

Alma Mater Studiorum Università di Bologna
Archivio istituzionale della ricerca

The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Mancuso F.P., D'Agostaro R., Milazzo M., Badalamenti F., Musco L., Mikac B., et al. (2022). The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea. *MARINE ENVIRONMENTAL RESEARCH*, 173, 1-11 [10.1016/j.marenvres.2021.105515].

Availability:

This version is available at: <https://hdl.handle.net/11585/839425> since: 2023-08-04

Published:

DOI: <http://doi.org/10.1016/j.marenvres.2021.105515>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).
When citing, please refer to the published version.

(Article begins on next page)

This is the final peer-reviewed accepted manuscript of:

Mancuso FP, D'Agostaro R, Milazzo M, Badalamenti F, Musco L, Mikac B, et al. The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea. *Marine Environmental Research*. 2022 Jan 1;173:105515.

The final published version is available online at:

<https://doi.org/10.1016/j.marenvres.2021.105515>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>)

When citing, please refer to the published version.

Marine Environmental Research

The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and biodiversity of native algal forests in the Mediterranean Sea --Manuscript Draft--

| | |
|------------------------------|--|
| Manuscript Number: | MERE-D-21-00590R2 |
| Article Type: | Full Length Article |
| Keywords: | habitat shift; alga; <i>Ericaria brachycarpa</i> ; epifauna diversity; <i>Cystoseira sensu lato</i> ; rocky shore; Marine Protected Area |
| Corresponding Author: | Francesco Paolo MANCUSO University of Palermo: Università degli Studi di Palermo Palermo, ITALY |
| First Author: | Francesco Paolo MANCUSO, PhD |
| Order of Authors: | Francesco Paolo MANCUSO, PhD Riccardo D'Agostaro Marco Milazzo, Associate Professor Fabio Badalamenti, Research Director Luigi Musco, Associate Professor Barbara Mikac, PhD Sabrina Lo Brutto, Associate Professor Renato Chemello, Associate Professor |
| Abstract: | Invasive seaweeds are listed among the most relevant threats to marine ecosystems worldwide. Biodiversity hotspots, such as the Mediterranean Sea, are facing multiple invasions and are expected to be severely affected by the introduction of new non-native seaweeds in the near future. In this study, we evaluated the consequences of the shift from the native <i>Ericaria brachycarpa</i> to the invasive <i>Asparagopsis taxiformis</i> habitat on the shallow rocky shores of Favignana Island (Egadi Islands, MPA, Sicily, Italy). We compared algal biomass and species composition and structure of the associated epifaunal assemblages in homogenous and mixed stands of <i>E. brachycarpa</i> and <i>A. taxiformis</i> . The results showed that the biomass of primary producers is reduced by 90% in the <i>A. taxiformis</i> invaded habitat compared to the <i>E. brachycarpa</i> native habitat. The structure of the epifaunal assemblages displayed significant variations among homogenous and mixed stands. The abundance, species richness and Shannon-Wiener diversity index of the epifaunal assemblages decreased by 89%, 78% and 40%, respectively, from homogenous stands of the native <i>E. brachycarpa</i> to the invasive <i>A. taxiformis</i> . Seaweed biomass was the structural attribute better explaining the variation in epifaunal abundance, species richness and diversity. Overall, our results suggest that the shift from <i>E. brachycarpa</i> to <i>A. taxiformis</i> habitat would drastically erode the biomass of primary producers and the associated biodiversity. We hypothesize that a complete shift from native to invasive seaweeds could ultimately lead to bottom-up effects on rocky shore habitats, with negative consequences for the ecosystem structure, functioning, and the services provided. |
| Suggested Reviewers: | Antonia Chiarore, PhD Stazione Zoologica Anton Dohrn Napoli antonia.chiarore@szn.it For her scientific skills and publications on the topic of the paper Pedro Augusto Dos Santos Longo, PhD State University of Campinas: Universidade Estadual de Campinas pedro.slongo@gmail.com For his scientific skills and publications on the subject of the paper Javier Urrea Instituto Español de Oceanografía: Instituto Espanol de Oceanografía |

| | |
|-------------------------------|--|
| | javier.urrea@ieo.es For his scientific skills and publications on the subject of the paper |
| | Valentina Pitacco National Institute of Biology: Nacionalni institut za biologijo valentina.pitacco@mbss.org For her scientific skills and publications on the topic of the paper |
| Response to Reviewers: | |

Highlights:

- Primary producer biomass is 90% lower in *A. taxiformis* than in *E. brachycarpa* habitat.
- From native to invasive seaweeds, epifaunal assemblages lost 40% of their diversity.
- Seaweed biomass was the structural attribute explaining the epifaunal variation.
- We suggest a complete shift from native to invasive seaweeds could impair rocky shore habitats.

1 **The invasive seaweed *Asparagopsis taxiformis* erodes the habitat structure and**
2
3 **biodiversity of native algal forests in the Mediterranean Sea**

4
5
6
7
8 F. Paolo Mancuso^a, Riccardo D'Agostaro^b, Marco Milazzo^{b,c}, Fabio Badalamenti^d, Luigi Musco^{c,e},
9
10 Barbara Mikac^f, Sabrina Lo Brutto^g, Renato Chemello^{b,c}

11
12
13 ^aDepartment of Earth and Marine Sciences (DiSTeM), University of Palermo, viale delle Scienze Ed. 16, 90128 Palermo,
14
15 Italy

16
17 ^bDepartment of Earth and Marine Sciences (DiSTeM), University of Palermo, via Archirafi 20-22, 90123 Palermo, Italy

18
19 ^cConsorzio Nazionale Interuniversitario per le Scienze del Mare (CoNISMa), Rome, Italy

20
21 ^dInstitute of Anthropic Impacts and Sustainability in Marine Environment (CNR-IAS), via Lungomare Cristoforo
22
23 Colombo 4521, 90149, Palermo, Italy

24
25 ^eDepartment of Biological and Environmental Sciences and Technologies, University of Salento, Lecce, Italy

26
27 ^fDepartment of Biological, Geological and Environmental Sciences, University of Bologna, via Sant'Alberto 16,
28
29 48123 Ravenna, Italy

30
31 ^gDipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche (STEBICEF), University of Palermo,
32
33 Palermo, Italy

34
35
36
37 Corresponding author: Mancuso F.P. email: francesco.mancuso@unipa.it

38
39
40
41
42
43
44
45
46
47
48
49 **Abstract**

50 Invasive seaweeds are listed among the most relevant threats to marine ecosystems worldwide.

51
52 Biodiversity hotspots, such as the Mediterranean Sea, are facing multiple invasions and are expected
53
54 to be severely affected by the introduction of new non-native seaweeds in the near future. In this
55
56 study, we evaluated the consequences of the shift from the native *Ericaria brachycarpa* to the
57
58 invasive *Asparagopsis taxiformis* habitat on the shallow rocky shores of Favignana Island (Egadi
59
60 Islands, MPA, Sicily, Italy). We compared algal biomass and species composition and structure of
61
62

29 the associated epifaunal assemblages in homogenous and mixed stands of *E. brachycarpa* and *A.*
30 *taxiformis*. The results showed that the biomass of primary producers is reduced by 90% in the *A.*
31 *taxiformis* invaded habitat compared to the *E. brachycarpa* native habitat. The structure of the
32 epifaunal assemblages displayed significant variations among homogenous and mixed stands. The
33 abundance, species richness and Shannon-Wiener diversity index of the epifaunal assemblages
34 decreased by 89%, 78% and 40%, respectively, from homogenous stands of the native *E. brachycarpa*
35 to the invasive *A. taxiformis*. Seaweed biomass was the structural attribute better explaining the
36 variation in epifaunal abundance, species richness and diversity. Overall, our results suggest that the
37 shift from *E. brachycarpa* to *A. taxiformis* habitat would drastically erode the biomass of primary
38 producers and the associated biodiversity. We hypothesize that a complete shift from native to
39 invasive seaweeds could ultimately lead to bottom-up effects on rocky shore habitats, with negative
40 consequences for the ecosystem structure, functioning, and the services provided.

41
42 **Keywords:** habitat shift; alga; *Ericaria brachycarpa*; epifauna diversity; *Cystoseira sensu lato*; rocky
43 shore; Marine Protected Area

44 45 **Introduction**

46 Invasive species are globally recognized among the main drivers of habitat shift in both terrestrial
47 and marine ecosystems (Gallardo et al., 2016; Mačić et al., 2018). In marine environments, decades
48 of human activities related to global aquatic trade have enabled the dispersion of invasive species
49 among distant geographic areas worldwide (Bax et al., 2003; Williams and Smith, 2007; Molnar et
50 al., 2008; Servello et al., 2019). In addition, the rise in seawater temperature caused by global
51 warming has allowed non-native species to cross environmental and geographical barriers, facilitating
52 their expansion and in turn eroding indigenous resistance (Occhipinti-Ambrogi and Galil, 2010; Lo
53 Brutto et al., 2019). Concerns over ecological and social-economic consequences have led researches
54 to investigate the effects of invasive species on many marine ecosystems around the world.

55 Seaweeds are a significant component of marine non-native and invasive species (227 taxa
1
26 globally), with some of them being responsible for drastic habitat shifts (Williams and Smith, 2007).
3
4
57 Studies have highlighted how invasive seaweeds can negatively impact the recipient habitats by
6
78 reducing biomass of primary producers, biodiversity, and nutrient flows, compromising ecosystem
8
9
59 functioning (Boudouresque et al., 2005; Streftaris and Zenetos, 2006; Thomsen et al., 2014; Maggi
10
11
60 et al., 2015; Ramsay-Newton et al., 2017; Geburzi and McCarthy, 2018). Interestingly, the effects of
12
13
61 non-native seaweeds seem to change depending on the complexity of the recipient habitat (Thomsen
14
15
16
62 et al., 2014). In less structured habitats (e.g. soft bottoms), the introduction of non-native seaweeds
17
18
63 enhances structural complexity that may favor the increase in biodiversity and food web length
19
20
21
64 (Dijkstra et al., 2017). Conversely, the introduction in well-structured habitats (e.g. seagrass
22
23
65 meadows, algal canopies) may alter the diversity and function, depending on the structural features
24
25
26
66 of the recipient habitat (Engelen et al., 2013; Veiga et al., 2014, 2018).
27

67 Macroalgal complexity plays a significant role in shaping the abundance, richness and structure of
28
29
30
68 epifaunal assemblages associated with both non-native and native seaweeds (Chemello and Milazzo,
31
32
33
69 2002; Jormalainen and Honkanen, 2008; Pitacco et al., 2014; Veiga et al., 2014; Maggi et al., 2015;
34
35
70 Dijkstra et al., 2017; Veiga et al., 2018; Chiarore et al., 2019). Algae with a high structural
36
37
38
71 complexity, expressed as a combination of attributes, such as degree of branching, thallus width and
39
40
41
72 height, and wet weight, can support well-structured epifaunal communities (Hacker and Steneck,
42
43
44
73 1990; Chemello and Milazzo, 2002; Jormalainen and Honkanen, 2008; Pitacco et al., 2014; Veiga et
45
46
74 al., 2014; Bitlis, 2019; Chiarore et al., 2019). Studies comparing the epifaunal diversity between
47
48
49
75 invasive and native seaweeds revealed that, when invasive species are structurally less complex than
50
51
76 native ones, they support low abundance and richness, and a simplified structure of epifaunal
52
53
77 assemblages (Navarro-Barranco et al., 2018; Veiga et al., 2018). However, when native macroalgae
54
55
78 are less complex, the abundance and diversity of epifauna associated with invasive seaweeds may be
56
57
79 higher (Veiga et al., 2014; Dijkstra et al., 2017). This indicates that the effects of invasive seaweeds
58
59
80 on epifaunal assemblages may change depending on both the invasive and the native seaweed
60
61
62
63
64
65

81 structural features. However, other studies have shown that native and invasive seaweeds with similar
1
82 morphologies can host either similar (Suárez-Jiménez et al., 2017) or different epifaunal diversity
3
83 (Navarro-Barranco et al., 2019). Overall, these contrasting evidences suggest that, apart from
4
6
84 seaweed morphology, other factors can be involved in structuring the associated assemblages.
8

