be a direct consequence of local *P. lividus* grazing: this species, by consuming and removing the entire canopy and the base of the alga, prepares naked substratum which can later be colonized by encrusting algae and its associated “cryptic fauna” (Agnetta et al. 2013). Then *A. lixula*, which settles preferentially in encrusting coralline algae, can colonize the barren (Privitera et al. 2011) and maintain it (Bonaviri et al. 2011). According to this facilitative model, in contrast to the traditional hypothesis of a competitive scenario, the decrease in *P. lividus* density, currently affected by cumulative human impact, should reduce the likelihood of widespread barren formation. Furthermore, because *Cystoseira* spp. needs naked substratum to recruit (Perkol-Finkel and Airoidi 2010) the timing of bare halos formation could be crucial in promoting the recovery of these algal forests. Thus another possible scenario is that when at low density *P. lividus* grazing on *Cystoseira* spp. (high density would make propagules more likely to be grazed) can trigger different habitat formation (algal forest vs. barren) depending on the seasonal time the substratum becomes naked

5. Conclusions

Foraging ability of the two sea urchins on *Cystoseira* canopy is very different and these algae can be particularly threatened by *P. lividus* grazing rather than *A. lixula*. This supports the hypothesis that *P. lividus* has a leading role in the formation of barren. Knowledge gained in this study fills important gaps in the understanding of functioning of rocky infralittoral ecosystems in particular barren formation process and furnishes new perspective to resources management also in Mediterranean Marine Protected Areas.

Acknowledgements

The authors are indebted to Dr. Nicola Galasso for their indispensable help during field work. The authors are indebted to Julie-Anne Buck for revising the English text. Experiments described in this paper comply with current Italian laws.

