

2020-03

Seasonal dynamics of native and invasive *Halophila stipulacea* populations A case study from the northern Gulf of Aqaba and the eastern Mediterranean Sea

Manh Nguyen, H

<http://hdl.handle.net/10026.1/15332>

10.1016/j.aquabot.2020.103205

Aquatic Botany

Elsevier BV

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

1 **Title:** Seasonal dynamics of native and invasive *Halophila stipulacea* populations – a case
2 study from the northern Gulf of Aqaba and the eastern Mediterranean Sea.

3 **Authors:**

4 Hung Manh Nguyen^{a,b,1}, Ioannis Savva^{c,d}, Periklis Kleitou^{c,e}, Demetris Kletou^{c,e}, Fernando P.
5 Lima^f, Yuval Sapir^b, and Gidon Winters^{a*}

6
7 ^aThe Dead Sea Arava Science Center, Tamar Regional Council, Dead-Sea Mobile Post
8 86910, Israel

9 ^bSchool of Plant Sciences and Food Security, The George S. Wise Faculty of Life Sciences,
10 Tel-Aviv University, Tel Aviv 69978, Israel

11 ^cMarine and Environmental Research (MER) Lab Ltd, Limassol 4533, Cyprus

12 ^dSchool of Biological Sciences and UWA Oceans Institute, The University of Western
13 Australia, Crawley, WA, Australia

14 ^eSchool of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

15 ^fCIBIO, Research Center in Biodiversity and Genetic Resources, University of Porto, Campus
16 de Vairão, Rua Padre Armando Quintas n° 7, 4485-661 Vairão, Portugal

17

18 ***Corresponding author:** Email: wintersg@adssc.org

19 **Short communication**

¹ Present address: Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy

20
21
22
23
24
25
26
27
28
29
30
31
32

33 **Abstract**

34 The tropical seagrass *Halophila stipulacea* is native to the Red Sea, Persian Gulf and the Indian
35 Ocean. Following the opening of the Suez Canal, *H. stipulacea* became a Lessepsian
36 immigrant, spreading to most of the eastern Mediterranean Sea. Its arrival in the Caribbean,
37 where it has changed the local seagrass landscapes, has led to concerns about its potential
38 effects on Mediterranean seagrass diversity. Surprisingly, morphological, growth, structural
39 and demographic and ecological traits have never been quantitatively compared between native
40 and invasive populations of *H. stipulacea*.

41 This study used a standardized methodology to provide the first quantitative comparison between
42 populations of native and invasive *Halophila stipulacea* and sheds ~~a~~ light on the importance of
43 long-term monitoring in both native (Red Sea) and invasive (Mediterranean and Caribbean
44 Seas) regions. Results from our study are important for understanding the current population
45 dynamics of *H. stipulacea* in both regions and could be used as baseline data ~~in~~ for future
46 assessments.

47

48 **Keywords:** *Halophila stipulacea*, seagrass monitoring, invasive species, seagrass cover

49

50

51

52

53

54

55

56

57

58

59 **1. Introduction**

60 The seagrass *Halophila stipulacea* (Forsskal) Ascherson is a dioecious, small tropical species,
61 native to the Red Sea, Persian Gulf, and Indian Ocean (Lipkin 1975). Soon after the opening
62 of the Suez Canal in 1869, *H. stipulacea* became a Lessepsian migrant. Since its first report in
63 the island of Rhodes in 1894, *H. stipulacea* has spread throughout most of the eastern and
64 southern Mediterranean basins (Lipkin 1975, Gambi et al. 2009, Sghaier et al. 2011).

65 In 2002, ~~*Halophila*~~ *H. stipulacea* was reported for the first time in Grenada, in the Caribbean
66 Sea (reviewed by Willette and Ambrose 2012). In just over 10 years, it has spread to most of

67 the Eastern Caribbean island nations (Willette and Ambrose 2012) and has even reached the
68 South American continent (Vera et al. 2014). Studies from the Caribbean have demonstrated
69 the invasiveness of *H. stipulacea* by showing that *H. stipulacea* is physically displacing local
70 Caribbean seagrass species (e.g. *Syringodium filiforme*, *Halophila decipiens*, and *Halodule*
71 *wrightii*; Willette and Ambrose 2012, Steiner and Willette 2015a), while in parallel it has also
72 expanded into sand ‘halos’ and the margins of coral reefs, where other seagrasses usually do
73 not grow (Steiner and Willette, 2015b). Taken together, these processes ~~–This phenomenon~~
74 ~~has~~ have transformed been changing the Caribbean’s seagrass landscapes (Steiner and Willette,
75 2015a).
76 ~~through three different schemes including (1) “native strongholds” of sheer native seagrasses,~~
77 ~~On a side note, I have included a link to the original article by Willette and Ambrose (2012) for reference.~~
78 Considering the highly invasive character displayed by *Halophila stipulacea* in the Caribbean,
79 the ongoing tropicalization of the Mediterranean Sea (Bianchi and Morri 2003) together with
80 the recent expansion of the Suez Canal (Galil et al. 2015) and the increasing mortality of the
81 Mediterranean’s native seagrasses in an era of rapid global change (Jordà et al. 2012), there is
82 growing concerns about the expansion of *H. stipulacea* in the Mediterranean and its potential
83 effects on the native temperate seagrass species in this basin. Thus, it is surprising to know that
84 only limited data are available regarding the year-round population dynamics of *H. stipulacea*
85 *stipulacea* in its original distributional ranges (e.g. within the Gulf of Aqaba [GoA]), where it
86 is considered as the dominant seagrass species (Wahbeh 1988; Cardini et al. 2018), and no
87 year-round data at all exists for *H. stipulacea* from the Mediterranean, where it has the potential
88 to trigger significant changes to the local seagrass communities (Sghaier et al. 2014).
89 Lack of information regarding the year-round dynamics of both native and invasive populations
90 of *Halophila stipulacea* limits our understanding of the current population dynamics of this
91 seagrass species in both these sites but also hinders future conservation and management efforts
92 directed at seagrasses in both habitats.
93 Here we report on the first-ever year-round quantitative comparison between native (Eilat,
94 Israel, northern Gulf of Aqaba, northern Red Sea) and invasive (Limassol, Cyprus, eastern
95 Mediterranean Sea) populations of *Halophila stipulacea*. The Results presented here provide
96 knowledge about the population dynamics of *H. stipulacea* from both its native and invasive
97 ranges. This knowledge, also, can serve as baseline data ~~to facilitate for~~ future monitoring
98 efforts in these regions.