9
85 In the last decades, the Mediterranean basin has witnessed an increase in the number of non-native
10
11
1286 and invasive seaweeds, with consequent modification of biodiversity and ecosystem functioning of
13
14
1587 coastal areas (Ribera Siguan, 2002; Streftaris et al., 2005; Streftaris and Zenetos, 2006; Piazzini and
16
1788 Balata, 2009; Musco et al., 2014; Bulleri et al., 2016; Corriero et al., 2016; Giangrande et al., 2020).
18
1989 In particular, *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon is listed among the 100 worst
20
21
2290 invasive species in this basin (Streftaris and Zenetos, 2006). The earliest reports of its presence in the
23
2491 Mediterranean Sea date back to 1798-1801 in Alexandria (Egypt) as a result of trading operations
25
26
2792 and the opening of the Suez Canal (Verlaque et al., 2015). It was first recorded along the Italian coast
28
293 on the western shore of Sicily, close to the city of Trapani, in May 2000 (Barone et al., 2003). While
30
31
3294 *A. taxiformis* has been suspected of producing harmful effects on native habitats (Barone et al., 2003),
33
3495 as far as we know, only one study assessed its effects on biodiversity, in particular by comparing the
35
3696 vagile macrofauna associated with this species to that of the native *Halopteris scoparia* (Linnaeus)
37
38
3997 Sauvageau indicating that *A. taxiformis* hosted less diverse epifaunal assemblages compared to native
40
4198 algae (Navarro-Barranco et al., 2018).
42

43
4499 Along the Italian coast, gametophytes of *A. taxiformis* can colonize coastal areas dominated by
45
46
47
48
49100 habitat-forming seaweeds, mainly belonging to the genus *Cystoseira* - recently divided into three
50
51
52
53
54101 genera *Cystoseira*, *Gongolaria* and *Ericaria* and hereafter referred to as *Cystoseira sensu lato* to
55
56
57
58
59102 include all three genera (Orellana et al., 2019; Molinari Novoa and Guiry, 2020). *Cystoseira sensu*
60
61
62
63
64
65103 *lato* species are important ecological engineers, greatly increasing the habitat surface, complexity and
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221
222
223
224
225
226
227
228
229
230
231
232
233
234
235
236
237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295
296
297
298
299
300
301
302
303
304
305
306
307
308
309
310
311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355
356
357
358
359
360
361
362
363
364
365
366
367
368
369
370
371
372
373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389
390
391
392
393
394
395
396
397
398
399
400
401
402
403
404
405
406
407
408
409
410
411
412
413
414
415
416
417
418
419
420
421
422
423
424
425
426
427
428
429
430
431
432
433
434
435
436
437
438
439
440
441
442
443
444
445
446
447
448
449
450
451
452
453
454
455
456
457
458
459
460
461
462
463
464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
480
481
482
483
484
485
486
487
488
489
490
491
492
493
494
495
496
497
498
499
500
501
502
503
504
505
506
507
508
509
510
511
512
513
514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539
540
541
542
543
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558
559
560
561
562
563
564
565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630
631
632
633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651
652
653
654
655
656
657
658
659
660
661
662
663
664
665
666
667
668
669
670
671
672
673
674
675
676
677
678
679
680
681
682
683
684
685
686
687
688
689
690
691
692
693
694
695
696
697
698
699
700
701
702
703
704
705
706
707
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724
725
726
727
728
729
730
731
732
733
734
735
736
737
738
739
740
741
742
743
744
745
746
747
748
749
750
751
752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773
774
775
776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804
805
806
807
808
809
810
811
812
813
814
815
816
817
818
819
820
821
822
823
824
825
826
827
828
829
830
831
832
833
834
835
836
837
838
839
840
841
842
843
844
845
846
847
848
849
850
851
852
853
854
855
856
857
858
859
860
861
862
863
864
865
866
867
868
869
870
871
872
873
874
875
876
877
878
879
880
881
882
883
884
885
886
887
888
889
890
891
892
893
894
895
896
897
898
899
900
901
902
903
904
905
906
907
908
909
910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926
927
928
929
930
931
932
933
934
935
936
937
938
939
940
941
942
943
944
945
946
947
948
949
950
951
952
953
954
955
956
957
958
959
960
961
962
963
964
965
966
967
968
969
970
971
972
973
974
975
976
977
978
979
980
981
982
983
984
985
986
987
988
989
990
991
992
993
994
995
996
997
998
999
1000

107 of their related assemblages, leading to the development of well-structured food webs (Schiel and
108 Foster, 2006; Cheminée et al., 2013; Mineur et al., 2015; Mancuso et al., 2021b). According to the
109 European Water Framework Directive (2000/60), they are also considered indicators of good water
110 and environmental quality (European Commission, 2000).

111 In a recent study, we discovered that *A. taxiformis* had a less diverse and less structured molluscan
112 assemblage than *E. brachycarpa*; however, no information about other epifaunal components
113 associated with seaweeds was reported, nor information about intermediate states, such as mixed
114 stands of *E. brachycarpa* and *A. taxiformis* (Mancuso et al., 2021a). Here, we compared the structure
115 of the epifaunal community (amphipods, molluscs and annelids) associated with three plausible
116 alternative states of the transition between the native *Ericaria brachycarpa* (J.Agardth) Orellana &
117 Sansón and the invasive *A. taxiformis*. In particular, we characterized and compared the biomass and
118 the diversity (richness, evenness, structure and composition) of the epifauna associated with the
119 fronds of homogenous and mixed stands of *E. brachycarpa* and *A. taxiformis*. Moreover, we explored
120 the variation of the epifaunal diversity in relation to the structural features of the two algae (dry
121 weight, thallus volume, canopy volume, and interstitial volume). We hypothesize that shifting from
122 habitats dominated by *E. brachycarpa* to those dominated by *A. taxiformis* will have a negative
123 impact on the associated biodiversity, resulting in low abundances and diversity of each epifaunal
124 component.

126 **Materials and Methods**

127 Study area and algal species characteristics

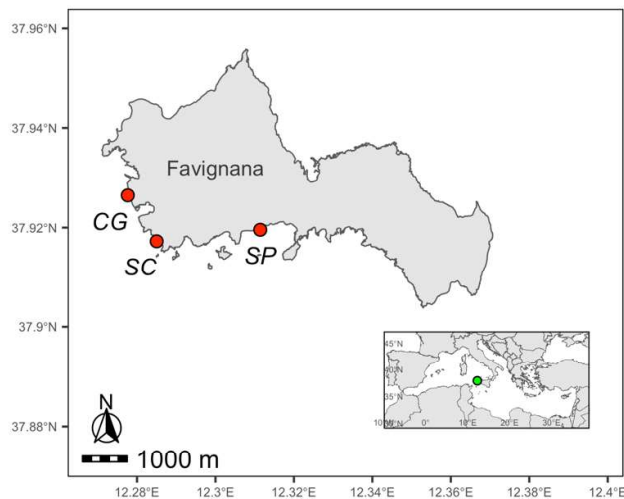
128 The research was performed on the southwestern, shallow rocky shore of Favignana Island
129 (Sicily, Italy), within the Egadi Islands Marine Protected Area (MPA) in June 2011 (Fig. 1). The
130 region consists of gently sloping (5°-10°) carbonate rocky platforms and scattered boulders (Pepe et
131 al., 2018) that provide substrates for well-developed macroalgal vegetation.

132 In this area, *A. taxiformis* was first recorded in 2000 (Barone et al., 2003). Since then, no studies
133 have explored the temporal effects of this invasive species on native habitats. Although today *A.*
134 *taxiformis* is well established in the area, previous surveys allowed the identification of three sites
135 with distinctive habitats corresponding to three possible alternative states of the transition from native
136 to invasive seaweed habitats: “Scoglio Corrente” (37° 55' 2.0778" N, 12° 17' 6.0432" E) characterized
137 by stands of *E. brachycarpa* (100% coverage); “Scoglio Palumbo” (37° 55' 10.4226" N, 12° 18'
138 41.097" E) hosting stands of *A. taxiformis* (100% coverage), and “Cala Grande” (37° 55' 35.385" N,
139 12° 16' 39.514" E) with mixed stands of *E. brachycarpa* (~50% coverage) and *A. taxiformis* (~50%
140 coverage) (Fig. 1). In this study, we decided to use these three sites to compare the epifaunal
141 communities associated with three plausible alternative states of the transition from native to invasive
142 habitats.

143 *Ericaria brachycarpa* is a brown seaweed (Fucales) characterized by caespitosis thalli up to 20-
144 25 cm in height with several perennial axes, up to 2-6 cm in height, connected to the substratum by a
145 more or less compact discoid base formed by haptera (Molinari Novoa and Guiry, 2020). The apices
146 of the axes are flattened, smooth and not very prominent. Branches are cylindrical with smooth bases,
147 or covered with tiny spinose appendages that are typically fertile in the spring-summer season
148 (Gómez-Garreta et al., 2002; Mannino and Mancuso, 2009; Cormaci et al., 2012). Like other
149 *Cystoseira sensu lato* species, *E. brachycarpa* displays seasonal differences in vegetative
150 development (Gómez-Garreta et al., 2002). At the study sites, new branches of *E. brachycarpa* grow
151 from the perennial axes in spring (May-June) providing new substrate and shelter for colonizing
152 fauna, while in autumn (September-October) *E. brachycarpa* starts to become quiescent, losing
153 almost all branches, leaving perennial axes that persist throughout the cold winter season.

154 *Asparagopsis taxiformis* is a red alga (Bonnemaisoniales) common in the tropics and subtropics
155 across the globe. The species experiences a heteromorphic life cycle, with an erect gametophyte
156 alternating with a filamentous sporophyte known as *Falkenbergia hillebrandii* (Bornet) Falkenberg
157 (Andreakis et al., 2004; Ní Chualáin et al., 2004). The gametophytes are characterized by sparsely

158 branched, creeping stolons and erect shoots from which several side branches grow in all directions.
1
159 The latter ramifies over and over again giving the thallus a plumose appearance. In the study area, *A.*
3
160 *taxiformis* develops in the upper sublittoral zone of the rocky substrate or as an epiphyte of other algal
4
6 species. The gametophytes are present during all seasons with a maximum occurrence in spring
7
8
9
162 (Barone et al., 2003).



164
165
166 **Fig. 1** Location of the three study sites (red dots) along the rocky-shore of Favignana Island MPA
167 (green dot), Trapani, Sicily, Italy. **SC** = Scoglio Corrente, **SP** = Scoglio Palumbo, **CG** = Cala Grande.

169 Sampling and analysis of epifauna

170 Samples were collected by scuba diving at a depth of 5-7 m. For each site (hereafter referred to
171 as habitat), two areas (5 x 5 m) were haphazardly selected. For each area, 10 thalli of *E. brachycarpa*
172 from homogenous stands (100% algal coverage), 10 thalli of *E. brachycarpa* from mixed stands and
173 10 gametophytes of *A. taxiformis* from homogenous stands (100% algal coverage) were collected (n
174 = 20 per habitat). Thalli were collected 50cm apart to avoid spatial autocorrelation among samples.
175 Underwater, each thallus and the associated epifauna were enveloped in a plastic bag, then the alga
176 was detached from the substrate and the plastic bag was immediately closed to prevent the escape of
177 vagile fauna. After collection, each sample was carefully drained of seawater in order to prevent

178 escape of small epifauna and stored at -20°C until laboratory analysis. In the laboratory, each thallus
1
179 of *E. brachycarpa* and gametophytes of *A. taxiformis* were transferred into buckets abundantly rinsed
3
180 under running water, allowing the associated fauna to detach from the algae. Then, the water was
4
6
181 sieved through a 1 mm mesh. After sorting, molluscs, amphipods, and annelids were stored in 70%
8
9
182 seawater ethanol solution and subsequently counted and identified to species, or the nearest possible
10
11
183 taxonomic level. Taxonomy and nomenclature were updated according to the World Register of
13
14
184 Marine Species database (WoRMS Editorial Board (2021)).
15
16
185

186 Seaweed structural attributes

187 For each thallus of *E. brachycarpa* and gametophyte of *A. taxiformis* collected, we measured 4
21
22
23
2488 structural features (thallus volume, canopy volume, interstitial volume, and biomass), to explore their
25
26
27
28
290 relationships with the diversity indices calculated for the epifaunal assemblages. Thallus volume was
30
31
32
33
3492 measured as the variation of volume, in ml, after the immersion of a thallus into a graduated cylinder
35
36
37
38
394 filled with seawater. Canopy and interstitial volumes were estimated according to Hacker and Steneck
40
41
42
43
4496 (1990). The canopy volume (*CV*, the volume, in ml, created by the overall dimension of a
45
46
47
48
49 thallus submerged in seawater) was defined as the volume of a theoretical cylinder ($CV = \pi \times r^2 \times$
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65 *h*), where $\pi = 3.14$, *h* is the length of the thallus from the base to its apical portion of the thallus,
including epiphytes, and *r* is the radius calculated as an average measure of the radius of the thallus
measured with a ruler (+/- 1 mm) at the apical, median, and basal parts. The interstitial volume (*IV*,
the volume, in ml, of water among the branches of the alga) was obtained by subtracting the thallus
volume (*TV*) from the canopy volume *CV* ($IV = CV - TV$).