References

1 Agnetta D, Bonaviri C, Badalamenti F, Scianna C, Vizzini S, Gianguzza P (2013) Functional traits of two co-occurring
2 sea urchins across a barren/forest patch system. *J Sea Res* 76: 170–177. <http://dx.doi.org/10.1016/j.seares.2012.08.009>
3
4 Airoidi L, Beck WM (2007) Loss, status and trends for coastal marine habitats of Europe. *Oceanogr Mar Biol Annu*
5 *Rev* 45:345–405.
6
7 Ballesteros E, Garrabau J, Hereu B, Zabala M, Cebrian E, Sala E (2009) Deep-water stands of *Cystoseira zosteroides*
8 (Fucales, Phaeophyta) in the Northwestern Mediterranean: insights into assemblage structure and population dynamics.
9 *Estuar. Coast Shelf Sci* 82:477–484.
10
11 Ballesteros E, Sala E, Garrabou J, Zabala M (1998) Community structure and frond size distribution of a deep water
12 stand of *Cystoseira spinosa* (Phaeophyta) in the northwestern Mediterranean. *Eur J Phycol* 33:121–128.
13
14 Bonaviri C, Vega Fernández T, Fanelli G, Badalamenti F, Gianguzza P (2011) Leading role of sea urchin *Arbacia lixula*
15 in maintaining barren state in southwestern Mediterranean. *Mar Biol* 158: 2505–2513.
16
17 <http://dx.doi.org/10.1007/s00227-011-1751-2>.
18
19 Bulleri (2013) Grazing by sea urchins at the margins of barren patches on Mediterranean rocky reefs. *Mar Biol*
20 160(9):2493-2501.
21
22 Bulleri F, Benedetti-Cecchi L, Cinelli F (1999) Grazing by the sea urchins *Arbacia lixula* L. and *Paracentrotus lividus*
23 Lam. in the Northwest Mediterranean. *J Exp Mar Biol Ecol* 241:81–95. [http://dx.doi.org/10.1016/S0022-](http://dx.doi.org/10.1016/S0022-0981(99)00073-8)
24 0981(99)00073-8.
25
26 Bulleri F, Bertocci I, Micheli F (2002) Interplay of encrusting coralline algae and sea urchins in maintaining alternative
27 habitats. *Mar Ecol Prog Ser* 243:101–109.
28
29 Conteras S, Castilla JC (1987) Feeding behavior and morphological adaptations in two sympatric sea urchin species in
30 central Chile. *Mar Ecol Prog Ser* 38:217-224.
31
32 Cardona L, Moranta J, Reñones O, Hereu B (2013) Pulses of phytoplanktonic productivity may enhance sea urchin
33 abundance and induce state shifts in Mediterranean rocky reefs. *Estuar. Coast. Shelf Sci.* 133: 88-96.
34
35 Estes JA; Terborgh T, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, et al. (2011) Trophic Downgrading
36 of Planet Earth. *Science* 333:301. doi: 10.1126/science.1205106
37
38 **Flukes EB., Johnson CR., Ling SD (2012) Forming sea urchin barrens from the inside out: an alternative pattern**
39 **of overgrazing. *Mar Ecol Prog Ser* 464: 179–194.**
40
41 Frantzis A, Gremare A (1992) Ingestion, absorption, and growth rates of *Paracentrotus lividus* (Echinodermata:
42 Echinoidea) fed different macrophytes. *Mar Ecol Prog Ser* 95:169–183.
43
44 Gianguzza P, Bonaviri C, Milisenda G, Barcellona A, Agnetta D, Vega Fernández T, Badalamenti F (2010) Macroalgal
45 assemblage type affects predation pressure on sea urchins by altering adhesion strength. *Mar Env Res* 70:82–86.
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2 Gianguzza P, Bonaviri C, Prato E, Fanelli G, Chiantore M, Privitera D, Luzzu F, Agnetta D (2013) Hydrodynamism
3 and its influence on the reproductive condition of the edible sea urchin *Paracentrotus lividus*. Mar Env Res 85:29-33.
4 <http://dx.doi.org/10.1016/j.marenvres.2012.12.007>
5
6 Graham M (2004) Effects of local deforestation on the diversity and structure of Southern California Giant Kelp forest
7 food webs. Ecosystems 7:341–357.
8
9 Guidetti P, Dulčić J (2007) Relationship among predatory fish, sea urchins and barrens in Mediterranean rocky reefs
10 across a latitudinal gradient. Mar Env Res 63:168–184. <http://dx.doi.org/10.1016/j.marenvres.2006.08.002>
11
12 Hereu B, Zabala M, Sala E (2008) Multiple controls of community structure and dynamics in a sublittoral marine
13 environment. Ecology 89:3423–3435. doi:10.1890/07-0613.1
14
15 Konar B, Estes JA (2003) The stability of boundary regions between kelp beds and deforested areas. Ecology 84
16 (1):174–185. <http://dx.doi.org/10.1890/0012-9658>
17
18 Lawrence JM (2013) Edible Sea urchins: Biology and Ecology, 3rd ed. Elsevier, Amsterdam
19
20 Mangialajo L, Chiantore M, Cattaneo-Viatti R (2008) Loss of fucoid algae along a gradient of urbanisation, and
21 structure of benthic assemblages. Mar Ecol Prog Ser 358:63–74.
22
23 Moore P, Hawkins SJ, Thompson RC (2007) Role of biological habitat amelioration in altering the relative responses of
24 congeneric species to climate change. Mar Ecol Prog Ser 334:11–19
25
26 Perkol-Finkel S, Airoidi L (2010) Loss and Recovery Potential of Marine Habitats: An Experimental Study of Factors
27 Maintaining Resilience in Subtidal Algal Forests at the Adriatic Sea. PLoS ONE 5(5): e10791.
28 doi:10.1371/journal.pone.0010791
29
30 Privitera D, Chiantore M, Mangialajo L, Glavic N, Kozul W, Cattaneo-Viatti R (2008) Inter- and intra-specific
31 competition between *Paracentrotus lividus* and *Arbacia lixula* in resource-limited barren areas. J Sea Res 60:184–192.
32 <http://dx.doi.org/10.1016/j.seares.2008.07.001>.
33
34 Privitera D, Noli M, Falugi C, Chiantore M (2011) Benthic assemblages and temperature effects on *Paracentrotus*
35 *lividus* and *Arbacia lixula* larvae and settlement. J Exp Mar Biol Ecol 407: 6–11.
36 <http://dx.doi.org/10.1016/j.jembe.2011.06.030>.
37
38 Rochette R, Hamel JF, Himmelman JH (1994) Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors,
39 current and feeding status. Mar Ecol Prog Ser 106:93–100. doi:10.3354/meps106093
40
41 Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F et al. (2012) The structure of Mediterranean rocky reef
42 ecosystems across environmental and human gradients, and conservation implications. PloS One 7 (2), e32742.
43 <http://dx.doi.org/10.1371/journal.pone.0032742>.
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 **Santos R, Flammang P (2005) Morphometry and mechanical design of tube foot stems in sea urchins: a**
2 **comparative study. J Exp Mar Biol Ecol 315:211–223.**