199 Finally, the biomass of the macroalgae was calculated as dry weight (*DW*, gr) after drying in a
52
53
200 stove at 60 °C for 48 h (Stein-Taylor et al., 1985). Biomass was used as a proxy for the primary
54
55
201 production of each habitat.
57
58
59
60
202

203 Data analysis

204 For each epifaunal species, we calculated total abundance (N), frequency (F%; the percentage of
1 samples in which a particular species is present) and dominance index (D%; the percentage of the
205 3 rate between the percentage of individuals of a particular species and the total number of individuals
4 5 6
206 7 within the sample) (Magurran, 1988). The epifaunal assemblages of each habitat were characterized
8
207 9 according to total abundance of individuals (N), rarefied species richness (S), Shannon-Wiener
10
208 11 diversity index (H') and Pielou's Evenness index (J). A two-way analysis of variance (ANOVA) was
12
209 13 used to test differences in the epifaunal indices (N, S, H', J) between habitats (fixed with 3 levels: *E.*
14
210 15 *brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*) and areas (random and nested within
16
211 17 habitat with 2 levels: area 1 and area 2). Cochran's test was used to check for the homogeneity of
18
212 19 variances (Underwood 1997). Tukey's HSD procedure was used to separate means (at $\alpha = 0.05$)
20
213 21 following significant effects in the ANOVAs (Underwood, 1996). The hierarchical structure of the
22
214 23 taxonomic classifications of the epifaunal assemblages of *E. brachycarpa*, *E. brachycarpa* in mixed
24
215 25 stands, and *A. taxiformis* was visualized using the "heat_tree" function in the "Metacoder" R- package
26
216 27 (Foster et al., 2017).
28
217 29

30
31
32
33
34
35
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

SIMPER analysis (Clarke, 1993) was performed to identify those taxa that contributed to the
dissimilarity of the epifaunal assemblages between habitats ($\delta_i\%$). The ratio $\delta_i/SD_{(\delta_i)}$ was used to
measure the consistency of the contribution of a particular taxon to the average dissimilarity in the
comparison between habitats. A cut-off value of 70% was used to exclude low contributions.

Differences in the epifaunal community structure (which takes into account species identity and
relative abundance) and composition (presence/absence, which only takes into account species
identity) among habitats and areas were assessed by Permutational Multivariate Analysis of Variance
(PERMANOVA). The analyses were based on a Bray-Curtis distance matrix of square-root
transformed epifaunal abundances (structure) and on a Jaccard distance matrix of presence/absence
data (composition) using 9999 permutations. PERMANOVA was also performed separately for each
component of the epifauna (molluscs, annelids and amphipods). Permutational analysis of
multivariate dispersion (PERMDISP) was used to test differences in multivariate dispersion

230 (Anderson et al., 2008). A principal coordinate analysis (PCoA) plot was generated to visualize the
1
231 variation of the epifaunal community structure (based on a Bray-Curtis distance matrix) and
2
3
232 composition (based on a Jaccard distance matrix).
4
5
6

233 Differences in each of the structural attributes (*CV*, *IV*, *TV*, *DW*) among habitats and areas were
7
8
234 analyzed by two-way ANOVAs according to the above mentioned design. Cochran's test was used
9
10
11
235 to check for the homogeneity of variances (Underwood, 1996).
12
13

14
15
236 Linear regression (LM) analysis was used to test which algal structural attributes explained better
16
17
237 the variation of total abundance (N), rarefied species richness (S), Shannon-Wiener diversity (H')
18
19
238 and Pielou's Evenness (J) of the whole epifaunal assemblages and its individual components
20
21
239 (molluscs, annelids and amphipods). If a non-linear relationship between response and depended
22
23
240 variables was detected, we examined the significance of applying a quadratic term in the model. In
24
25
241 addition, a distance-based redundancy analysis (dbRDA, Legendre and Anderson, 1999) was used to
26
27
28
242 investigate the relationship between structural attributes and the epifaunal multivariate structure.
29
30
243 Since dbRDA is susceptible to multicollinearity (i.e. high correlation between environmental
31
32
33
244 variables), draftsman plots were used to verify skewness or identify clear correlations between
34
35
245 structural attributes. A $\log(x + 1)$ transformation was used to correct the right-skewness of thallus
36
37
246 volume (*TV*) and biomass (*DW*). Moreover, due to the high correlation between canopy volume (*CV*)
38
39
40
247 and interstitial volume (*IV*) we removed *CV* from the subsequent analyses. Then, the structural
41
42
248 attributes were normalised using a z-score transformation due to their varying measurement scales.
43
44
45
249 Finally, forward selection was used to identify the structural properties that mostly contributed to the
46
47
250 heterogeneity in the multivariate structure of the epifaunal assemblages.
48
49
50

251 Statistical analyses were performed using R open access statistical software 3.5.1 (R Core Team,
51
52
252 2018). See the "*Data availability and reproducible research*" section for further details.
53
54
55

254 **Results**

56
57

255 Epifauna

58
59
60
61
62
63
64
65

256 Overall, we identified 5676 individuals of epifauna belonging to 199 taxa (74 molluscs, 50
1
257 amphipods, and 75 annelids). Of these, 46 and 38 taxa were exclusively found on homogenous and
3
258 mixed stands of the native *E. brachycarpa* respectively, while the invasive *A. taxiformis* hosted only
4
6
259 12 unique taxa (Fig. 2, Table S1-S2). Syllidae (annelids) and Rissoidae (molluscs) were the most
8
9
260 species rich families (35 spp. and 21 spp. respectively), while all the other families contained less
10
11
261 than 10 species each (Fig. 2, Table S1). Among molluscs, the most abundant species were *Eatonina*
13
14
262 *cossurae* (Calcara, 1841) on both *E. brachycarpa* (186 ind.) and *A. taxiformis* (12 ind.) and *Setia*
15
16
263 *ambigua* (Brugnone, 1873) on *E. brachycarpa* from mixed stands (161 ind.). The most abundant
18
19
264 species among amphipods were *Ampithoe ramondi* on *E. brachycarpa* (164 ind.), *Apherusa*
20
21
265 *alacris* (Krapp-Schickel, 1969) on *E. brachycarpa* from mixed stands (253 ind.) and *Caprella*
23
266 *acanthifera* (Leach, 1814) on *A. taxiformis* (33 ind.). Finally, annelids were mostly represented by
25
26
267 *Amphiglena mediterranea* (Leydig, 1851) on *E. brachycarpa* (457 ind.) and *Syllis prolifera* (Krohn,
28
268 1852) on both *E. brachycarpa* in mixed stands (171 ind.) and *A. taxiformis* (17 ind.) (Fig. 2, Table
30
31
269 S1).

33
34
35
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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
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

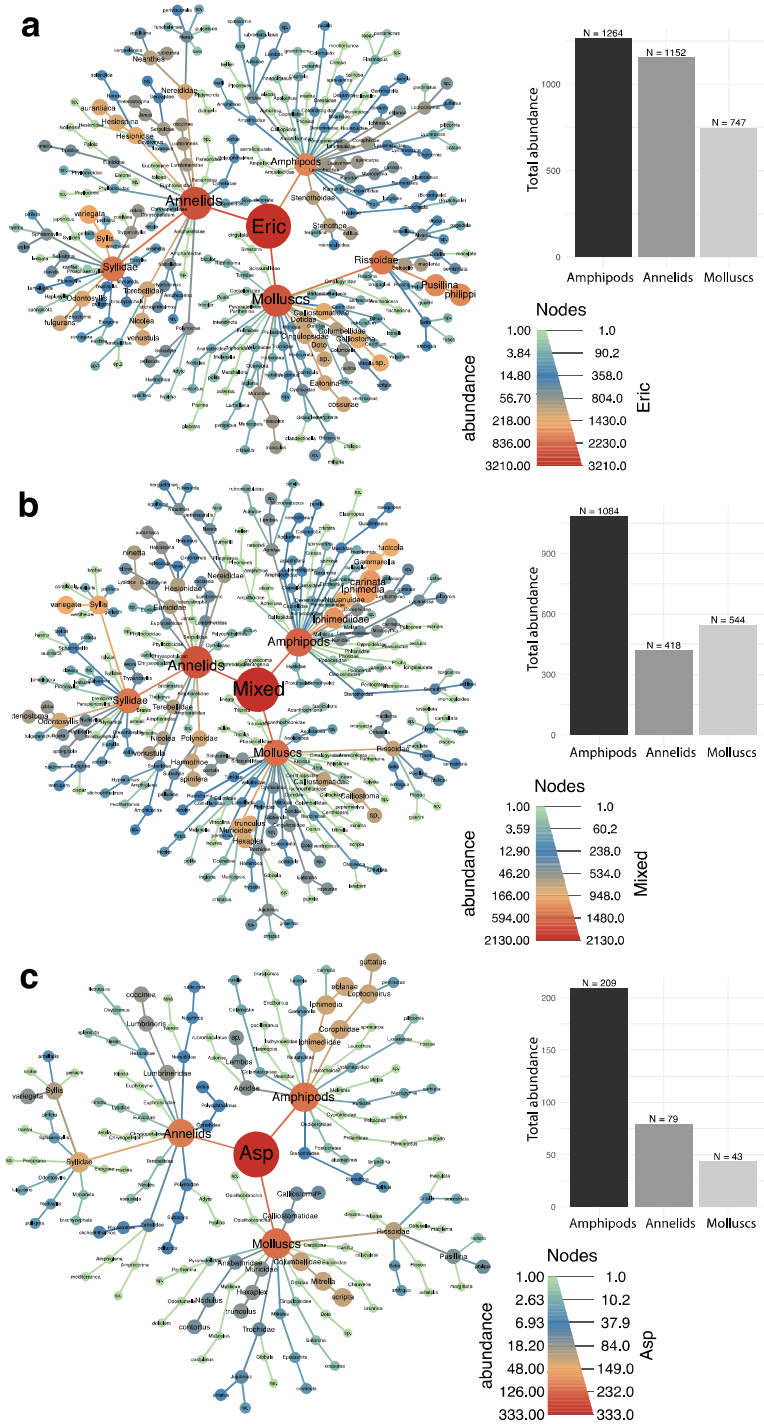


Fig. 2 Differences in the epifaunal assemblages among habitats. Heat trees show the abundances of taxa classified at the lowest taxonomic level possible on *E. brachycarpa* (a), *E. brachycarpa* in mixed stands (b) and *A. taxiformis* (c). Bar charts show the total abundance of amphipods, annelids, and molluscs for each habitat.

280
1
281
3
4
282
5
6
283
7
8
284
9
10
11
285
12
13
286
14
15
16
287
17
18
288
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
289
56
57
290
58
59
291
60
61
62
63
64
65

Total abundance (**N**) and rarefied species richness (**S**), differed significantly among habitats, with values that were higher in *E. brachycarpa* compared to *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. 3, Table S3). Shannon-Wiener diversity (**H'**) varied significantly across habitats, with *E. brachycarpa* and *E. brachycarpa* in mixed stands exhibiting closer and higher values than *A. taxiformis*.

Conversely, Pielou's evenness (**J**) was higher in *A. taxiformis* compared to the other two habitats, which showed comparable values (Fig. 3, Table S3).

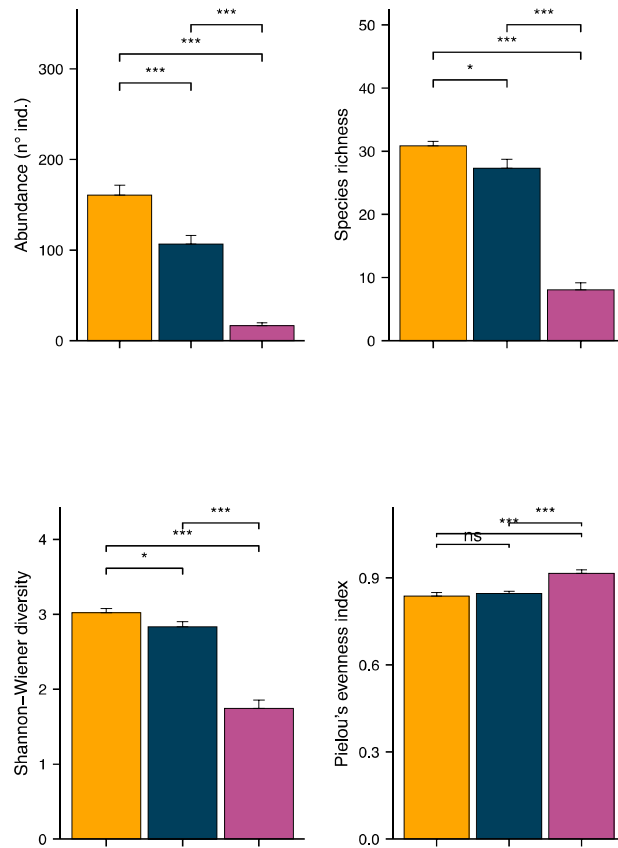
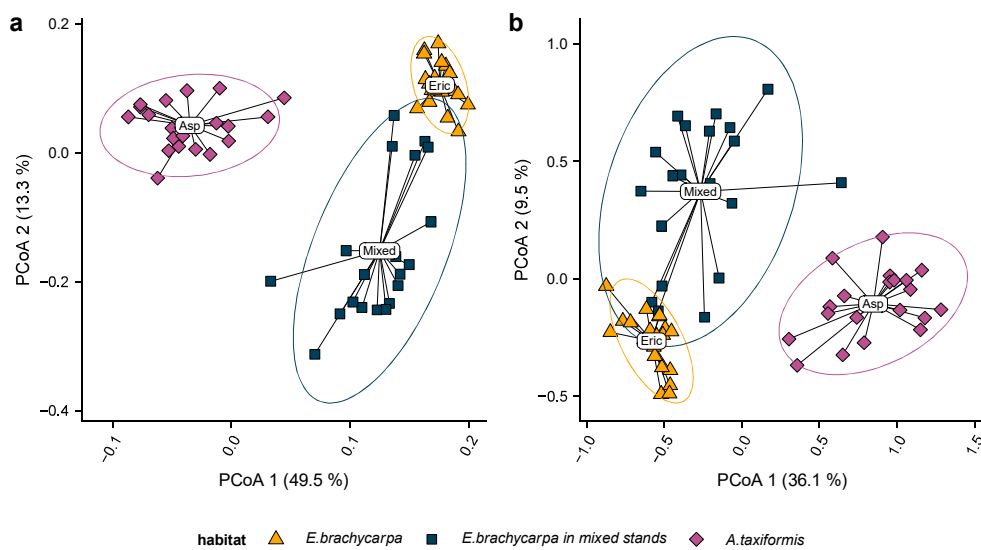


Fig. 3 Comparison of the alpha diversity indices among habitats. Abundance (a), rarefied species richness (b), Shannon-Wiener diversity (c), and Pielou's evenness index (d) of the epifaunal

292 assemblage associated with *E. brachycarpa*, *E. brachycarpa* in mixed stands, and *A. taxiformis*. Bar
 1
 293 plots show mean \pm 1 standard error (n = 20). Significant codes: *** $p \leq 0.001$, * $p \leq 0.05$, ns
 3
 4
 294 $p > 0.05$. See Table S3 for further details.
 5
 6

295
 8
 9
 296 PERMANOVA showed that the structure and composition of the epifaunal assemblages
 10
 11 differed significantly among habitats (Table S4). PERMDISP analysis revealed a high dispersion of
 12
 13 samples within habitats, especially for *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. 4).
 14
 15
 16 Notwithstanding this high dispersion, the epifaunal assemblages of the three habitats were clearly
 17
 18 separated, as shown by the PCoA ordination plot (Fig. 4). The proportion of variance explained by
 19
 20 the first two axes was 62.8% for structure and 45.6% for composition. The first axis accounted for
 21
 22 the larger part of the variance (structure = 49.5% and composition = 36.1%) and highlighted a shift,
 23
 24 in both structure and composition, from *E. brachycarpa* to *A. taxiformis*, with *E. brachycarpa* in
 25
 26 mixed stands placed between the two homogeneous stands of native and invasive seaweeds (Fig. 4).
 27
 28
 29 The second axis explained lower variation (structure = 13.3% and composition = 9.5%) and separated
 30
 31 *E. brachycarpa* and *A. taxiformis* from *E. brachycarpa* in mixed stands (Fig. 4).
 32
 33
 34
 35



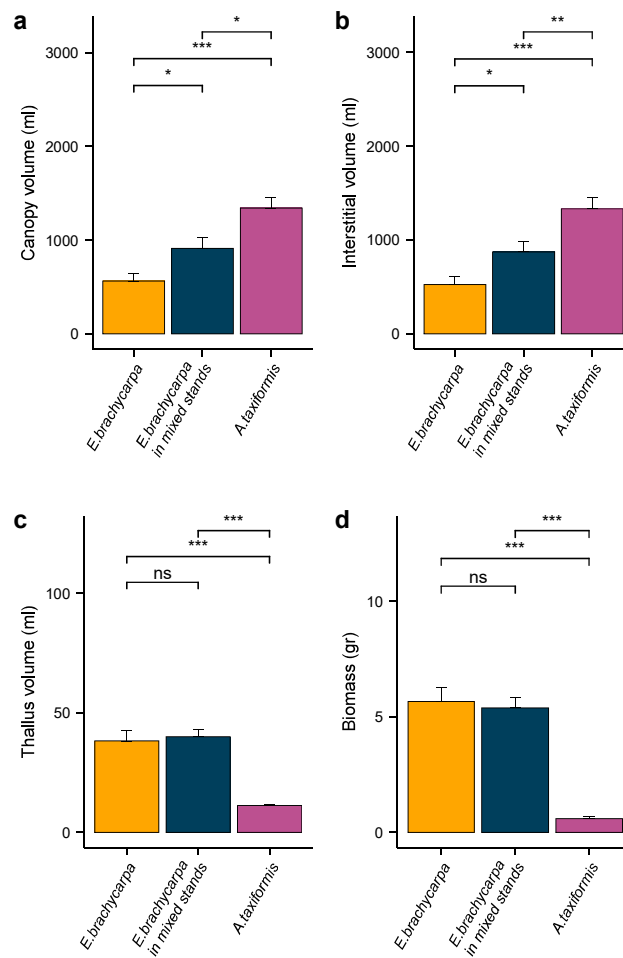
309 **Fig. 4 Structure (a) and composition (b) of the epifaunal assemblages associated with the three**
1
310 **habitats.** The Principal coordinate analysis plot (PCoA) based on a Bray-Curtis distance matrix of
3
311 square-root transformed relative abundances (structure) or on a Jaccard distance matrix of
4
6
312 presence/absence data (composition). The circles show the 90% confidence interval for each seaweed.
8

9
313
10
11
124 The SIMPER analysis revealed that 28 taxa contributed 70% to the dissimilarity between *E.*
13
14
15 *brachycarpa* and *A. taxiformis*; 37 taxa contributed 70% to the dissimilarity between *E. brachycarpa*
16
17 and *E. brachycarpa* in mixed stands; and 30 taxa contributed 70% to the dissimilarity between *E.*
18
19 *brachycarpa* in mixed stand and *A. taxiformis* (Fig. S1, Table S5). Most of the species contributing
20
21 to the dissimilarities belonged to amphipods. The polychaete *Amphiglena mediterranea* (Leydig,
22
23 1851) was the species mostly contributing to the differences observed between both *E. brachycarpa*
24
25 and *A. taxiformis* and between *E. brachycarpa* and *E. brachycarpa* in mixed stands, contributing
26
27 respectively to 8% and 6% of the observed differences. The amphipod *Apherusa alacris* Krapp-
28
29 Schickel, 1969 was the species most contributing to the differences (7%) between *E. brachycarpa* in
30
31 mixed stands and *A. taxiformis*. In addition, the gastropod *Obtusella macilenta* (Monterosato, 1880)
32
33 was the species that contributed consistently (higher $\delta_i/SD(\delta_i)$ values) to the difference between *E.*
34
35 *brachycarpa* and *A. taxiformis* (Fig. S1, Table S5), while the amphipod *Stenothoe monoculoides*
36
37 (Montagu, 1813) and the gastropod *Eatonina cossurae* (Calcara, 1841) were the species that
38
39 contributed consistently to the differences between *E. brachycarpa* in mixed stands and *E.*
40
41 *brachycarpa*, and between *E. brachycarpa* in mixed stands and *A. taxiformis* (Fig. S1, Table S5). The
42
43 polychaete *S. prolifera* was among the first 5 species contributing to the differences between each
44
45 couple of habitats (Fig. S1, Table S5).
46
47
48
49
50
51
52

53
54 Multivariate analyses conducted separately for the three dominant epifaunal groups (molluscs,
55
56 annelids, and amphipods) revealed patterns of variation comparable to those of the whole epifaunal
57
58 assemblage (Table S6). Only, amphipods showed less variability among habitats (Table S6).
59
60
61
62
63
64
65

335 Seaweed structural attributes and relationships with the epifaunal assemblages.

336 Canopy volume (CV) and interstitial volume (IV) differed significantly among habitats with
337 higher values in *A. taxiformis* compared to *E. brachycarpa* in mixed stands and *E. brachycarpa* (Fig.
338 5 a-b, Table S7). Biomass (DW) and thallus volume (TV) showed similar values between *E.*
339 *brachycarpa* and *E. brachycarpa* in mixed stands and were significantly higher compared to those of
340 *A. taxiformis* (Fig. 5 c-d, Table S7).



342
343 **Fig. 5 Differences in structural attributes among habitats.** Canopy volume (CV), interstitial
344 volume (IV), thallus volume (TV) and biomass (expressed as dry weight, DW) of the epifaunal
345 assemblages associated with *E. brachycarpa*, *E. brachycarpa* in mixed stands and *A. taxiformis*. Bar

346 plots show mean \pm 1 standard error (n = 20). Significant codes: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq$
1
347 0.05, ns $p > 0.05$. See Table S7 for further details.
3
4

348
6
349 The linear regression analysis revealed that biomass (DW) was the attribute that explained better the
8
9
350 variation in abundance ($R^2_N = 0.51$), rarefied species richness ($R^2_S = 0.58$), Shannon-Wiener diversity
11
12
351 ($R^2_{H'} = 0.54$) and Pielou's evenness index ($R^2_J = 0.2$) of the epifaunal assemblages (Table S8). The
13
14
352 variance explained by algal biomass increased if we considered a quadratic relationship between
15
16
353 those variables (Fig. 6). The relationship was positive for N, S and H' , while J presented and opposite
18
19
354 pattern of variation (Fig. 6). Otherwise, canopy volume (CV) interstitial volume (IV) and thallus
20
21
355 volume (TV) explained less variation (and it was significant for N, S and H' but not for J) of the
23
24
356 epifaunal attributes (R-squared < 0.5 , Table S8). The analysis conducted separately on the three
25
26
357 dominant epifaunal groups (molluscs, annelids, and amphipods) revealed similar results however for
28
29
358 amphipods and annelids the relationship between assemblage parameters and algal biomass was
30
31
359 weaker (annelids: $R^2_N = 0.35$, $R^2_S = 0.52$, $R^2_{H'} = 0.49$, $R^2_J = 0.03$; amphipods: $R^2_N = 0.23$, $R^2_S = 0.43$,
32
33
360 $R^2_{H'} = 0.31$, $R^2_J = 0.01$) although remaining the most important explanatory variable for both groups.
35
36
361 Meanwhile, molluscs revealed patterns of variation similar to the whole assemblage ($R^2_N = 0.5$, R^2_S
37
38
362 $= 0.53$, $R^2_{H'} = 0.48$, $R^2_J = 0.12$) (Table S8). As for the other algal structural features, annelids showed
40
41
363 a weaker and not significant relationship with the canopy and interstitial volumes, differing from
42
43
364 amphipods and molluscs (Table S8).
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
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