3
4 Santos R, Flammang P (2007) Intra- and interspecific variation of attachment strength in sea urchins. Mar Ecol Prog Ser
5 332:129–142.

6
7 Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate
8 reef. Oecologia 132:131–142.

9
10 Thibaut T, Pinedo S, Torras X, Ballesteros E (2005) Long-term decline of the populations of Fucales (*Cystoseira* spp.
11 And *Sargassum* spp.) in the Albères coast (France, northwestern Mediterranean). Mar Pollut Bull 50:1472–1489.

12
13 Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variances.
14 Cambridge University Press, Cambridge.

15
16 Winer BJ, Brown DR, Michels KM (1991) Statistical principles in experimental designs, 3rd ed. McGraw-Hill, Sydney

17 18 19 20 21 22 **Figure legends**

23
24 **Fig. 1** Not consumed vs consumed *Cystoseira* spp. (arrows) canopy by *A. lixula* (A) and *P. lividus* (B) at the end of the
25 foraging experiment (30 and 3 days respectively).

26
27 **Fig. 2** Percentage of *Cystoseira* spp. in sea urchin gut contents from the field study. Differences between the two sea
28 urchin species were consistent with season: Summer (S), Autumn (A) 2007 and Winter (W), Spring (Sp) 2008.

29 30 31 32 **Table legends**

33
34 **Table 1 Results** of the 2 - way ANOVA on consumed *Cystoseira* spp. (percent wet weight (g)) **at the end of the**
35 **experiment.** Factors include: “Urchin” (Ur; three levels: *P. lividus*, *A. lixula* and no urchins), fixed, and “Aquarium”
36 (Aq; three levels), random and nested in Ur (n = 3). **Transformation: $x^{0.25}$, Cochran's Test: $C = 0.3743$ ns**
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Table 1 Results of the 2 - way ANOVA on consumed *Cystoseira* spp. (percent wet weight (g)) **at the end of the experiment**. Factors include: “Urchin” (Ur; three levels: *P. lividus*, *A. lixula* and no urchins), fixed, and “Aquarium” (Aq; three levels), random and nested in Ur (n = 3).

Transformation: $x^{0.25}$, Cochran's Test: C = 0.3743 ns

Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Urchin = Ur	2	23.0361	209.64	0.0000
Aquarium(Ur)	6	0.1099	0.43	0.8493
Residual	18	0.2555		
Total	26			