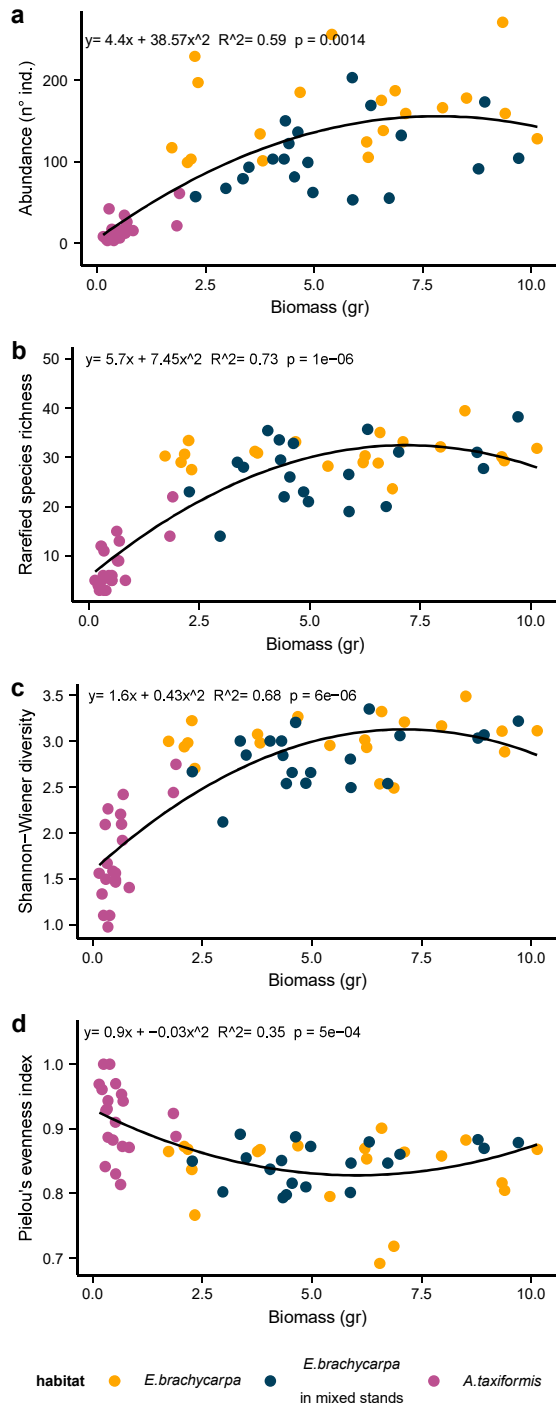


Fig. 6 Relationship between seaweed structural attributes and epifaunal diversity. Results of the linear regression analysis (LM) between the algal biomass (expressed as dry weight, DW) and the abundance (a), rarefied species richness (b), Shannon-Wiener diversity (c) and Pielou's evenness index (d) of the epifaunal assemblages.

Biomass (DW) was also the structural attribute selected for constrained db-RDA, explaining 24.7% of the variation in the structure of the epifaunal assemblages (Table S9). The first two axes of the dbRDA plot explained 15.6% of the total variance of the multivariate structure of the epifaunal assemblages, with 12.4% for axis 1 and 3.2% for axis 2 (Fig. 7).

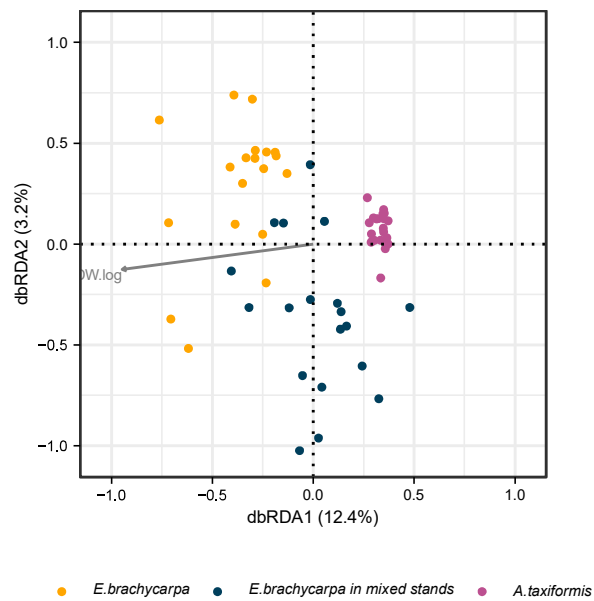


Fig. 7 Relationship between structural attributes and the multivariate structure of the epifaunal assemblages associated to the three habitats. The distance-based redundancy (dbRDA) plot illustrates the structural attribute better explaining the multivariate structure of the three habitats.

DW.log = seaweed biomass (log + 1).

388 **Discussion**

1
389 The biodiversity and the socio-economic value of marine ecosystems are threatened by biological
3
4
390 invasions around the world (Bax et al., 2003; Molnar et al., 2008). Understanding how invasive
5
6
391 seaweeds modify the functioning of recipient ecosystems may allow us to better understand large
7
8
9
392 scale effects on native rocky shore habitats. Here we investigated the effects of the invasive *A.*
10
11
393 *taxiformis* on the native *E. brachycarpa* by comparing the epifaunal assemblage associated with three
12
13
14
394 alternative states of the transition between native and invasive seaweeds, homogenous and mixed
15
16
395 stands of the two seaweeds. Our results showed differences in abundance and diversity of the
17
18
19
396 epifaunal assemblages between three alternative states of the transition from native *E. brachycarpa*
20
21
22
397 to invasive *A. taxiformis*. In particular, *A. taxiformis* hosted almost 6 times less epifaunal individuals
23
24
25
398 compared to *E. brachycarpa* in mixed stands, and 10 folds less individuals compared to homogenous
26
27
28
399 stands of *E. brachycarpa*. Also, the number of epifaunal species was more than 4 folds lower in the
29
30
31
400 invasive compared to the native habitat, while diversity reduced by half. These results confirm that
32
33
34
401 generally invasive seaweeds exhibit a less diverse epifaunal component compared to native seaweeds
35
36
37
402 (Guerra-García et al., 2012; Janiak and Whitlatch, 2012; Maggi et al., 2015; Navarro-Barranco et al.,
38
39
403 2018; Veiga et al., 2018).

40
404 We found that variation in diversity and multivariate structure of the epifaunal assemblages was
41
42
405 related to changes in algal structural features. In particular, biomass was the variable better explaining
43
44
406 the variation in abundance, number of species, and the multivariate structure of the epifaunal
45
46
407 assemblages. The role of macroalgal complexity in shaping the associated biota has been highlighted
47
48
408 in several studies, with complex algae hosting a larger abundance and diversity of epifauna than
49
50
51
409 simpler ones (Chemello and Milazzo, 2002; Pitacco et al., 2014; Veiga et al., 2014; Lolas et al., 2018;
52
53
54
410 Veiga et al., 2018; Bitlis, 2019; Chiarore et al., 2019; Poursanidis et al., 2019; Mancuso et al., 2021b).
55
56
411 In general, studies have highlighted that invasive seaweeds host lower (Guerra-García et al., 2012;
57
58
59
412 Navarro-Barranco et al., 2018; Rubal et al., 2018; Veiga et al., 2018) or higher (Veiga et al., 2014)
60
61
413 epifaunal abundance, species richness, and diversity, depending on whether their structural
62
63
64
65

414 complexity is respectively lower or higher compared to native seaweeds. Navarro-Barranco et al.
1
415 (2018) showed that *A. taxiformis* had low fractal complexity and hosted an impoverished faunal
3
416 assemblage compared to native seaweeds. Guerra-García et al., (2012) found that *A. armata* had low
4
6
417 algal volume and showed lower abundance, species richness, and diversity of associated isopods
8
9
418 fauna compared to the native *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders.
10
11
419 Moreover, lower dry weight and fractal dimension in the invasive *S. muticum* compared to native
12
13
420 seaweeds have been shown to play a major role in shaping the associated faunal assemblages (Veiga
14
15
421 et al., 2014, 2018). Likewise other studies (Janiak and Whitlatch, 2012; Veiga et al., 2014; Rubal et
16
17
422 al., 2018), our results indicated that the quantity of habitat (biomass) was the best predictor variable
18
19
423 explaining variation in terms of abundance, species richness, as well as multivariate structure of the
20
21
424 associated epifauna.
22
23
24
25

425 Interestingly, our results highlight that *A. taxiformis* affected each component (molluscs, annelids,
26
27
28
426 and amphipods) of the epifaunal assemblages in the same way. However, in the available literature
29
30
31
427 on the epifaunal assemblages of invasive seaweeds, we can find distinct responses among epifaunal
32
33
428 components (Schmidt and Scheibling, 2006; Gestoso et al., 2010; Guerra-García et al., 2012; Bedini
34
35
429 et al., 2014; Veiga et al., 2018; Navarro-Barranco et al., 2019). For example, species richness,
36
37
38
430 Shannon diversity and total abundance of isopods were significantly lower in *A. armata* compared to
39
40
41
431 native algae (Guerra-García et al., 2012). Bedini et al. (2014) found that the invasive *Lophocladia*
42
43
432 *lallemandii* (Montagne) F. Schmitz hosted a higher abundance of amphipods, isopods, and
44
45
433 polychaetes, while native habitats harbored a greater abundance of molluscs and decapods. Bivalves
46
47
434 associated with the invasive *S. muticum* were more abundant compared to native seaweeds, which, in
48
49
50
435 contrast, hosted more gastropods (Veiga et al., 2018), and Gestoso et al. (2010) found that isopods
51
52
436 and amphipods were more abundant in *S. muticum* than in native seaweeds. Moreover, the invasive
53
54
55
437 *Codium fragile* subsp. *fragile* (Suringar) Hariot supported higher densities of nematodes, bivalves,
56
57
58
438 and specialist herbivores compared to fronds of the native kelp, which, in contrast, supported greater
59
60
439 densities of gastropods and asteroids (Schmidt and Scheibling, 2006). Other authors revealed that
61
62
63
64
65

440 differences between invasive and native seaweeds in single components of epifaunal assemblages
1
441 changed depending on the site and the identity of the algal species (Navarro-Barranco et al., 2019).
3
442 The fact that in our study, the *A. taxiformis* habitat showed lower abundance, species richness, and
4
5
6
443 diversity values for all the epifaunal organisms, regardless of the groups investigated in this study
8
9
444 (molluscs, amphipods and annelids), led us to hypothesize that a potential shift from the native (i.e.
10
11
445 *E. brachycarpa*) to the invasive (i.e. *A. taxiformis*) habitat could cause large negative cascade effects
13
14
446 on the benthic ecosystem.
15

16
447 Although differences in the epifaunal assemblages among native and invasive seaweeds have
18
448 been largely explored, our results also suggest that the presence of *A. taxiformis* affects the epifaunal
20
449 assemblages associated with *E. brachycarpa* in mixed stands. This result could be explained by other
21
22
450 attributes that differed between native and invasive seaweeds, such as the amount of epiphytes and/or
25
26
451 the presence of chemical defenses, that have been related to the ability of seaweeds to shape their
27
28
452 associated fauna (Hay et al., 1987; Viejo, 1999; Paul et al., 2006; Cacabelos et al., 2010; Máximo et
30
31
453 al., 2018; Gache et al., 2019). Invasive seaweeds can release secondary metabolites (e.g. halogenated
32
33
454 compounds) able to act as deterrents against epiphytes, and herbivores (Paul et al., 2006; Cacabelos
35
36
455 et al., 2010; Vega Fernández et al., 2019). Secondary metabolites released by *A. taxiformis* can affect
37
38
456 the survival of fish in the post-larval stages, eventually leading to alteration of the grazing pressure
39
40
457 on the surrounding habitat (Máximo et al., 2018; Gache et al., 2019). Other studies suggest that
42
43
458 invasive seaweeds can alter the trophic web by changing the composition of epiphytes which reduces
44
45
459 suitable habitat for many epifaunal species (Viejo, 1999; Wikström and Kautsky, 2004). Several
47
48
460 authors suggested that the amount of epiphytes could explain the higher species richness found in the
49
50
461 invasive *S. muticum* compared to native seaweeds (Viejo, 1999; Cacabelos et al., 2010). In our study,
52
53
462 *A. taxiformis* had no or fewer epiphytes compared to *E. brachycarpa* (R.C. personal observation). As
54
55
463 epifauna is mostly represented by microalgae grazers, we can hypothesize that differences in the
57
58
464 abundance of epiphytes between *A. taxiformis* and *E. brachycarpa* could contribute to the variation
59
60
465 in epifaunal assemblages observed in this study. It is therefore arguable that further studies analyzing
61
62
63
64
65

466 the direct and indirect role of epiphyte abundance and secondary metabolites released by *A. taxiformis*
1
467 in structuring its associated epifauna would allow us to better clarify the effects of this seaweed on
3
468 the recipient habitats.
4
5
6

469 Moreover, as suggested by other authors (Navarro-Barranco et al., 2019), landscape features
8
470 could be another key aspect explaining the effect of *A. taxiformis* on *E. brachycarpa* associated
9
10
11
471 assemblages in mixed stands. In fact, the presence of invasive seaweeds may contribute to the
12
13
472 fragmentation of native habitats, reducing the patch size of native seaweeds, and at the same time
14
15
473 increasing their isolation (Roberts and Poore, 2006; Lanham et al., 2015). It has been observed that
16
17
474 the reduction in patch size of *Cystoseira sensu lato* habitats reduces the diversity of associated faunal
18
19
20
475 assemblages (Mancuso et al., 2021b). Thus, we can hypothesize that the presence of *A. taxiformis* in
21
22
23
476 mixed stands can act as a physical barrier to the dispersal of vagile fauna, reducing connectivity on a
24
25
477 small scale and ultimately eroding the diversity of native habitats (Lanham et al., 2015). However,
26
27
28
478 another possibility to consider is that some epifaunal groups may be able to disperse through the
29
30
479 different seaweeds (Taylor, 1998) in mixed stands. In this case, the lower epifaunal abundance and
31
32
33
480 diversity observed on *E. brachycarpa* from mixed stands could be because part of this diversity may
34
35
481 have preferentially dispersed to the *A. taxiformis* portion of these mixed stands. Our study, however,
36
37
38
482 cannot address the effects of epifauna movement among seaweeds on the observed results, and more
39
40
483 studies are necessary to understand the possible role of mobile epifaunal assemblage movement
41
42
43
484 patterns within mixed stands of *E. brachycarpa*.
44
45

485 One inherent weakness of this study concerns the impossibility of separating the effects of *A.*
46
486 *taxiformis* from natural spatial variability. This should be accounted for by using more interspersed
47
48
49
50
51
487 sites for each condition (mono and mixed stands of native and invasive seaweeds). Unfortunately, we
52
53
488 were not able to find more interspersed sites in the area of study. However, the three sites selected
54
55
489 had the same average values of different environmental variables (surface temperature, salinity,
56
57
58
490 nitrate and phosphate concentrations, dissolved oxygen, chlorophyll and photosynthetic active
59
60
491 radiation, Table S10), indicating that spatial variability had little effect. Then, we think that the data
61
62
63
64
65

492 presented in this study is still valuable, albeit with its limitations, for understanding epifaunal
1
493 community changes between plausible alternative states of the transition between *E. brachycarpa*
3
494 and *A. taxiformis*.
4
5
6

495
8
9
496 In summary, our study suggests that shifting from native to invasive habitats may pose a serious
10
11
497 threat to biodiversity in coastal areas (Martin et al., 1992; Heck et al., 2003), potentially leading to
12
13
498 bottom-up effects on rocky shore ecosystems. In addition, the low biomass supplied by the herein
14
15
499 studied invasive species suggests that the shift from native canopy-forming algae to the invasive *A.*
16
17
500 *taxiformis* habitat would also drastically reduce the biomass of primary producers in affected coastal
18
19
501 areas. Predicting the ecological effects of invasive seaweeds is one of the main goals in the study of
20
21
502 biological invasions. Previous research has highlighted the context-dependent effects of invasive
22
23
503 seaweeds, with larger impact caused by invasive species exerting a different functional role compared
24
25
504 to native habitat forming species (Ricciardi and Atkinson, 2004; Ricciardi et al., 2013; Navarro-
26
27
505 Barranco et al., 2019). Our results not only remark the negative effect of *A. taxiformis* on *E.*
28
29
506 *brachycarpa* epifaunal assemblages, but also suggest that invasive species are able to affect native
30
31
507 habitats in a transitional phase (mixed stands) of the habitat shift, facilitating fragmentation and
32
33
508 isolation. Further studies aimed at understanding the effects of the habitat shift from native to invasive
34
35
509 seaweeds should include multiple transitional phases (different percentage coverage), as well as the
36
37
510 analysis of changes in the trophic structure of the associated epifaunal assemblages.
38
39
40
41
42
43
44
45

511 **Declarations**

512
513 Not applicable
514

515 **Funding**

516 This work was partially supported by the University of Palermo (FFR grant).
517
518
519
520
521
522
523
524
525

518
1
519
3
520
4
6
521
8
522
10
11
523
13
524
14
15
525
16
18
526
19
20
21
527
22
23
528
25
529
26
27
28
530
30
531
31
32
33
532
35
533
36
37
534
38
39
40
535
42
43
536
44
45
537
47
48
538
49
50
539
52
540
53
54
55
541
57
542
58
59
60
543
61
62
63
64
65

Conflicts of interest/Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability and reproducible research

The repository with all the data and the scripts used to reproduce the research in this paper is available at <http://dx.doi.org/10.17632/h3r8ygnjfd.1>

Acknowledgements

We would like to thank the three anonymous reviewers for their constructive and valuable comments and critical revision.

Author Contributions

Conceptualization, C.R., M.M. and D.R.; Methodology, C.R. and M.M.; Investigation, D.R.; Formal Analysis, M.F.P.; Data curation, M.F.P.; Writing – Original Draft Preparation, M.F.P.; Writing – Review & Editing, M.F.P., M.M., C.R., B.F., M.L., M.B., L.B.S.; Visualization, M.F.P.; Validation, M.F.P.; Supervision, C.R.; Project Administration, C.R.; Funding Acquisition, C.R.; Resources, C.R.; molluscs identification, C.R., D.R.; amphipods identification , L.B.S; annelids identification ; B.F., M.B., M.L.

544 **3 References**

- 1
2
3
545 Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to
4
5
546 Software and Statistical Methods, Plymouth, UK. PRIMER-E, Plymouth.
7
8
547 doi:10.13564/j.cnki.issn.1672-9382.2013.01.010
9
10
548 Andreakis, N., Procaccini, G., Kooistra, W.H.C.F., 2004. *Asparagopsis taxiformis* and
11
12
549 *Asparagopsis armata* (Bonnemaisoniales, Rhodophyta): Genetic and morphological
13
14
550 identification of Mediterranean populations. *Eur. J. Phycol.* 39, 273–283.
15
16
551 doi:10.1080/0967026042000236436
17
18
552 Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Cebrian, E., Sala, E., 2009. Deep-water stands
19
20
553 of *Cystoseira zosteroides* C. Agardh (Fucales, Ochrophyta) in the Northwestern
21
22
554 Mediterranean: Insights into assemblage structure and population dynamics. *Estuar. Coast.*
23
24
555 *Shelf Sci.* 82, 477–484. doi:10.1016/j.ecss.2009.02.013
25
26
556 Barone, R., Mannino, A., Marino, M., 2003. *Asparagopsis taxiformis* (Bonnemaisoniales,
27
28
557 Rhodophyta): first record of gametophytes on the Italian coast. *Bocconea* 16, 1021–1025.
29
30
558 Bax, N., Williamson, A., Aguero, M., Gonzalez, E., Geeves, W., 2003. Marine invasive alien
31
32
559 species: a threat to global biodiversity. *Mar. Policy* 27, 313–323. doi:10.1016/S0308-
33
34
560 597X(03)00041-1
35
36
561 Bedini, R., Bonechi, L., Piazzini, L., 2014. Mobile epifaunal assemblages associated with *Cystoseira*
37
38
562 beds: comparison between areas invaded and not invaded by *Lophocladia lallemandii*. *Sci.*
39
40
563 *Mar.* 78, 425–432. doi:10.3989/scimar.03995.28B
41
42
564 Bitlis, B., 2019. Mollusk fauna associated with *Cystoseira barbata* (Stockhouse) C. Agardh, 1820
43
44
565 in the Sea of Marmara (Turkey). *Oceanol. Hydrobiol. Stud.* 48, 174–183. doi:10.1515/ohs-
45
46
566 2019-0016
47
48
567 Boudouresque, C.F., Ruitton, S., Verlaque, M., 2005. Large-Scale Disturbances , Regime Shift and
49
50
568 Recovery in Littoral Systems Subject To Biological Invasions. UNESCO-ROSTE/BAS Work.
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

569 regime shifts 85–101.
1
570 Bulleri, F., Badalamenti, F., Iveša, L., Mikac, B., Musco, L., Jaklin, A., Rattray, A., Vega
3
571 Fernández, T., Benedetti-Cecchi, L., 2016. The effects of an invasive seaweed on native
4
6 communities vary along a gradient of land-based human impacts. PeerJ 4, e1795.
572
8
573 doi:10.7717/peerj.1795
9
10
11
574 Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F., Hawkins, S.J., 2002. The influence of
13
14
575 canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in
15
16
576 the northwest Mediterranean. J. Exp. Mar. Bio. Ecol. 267, 89–106. doi:10.1016/S0022-
18
19
577 0981(01)00361-6
20
21
578 Cacabelos, E., Olabarria, C., Incera, M., Troncoso, J.S., 2010. Effects of habitat structure and tidal
23
24
579 height on epifaunal assemblages associated with macroalgae. Estuar. Coast. Shelf Sci. 89, 43–
25
26
580 52. doi:10.1016/j.ecss.2010.05.012
27
28
581 Chemello, R., Milazzo, M., 2002. Effect of algal architecture on associated fauna: Some evidence
30
31
582 from phytal molluscs. Mar. Biol. 140, 981–990. doi:10.1007/s00227-002-0777-x
32
33
583 Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., Cottalorda, J.M.,
35
36
584 Francour, P., 2013. Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes. J.
37
38
585 Exp. Mar. Bio. Ecol. 442, 70–79. doi:10.1016/j.jembe.2013.02.003
39
40
586 Chiarore, A., Bertocci, I., Fioretti, S., Meccariello, A., Saccone, G., Crocetta, F., Patti, F.P., 2019.
42
43
587 Syntopic *Cystoseira* taxa support different molluscan assemblages in the Gulf of Naples
44
45
588 (southern Tyrrhenian Sea). Mar. Freshw. Res. 70, 1561–1575. doi:10.1071/MF18455
47
48
589 Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust.
49
50
590 J. Ecol. 18, 117–143. doi:10.1111/j.1442-9993.1993.tb00438.x
52
53
591 Cormaci, M., Furnari, G., Catra, M., Alongi, G., Giaccone, G., 2012. Flora marina bentonica del
54
55
592 Mediterraneo: Phaeophyceae*. Boll. dell'Accademia Gioenia di Sci. Nat. 45, 1–508.
56
57
593 Corriero, G., Pierri, C., Accoroni, S., Alabiso, G., Bavestrello, G., Barbone, E., Bastianini, M.,
59
60
594 Bazzoni, A.M., Bernardi Aubry, F., Boero, F., Buia, M.C., Cabrini, M., Camatti, E., Cardone,
61
62
63
64
65