SNK test: *P. lividus* > *A. lixula* = Control

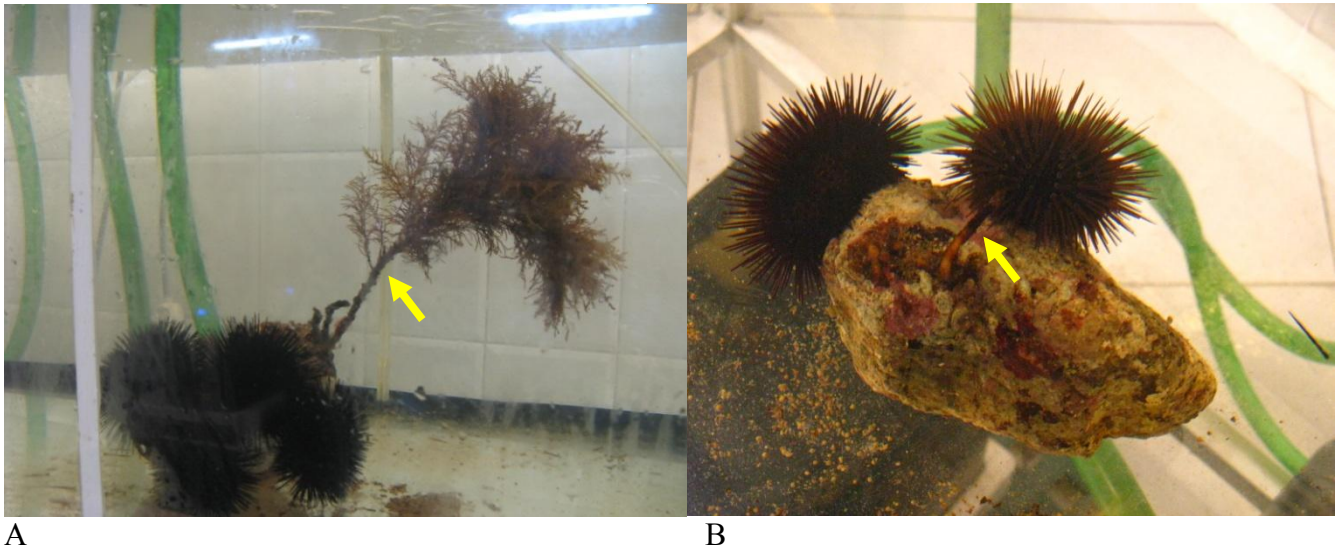


Fig. 1 Not consumed vs consumed *Cystoseira* spp. (arrows) canopy by *A. lixula* (A) and *P. lividus* (B) at the end of the foraging experiment (30 and 3 days respectively).

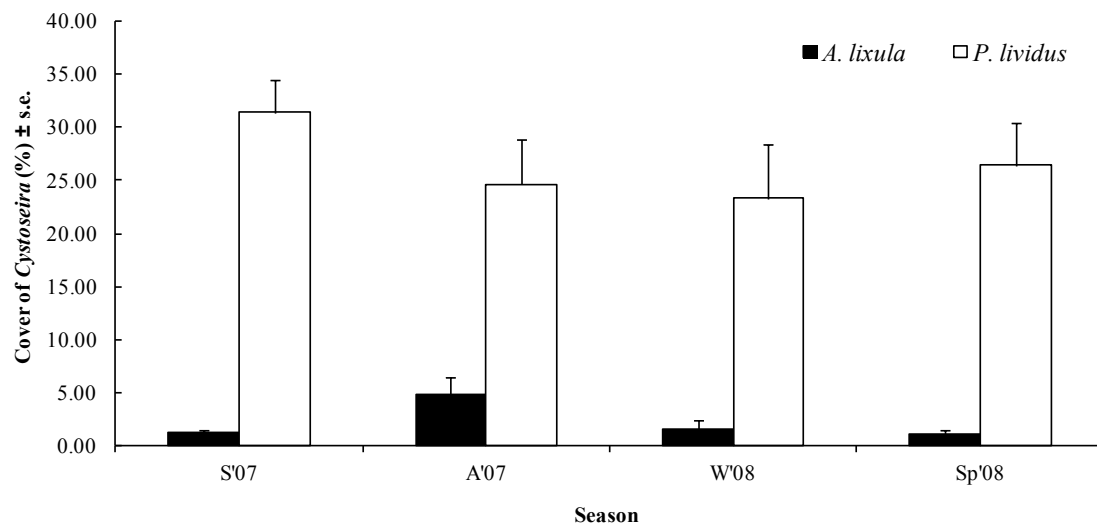


Fig. 2 Percentage of *Cystoseira* spp. in sea urchin gut contents from the field study. Differences between the two sea urchin species were consistent with season: Summer (S), Autumn (A) 2007 and Winter (W), Spring (Sp) 2008.