- 595 F., Cataletto, B., Cattaneo Vietti, R., Cecere, E., Cibic, T., Colangelo, P., De Olazabal, A.,
 1
 596 D'onghia, G., Finotto, S., Fiore, N., Fornasaro, D., Frascchetti, S., Gambi, M.C., Giangrande,
 3
 597 A., Gravili, C., Guglielmo, R., Longo, C., Lorenti, M., Lugliè, A., Maiorano, P., Mazzocchi,
 4
 6 M.G., Mercurio, M., Mastrototaro, F., Mistri, M., Monti, M., Munari, C., Musco, L., Nonnis-
 598
 8
 599 Marzano, C., Padedda, B.M., Patti, F.P., Petrocelli, A., Piraino, S., Portacci, G., Pugnetti, A.,
 9
 10
 600 Pulina, S., Romagnoli, T., Rosati, I., Sarno, D., Satta, C.T., Sechi, N., Schiaparelli, S.,
 11
 13
 601 Scipione, B., Sion, L., Terlizzi, A., Tirelli, V., Totti, C., Tursi, A., Ungaro, N., Zingone, A.,
 14
 15
 602 Zupo, V., Basset, A., 2016. Ecosystem vulnerability to alien and invasive species: A case study
 16
 18
 603 on marine habitats along the Italian coast. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 26, 392–
 19
 20
 604 409. doi:10.1002/aqc.2550
 21
 23
 605 Dijkstra, J.A., Harris, L.G., Mello, K., Litterer, A., Wells, C., Ware, C., 2017. Invasive seaweeds
 25
 26
 606 transform habitat structure and increase biodiversity of associated species. *J. Ecol.* 105, 1668–
 27
 28
 607 1678. doi:10.1111/1365-2745.12775
 30
 31
 608 Engelen, A.H., Primo, A.L., Cruz, T., Santos, R., 2013. Faunal differences between the invasive
 32
 33
 609 brown macroalga *Sargassum muticum* and competing native macroalgae. *Biol. Invasions* 15,
 35
 36
 610 171–183. doi:10.1007/s10530-012-0276-z
 37
 38
 611 European Commission, 2000. Water Framework Directive (2000/60/EC), Official Journal of the
 40
 41
 612 European Communities. doi:2004R0726 - v.7 of 05.06.2013
 42
 43
 613 Falace, A., Bressan, G., 2006. Seasonal variations of *Cystoseira barbata* (Stackhouse) C. Agardh
 45
 46
 614 frond architecture. *Hydrobiologia* 555, 193–206. doi:10.1007/s10750-005-1116-2
 47
 48
 615 Foster, Z.S.L., Sharpton, T.J., Grünwald, N.J., 2017. Metacoder: An R package for visualization
 49
 50
 616 and manipulation of community taxonomic diversity data. *PLoS Comput. Biol.* 13, 1–15.
 52
 53
 617 doi:10.1371/journal.pcbi.1005404
 54
 55
 618 Gache, C., Bertucci, F., Guerra, A.S., Calandra, M., Berr, T., Lafaye, J., Jorissen, H., Nugues, M.,
 57
 58
 619 Cossy, J., Lecchini, D., 2019. Effects of *Asparagopsis taxiformis* metabolites on the feeding
 59
 60
 620 behaviour of post- larval *Acanthurus triostegus*. *J. Fish Biol.* 95, 1355–1358.
 61
 62
 63
 64
 65

- 621 doi:10.1111/jfb.14140
1
- 622 Gallardo, B., Clavero, M., Sánchez, M.I., Vilà, M., 2016. Global ecological impacts of invasive
3
623 species in aquatic ecosystems. *Glob. Chang. Biol.* 22, 151–163. doi:10.1111/gcb.13004
4
6
624 Geburzi, J.C., McCarthy, M.L., 2018. How Do They Do It? – Understanding the Success of Marine
8
625 Invasive Species, in: *YOUMARES 8 – Oceans Across Boundaries: Learning from Each Other.*
9
10
626 Springer International Publishing, Cham, pp. 109–124. doi:10.1007/978-3-319-93284-2_8
11
13
627 Gestoso, I., Olabarria, C., Troncoso, J.S., 2010. Variability of epifaunal assemblages associated
14
15
628 with native and invasive macroalgae. *Mar. Freshw. Res.* 61, 724–731. doi:10.1071/MF09251
16
18
629 Giaccone, G., Alongi, G., Pizzuto, F., Cossu, A.V.L., 1994. La Vegetazione marina bentonica
19
20
630 fotofila del Mediterraneo: 2. Infralitorale e Circalitorale: proposte di aggiornamento. *Boll.*
21
22
631 dell'Accademia Gioenia di Sci. Nat. 27, 111–157.
23
25
632 Giangrande, A., Pierri, C., Del Pasqua, M., Gravili, C., Gambi, M.C., Gravina, M.F., 2020. The
26
27
633 Mediterranean in check: Biological invasions in a changing sea. *Mar. Ecol.* 41.
28
30
634 doi:10.1111/maec.12583
31
32
33
635 Gómez-Garreta, A., Barceló, M., Gallardo, T., Pérez-Ruzafa, I., Ribera, M.A., Rull, J., 2002. *Flora*
35
636 *Phycologica Iberica*. Vol. 1. Fucales, Universida. ed. Murcia.
36
37
637 Guerra-García, J.M., Ros, M., Izquierdo, D., Soler-Hurtado, M.M., 2012. The invasive
38
40
638 *Asparagopsis armata* versus the native *Corallina elongata*: Differences in associated peracarid
41
42
639 assemblages. *J. Exp. Mar. Bio. Ecol.* 416–417, 121–128. doi:10.1016/j.jembe.2012.02.018
43
44
45
640 Hacker, S.D., Steneck, R.S., 1990. Habitat Architecture and the Abundance and Body-Size-
46
47
641 Dependent Habitat Selection of a Phytal Amphipod. *Ecology* 71, 2269–2285.
48
49
50
642 doi:10.2307/1938638
51
52
53
643 Hay, M.E., Duffy, J.E., Pfister, C.A., Fenical, W., 1987. Chemical Defense Against Different
54
55
644 Marine Herbivores: Are Amphipods Insect Equivalents? *Ecology* 68, 1567–1580.
56
57
645 doi:10.2307/1939849
58
59
60
646 Heck, K.L., Hays, G., Orth, R.J., Heck Hay, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of
61
62
63
64
65

- 647 the nursery role hypothesis for seagrass meadows. *Mar. Ecol. Prog. Ser.* 253, 123–136.
 1
 648 doi:10.3354/meps253123
 3
 649 Janiak, D.S., Whitlatch, R.B., 2012. Epifaunal and algal assemblages associated with the native
 6
 650 *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern
 8
 651 Long Island Sound. *J. Exp. Mar. Bio. Ecol.* 413, 38–44. doi:10.1016/j.jembe.2011.11.016
 10
 652 Jormalainen, V., Honkanen, T., 2008. Macroalgal chemical defenses and their roles in structuring
 13
 653 temperate marine communities. *Algal Chem. Ecol.* 9783540741, 57–89. doi:10.1007/978-3-
 15
 654 540-74181-7_3
 18
 655 Lanham, B.S., Gribben, P.E., Poore, A.G.B., 2015. Beyond the border: Effects of an expanding
 20
 656 algal habitat on the fauna of neighbouring habitats. *Mar. Environ. Res.* 106, 10–18.
 23
 657 doi:10.1016/j.marenvres.2015.02.006
 25
 658 Legendre, P., Anderson, M.J., 1999. Distance-Based Redundancy Analysis: Testing Multispecies
 28
 659 Responses in Multifactorial Ecological Experiments. *Ecol. Monogr.* 69, 1–24.
 30
 660 doi:10.2307/2657192
 32
 661 Lo Brutto, S., Iacofano, D., Guerra García, J.M., Lubinevsky, H., Galil, B.S., 2019. Desalination
 35
 662 effluents and the establishment of the non-indigenous skeleton shrimp *Paracaprella pusilla*
 37
 663 Mayer, 1890 in the south -eastern Mediterranean. *BioInvasions Rec.* 8, 661–669.
 40
 664 doi:10.3391/bir.2019.8.3.23
 42
 665 Lolás, A., Antoniadou, C., Vafidis, D., 2018. Spatial variation of molluscan fauna associated with
 45
 666 *Cystoseira* assemblages from a semi-enclosed gulf in the Aegean Sea. *Reg. Stud. Mar. Sci.* 19,
 47
 667 17–24. doi:10.1016/j.rsma.2018.03.003
 49
 668 Mačić, V., Albano, P.G., Almpandou, V., Claudet, J., Corrales, X., Essl, F., Evagelopoulos, A.,
 52
 669 Giovos, I., Jimenez, C., Kark, S., Marković, O., Mazaris, A.D., Ólafsdóttir, G.Á., Panayotova,
 54
 670 M., Petović, S., Rabitsch, W., Ramdani, M., Rilov, G., Tricarico, E., Vega Fernández, T., Sini,
 57
 671 M., Trygonis, V., Katsanevakis, S., 2018. Biological Invasions in Conservation Planning: A
 59
 672 Global Systematic Review. *Front. Mar. Sci.* 5. doi:10.3389/fmars.2018.00178
 62
 63
 64
 65

- 673 Maggi, E., Benedetti- Cecchi, L., Castelli, A., Chatzinikolaou, E., Crowe, T.P., Ghedini, G., Kotta,
1
674 J., Lyons, D.A., Ravaglioli, C., Rilov, G., Rindi, L., Bulleri, F., 2015. Ecological impacts of
3
675 invading seaweeds: a meta- analysis of their effects at different trophic levels. *Divers. Distrib.*
4
6 21, 1–12. doi:10.1111/ddi.12264
- 676
8
677 Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*, Transactions of the American
9
10
678 Institute of Electrical Engineers. Springer Netherlands, Dordrecht. doi:10.1007/978-94-015-
11
13 7358-0
- 679
14
680 Mancuso, F.P., D’Agostaro, R., Milazzo, M., Chemello, R., 2021a. The invasive *Asparagopsis*
15
16
681 *taxiformis* hosts a low diverse and less trophic structured molluscan assemblage compared
18
682 with the native *Ericaria brachycarpa*. *Mar. Environ. Res.* 166, 105279.
19
20
683 doi:10.1016/j.marenvres.2021.105279
21
22
23
684 Mancuso, F.P., Milazzo, M., Chemello, R., 2021b. Decreasing in patch-size of *Cystoseira* forests
24
25
685 reduces the diversity of their associated molluscan assemblage in Mediterranean rocky reefs.
26
27
686 *Estuar. Coast. Shelf Sci.* 250, 107163. doi:10.1016/j.ecss.2020.107163
28
29
30
31
687 Mannino, A.M., Mancuso, F.P., 2009. Guida all’identificazione delle Cistoseire (Area Marina
32
33
688 Protetta “Capo Gallo-Isola delle Femmine”). Palermo.
34
35
36
37
689 Martin, T.H., Crowder, L.B., Dumas, C.F., Burkholder, J.M., 1992. Indirect effects of fish on
38
39
690 macrophytes in Bays Mountain Lake: evidence for a littoral trophic cascade. *Oecologia* 89,
40
41
691 476–481. doi:10.1007/BF00317152
42
43
44
45
692 Máximo, P., Ferreira, L., Branco, P., Lima, P., Lourenço, A., 2018. Secondary Metabolites and
46
47
693 Biological Activity of Invasive Macroalgae of Southern Europe. *Mar. Drugs* 16, 265.
48
49
50
694 doi:10.3390/md16080265
51
52
53
695 Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E., Thibaut, T.,
54
55
696 Van Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E. a., De Clerck, O., 2015. European
56
57
697 seaweeds under pressure: Consequences for communities and ecosystem functioning. *J. Sea*
58
59
698 *Res.* 98, 91–108. doi:10.1016/j.seares.2014.11.004
60
61
62
63
64
65

- 699 Molinari Novoa, E.A., Guiry, M.D., 2020. Reinstatement of the genera *Gongolaria* Boehmer and
1
700 *Ericaria* Stackhouse (Sargassaceae, Phaeophyceae). Not. Algarum 172, 1–10.
3
- 701 Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of
4
6
702 invasive species to marine biodiversity. Front. Ecol. Environ. 6, 485–492. doi:10.1890/070064
8
- 703 Musco, L., Andaloro, F., Mikac, B., Mirto, S., Vega Fernandex, T., Badalamenti, F., 2014. Concern
9
10
704 about the spread of the invader seaweed *Caulerpa taxifolia* var. *distichophylla* (Chlorophyta:
11
13
705 Caulerpales) towards the West Mediterranean. Mediterr. Mar. Sci. 15, 532.
15
16
706 doi:10.12681/mms.742
18
- 707 Navarro-Barranco, C., Florido, M., Ros, M., González-Romero, P., Guerra-García, J.M., 2018.
20
21
708 Impoverished mobile epifaunal assemblages associated with the invasive macroalga
22
23
709 *Asparagopsis taxiformis* in the Mediterranean Sea. Mar. Environ. Res. 141, 44–52.
25
26
710 doi:10.1016/j.marenvres.2018.07.016
27
28
- 711 Navarro-Barranco, C., Muñoz-Gómez, B., Saiz, D., Ros, M., Guerra-García, J.M., Altamirano, M.,
30
31
712 Ostalé-Valriberas, E., Moreira, J., 2019. Can invasive habitat-forming species play the same
32
33
713 role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the
35
36
714 Strait of Gibraltar. Biol. Invasions 21, 3319–3334. doi:10.1007/s10530-019-02049-y
37
- 715 Ní Chualáin, F., Maggs, C.A., Saunders, G.W., Guiry, M.D., 2004. The invasive genus
38
40
716 *Asparagopsis* (Bonnemaisoniaceae, Rhodophyta): Molecular systematics, morphology, and
42
43
717 ecophysiology of Falkenbergia isolates. J. Phycol. 40, 1112–1126. doi:10.1111/j.1529-
44
45
718 8817.2004.03135.x
47
- 719 Occhipinti-Ambrogi, A., Galil, B., 2010. Marine alien species as an aspect of global change. Adv.
48
49
50
720 Oceanogr. Limnol. 1, 199–218. doi:10.1080/19475721003743876
52
- 721 Orellana, S., Hernández, M., Sansón, M., 2019. Diversity of *Cystoseira* sensu lato (Fucales,
53
54
55
722 Phaeophyceae) in the eastern Atlantic and Mediterranean based on morphological and DNA
57
58
723 evidence, including *Carpodesmia* gen. emend. and *Treptacantha* gen. emend. Eur. J. Phycol.
59
60
724 54, 447–465. doi:10.1080/09670262.2019.1590862
62
63
64
65

- 725 Paul, N., de Nys, R., Steinberg, P., 2006. Seaweed-herbivore interactions at a small scale: direct
1 tests of feeding deterrence by filamentous algae. *Mar. Ecol. Prog. Ser.* 323, 1–9.
726
3
727 doi:10.3354/meps323001
4
6
- 728 Pepe, F., Corradino, M., Parrino, N., Besio, G., Presti, V. Lo, Renda, P., Calcagnile, L., Quarta, G.,
8
9
729 Sulli, A., Antonioli, F., 2018. Boulder coastal deposits at Favignana Island rocky coast (Sicily,
10
11
730 Italy): Litho-structural and hydrodynamic control. *Geomorphology* 303, 191–209.
12
13
731 doi:10.1016/j.geomorph.2017.11.017
14
15
16
- 732 Piazzì, L., Balata, D., 2009. Invasion of alien macroalgae in different Mediterranean habitats. *Biol.*
17
18
733 *Invasions* 11, 193–204. doi:10.1007/s10530-008-9224-3
19
20
21
- 734 Pitacco, V., Orlando-Bonaca, M., Mavric, B., Popocic, A., Lipej, L., Orlando-Banaca, M.,
22
23
735 MAVRIČ, B., POPOVIĆ, A., Lipej, L., Mavric, B., Popocic, A., Lipej, L., 2014. Mollusc
24
25
736 fauna associated with the *Cystoseira* algal associations in the Gulf of Trieste (Northern
26
27
28
737 Adriatic Sea). *Mediterr. Mar. Sci.* 15, 225. doi:10.12681/mms.466
29
30
31
- 738 Poursanidis, D., Chatzigeorgiou, G., Dimitriadis, C., Koutsoubas, D., Arvanitidis, C., 2019. Testing
32
33
739 the robustness of a coastal biodiversity data protocol in the Mediterranean: insights from the
34
35
740 molluscan assemblages from the sublittoral macroalgae communities. *Hydrobiologia* 826,
36
37
741 159–172. doi:10.1007/s10750-018-3725-6
38
39
40
- 742 Ramsay-Newton, C., Drouin, A., Hughes, A.R., Bracken, M.E.S., 2017. Species, community, and
41
42
743 ecosystem-level responses following the invasion of the red alga *Dasysiphonia japonica* to the
43
44
744 western North Atlantic Ocean. *Biol. Invasions* 19, 537–547. doi:10.1007/s10530-016-1323-y
45
46
47
- 745 Ribera Siguan, M.A., 2002. Review of Non-Native Marine Plants in the Mediterranean Sea, in:
48
49
746 *Invasive Aquatic Species of Europe. Distribution, Impacts and Management.* Springer
50
51
747 Netherlands, Dordrecht, pp. 291–310. doi:10.1007/978-94-015-9956-6_31
52
53
54
- 748 Ricciardi, A., Atkinson, S.K., 2004. Distinctiveness magnifies the impact of biological invaders in
55
56
749 aquatic ecosystems. *Ecol. Lett.* 7, 781–784. doi:10.1111/j.1461-0248.2004.00642.x
57
58
59
- 750 Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L., 2013. Progress toward
60
61
62
63
64
65

- 751 understanding the ecological impacts of nonnative species. *Ecol. Monogr.* 83, 263–282.
1
752 doi:10.1890/13-0183.1
3
- 753 Roberts, D.A., Poore, A.G.B.B., 2006. Habitat configuration affects colonisation of epifauna in a
4
6
754 marine algal bed. *Biol. Conserv.* 127, 18–26. doi:10.1016/j.biocon.2005.07.010
8
- 755 Rubal, M., Costa-Garcia, R., Besteiro, C., Sousa-Pinto, I., Veiga, P., 2018. Mollusc diversity
9
10
11
1256 associated with the non-indigenous macroalga *Asparagopsis armata* Harvey, 1855 along the
13
14
157 Atlantic coast of the Iberian Peninsula. *Mar. Environ. Res.* 136, 1–7.
15
16
1758 doi:10.1016/j.marenvres.2018.02.025
18
- 1759 Schiel, D.R., Foster, M.S., 2006. The Population Biology of Large Brown Seaweeds: Ecological
19
20
21
2260 Consequences of Multiphase Life Histories in Dynamic Coastal Environments. *Annu. Rev.*
23
24
2561 *Ecol. Evol. Syst.* 37, 343–372. doi:10.1146/annurev.ecolsys.37.091305.110251
25
- 26
2762 Schmidt, A.L., Scheibling, R.E., 2006. A comparison of epifauna and epiphytes on native kelps
28
2963 (*Laminaria* species) and an invasive alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia,
30
31
3264 Canada. *Bot. Mar.* 49, 315–330. doi:10.1515/BOT.2006.039
33
- 3465 Servello, G., Andaloro, F., Azzurro, E., Castriota, L., Catra, M., Chiarore, A., Crocetta, F.,
35
3666 D’Alessandro, M., Denitto, F., Frogliola, C., Gravili, C., Langer, M.R., Lo Brutto, S.,
37
38
3967 Mastrototaro, F., Petrocelli, A., Pipitone, C., Piraino, S., Relini, G., Serio, D., Xentidis, N.J.,
40
41
4268 Zenetos, A., 2019. Marine alien species in Italy: A contribution to the implementation of
43
4469 descriptor D2 of the marine strategy framework directive. *Mediterr. Mar. Sci.* 18, 64–76.
45
4670 doi:10.12681/mms.18711
47
- 48
4971 Stein-Taylor, J.R., Littler, M.M., Littler, D.S., America, P.S. of, 1985. *Handbook of Phycological*
50
5172 *Methods: Volume 4: Ecological Field Methods: Macroalgae.* Cambridge University Press.
52
- 53
5473 Streftaris, N., Zenetos, A., 2006. Alien marine species in the Mediterranean - the 100 “worst
55
5674 invasives” and their impact. *Mediterr. Mar. Sci.* 7, 87–118. doi:10.12681/mms.180
57
- 5875 Streftaris, N., Zenetos, A., Papathanassiou, E., 2005. Globalisation in marine ecosystems: The story
59
60
6176 of non-indigenous marine species across European seas. *Oceanogr. Mar. Biol.* 43, 419–453.
62
63
64
65

- 777 Suárez-Jiménez, R., Hepburn, C., Hyndes, G., McLeod, R., Taylor, R., Hurd, C., 2017. The
 1
 778 invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds
 3
 779 with comparable morphologies. *Mar. Ecol. Prog. Ser.* 582, 45–55. doi:10.3354/meps12321
 4
 6
 780 Taylor, R.B., 1998. Short-term dynamics of a seaweed epifaunal assemblage. *J. Exp. Mar. Bio.*
 8
 781 *Ecol.* 227, 67–82. doi:10.1016/S0022-0981(97)00262-1
 9
 10
 782 Thomsen, M.S., Byers, J.E., Schiel, D.R., Bruno, J.F., Olden, J.D., Wernberg, T., Silliman, B.R.,
 11
 13
 783 2014. Impacts of marine invaders on biodiversity depend on trophic position and functional
 14
 15
 784 similarity. *Mar. Ecol. Prog. Ser.* 495, 39–47. doi:10.3354/meps10566
 16
 17
 785 Underwood, A.J., 1996. *Experiments in Ecology: Their Logical Design and Interpretation Using*
 19
 20
 786 *Analysis of Variance.* Cambridge University Press. doi:10.1017/CBO9780511806407
 21
 22
 23
 787 Vega Fernández, T., Badalamenti, F., Bonaviri, C., Di Trapani, F., Gianguzza, P., Noè, S., Musco,
 25
 26
 788 L., 2019. Synergistic reduction of a native key herbivore performance by two non-indigenous
 27
 28
 789 invasive algae. *Mar. Pollut. Bull.* 141, 649–654. doi:10.1016/j.marpolbul.2019.02.073
 30
 31
 790 Veiga, P., Rubal, M., Sousa-Pinto, I., 2014. Structural complexity of macroalgae influences
 32
 33
 791 epifaunal assemblages associated with native and invasive species. *Mar. Environ. Res.* 101,
 35
 792 115–123. doi:10.1016/j.marenvres.2014.09.007
 37
 38
 793 Veiga, P., Torres, A.C., Besteiro, C., Rubal, M., 2018. Mollusc assemblages associated with
 40
 794 invasive and native *Sargassum* species. *Cont. Shelf Res.* 161, 12–19.
 42
 43
 795 doi:10.1016/j.csr.2018.04.011
 44
 45
 796 Verlaque, M., Ruitton, S., Mineur, F., Boudouresque, C., Briand, F., 2015. *CIESM Atlas of Exotic*
 47
 48
 797 *Species in the Mediterranean. Volume 4. Macrophytes.*
 49
 50
 798 Viejo, R.M., 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local
 52
 799 seaweeds in northern Spain. *Aquat. Bot.* 64, 131–149. doi:10.1016/S0304-3770(99)00011-X
 53
 54
 800 Wikström, S.A., Kautsky, L., 2004. Invasion of a habitat-forming seaweed: Effects on associated
 56
 57
 801 biota. *Biol. Invasions* 6, 141–150. doi:10.1023/B:BINV.0000022132.00398.14
 59
 60
 802 Williams, S.L., Smith, J.E., 2007. *A Global Review of the Distribution, Taxonomy, and Impacts of*
 61
 62
 63
 64
 65

803 Introduced Seaweeds. *Annu. Rev. Ecol. Evol. Syst.* 38, 327–359.

1

804 doi:10.1146/annurev.ecolsys.38.091206.095543

3

805 WoRMS Editorial Board (2021), 2021. World Register of Marine Species (WoRMS).

4

806

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35

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

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRedit author statement

Conceptualization, C.R., M.M. and D.R.; Methodology, C.R. and M.M.; Investigation, D.R.; Formal Analysis, M.F.P.; Data curation, M.F.P.; Writing – Original Draft Preparation, M.F.P.; Writing – Review & Editing, M.F.P., M.M., C.R., B.F., M.L., M.B., L.B.S.; Visualization, M.F.P.; Validation, M.F.P.; Supervision, C.R.; Project Administration, C.R.; Funding Acquisition, C.R.; Resources, C.R.; molluscs identification, C.R., D.R.; amphipods identification , L.B.S; annelids identification ; B.F., M.B., M.L.



[Click here to access/download](#)

Supplementary Material

[Draft_shift_E.brachy.A.taxi_supp_final.docx](#)