99 2. Methods

100 2.1. Setup of monitoring sites

101 50-meter long permanent transects were set up at 3-4 m depth at both the native site (Eilat,
102 northern Gulf of Aqaba, northern Red Sea, Israel; 29°34'48"N, 34°57'33"E; Fig. 1c,e,g) and at
103 the invasive site (Limassol, eastern Mediterranean Sea, Cyprus; 34°42'20"N, 33°07'24"E; Fig.
104 1b,d,f). Transects were marked with labelled plastic poles and floats for easy identification,
105 allowing for revisiting once every three months. The transects (one in each site) were visited
106 seasonally in 2017 as follows: spring (Eilat: 18th March; Limassol: 9th April), summer (Eilat:
107 3rd July; Limassol: 9th July), autumn (Eilat: 03rd October; Limassol: 29th September) and winter
108 (Eilat: 25th December; Limassol: 2nd December) (Fig. 1h).

109 2.2. Sea surface temperature

110 To compare environmental temperatures between study locations in Eilat and Limassol, we
111 obtained daily average sea surface temperatures for the period of 2017 from the NOAA
112 dOISST.v2 dataset at www.ngdc.noaa.gov. We used Advanced Very High-Resolution
113 Radiometer (AVHRR) only data, due to its longer temporal span and because it has been shown
114 to out-perform other datasets in coastal areas (Lima and Wethey 2012).

115 2.3. Seagrass measurements

116 Roca et al. (2016) showed that in small seagrasses (e.g. *Halophila* sp.), morphological, growth,
117 structural and demographic traits were particularly responsive to both a suit of stressors and
118 the recovery from them. Following these traits provides a basic understanding of the
119 population's dynamics, seasonal changes, alongside basic population characteristics and
120 general environmental quality (Roca et al. 2016). These traits also tend to be relatively cheap
121 and easy to apply, providing an opportunity for citizen science programs to join future
122 monitoring of *H. stipulacea*.

123 Seagrass cover was assessed in replicated photo-quadrats (50x50 cm, n=10) every 5 m along
124 the 50 m transects and the taken photos were processed using the CoralNet Platform (Beijbom
125 et al. 2015) by applying 100 random points per quadrat.

126 Plant materials were collected from 25x25 cm quadrats (n=4 in each site and season), placed
127 along the transect (~10 m away from each other). Samples were collected and transported to
128 the laboratory in zip-lock bags filled with seawater for further measurements.

129 Shoot density was calculated as the total number of shoots per m².

130 Fresh plant material was separated into above-ground (leaves) and below-ground (rhizomes
131 and roots) compartments and oven-dried at 70°C for 24 hours to obtain above- and below-
132 ground dry biomass (g DW m⁻²) and their ratios.

133 Data from replicated quadrats in each season were then averaged and normalized to m².

134 Thirty mature-undamaged leaves from each quadrat were digitally scanned (CanoScan LiDE
135 220, Canon U.S.A., Inc, USA) and images were processed with ImageJ
136 (<https://imagej.nih.gov/ij/>) to estimate the leaf surface area (cm²).

137 Percentage of apical shoots (shoot apical meristems) and internode distance was assessed
138 throughout all collected samples.

139 2.4. Statistical analyses

140 ~~Statistically,~~ Permutational multivariate analysis of variance (PERMANOVA) was performed
141 to assess the significant difference between native vs. invasive sites, seasons (i.e. spring
142 [March-April 2017], summer [July 2017], autumn [Sep-Oct 2017], and winter [Dec 2017]) and
143 the interaction between sites and seasons. Data were analyzed on the resemblance matrix
144 (created by S17 BrayCurtis similarity) on Primer 6 v.6.1.16 + PERMANOVA v. 1.0.6
145 (Anderson et al. 2008) with site and season treated as fixed factors and 9999 permutations.
146 ~~Following PERMANOVA was followed by a pair-wise test was performed to detect~~
147 ~~significant differences between seasons of each population separately.~~

148

149 3. Results and discussion

150 Results show that percent of seagrass cover (Fig. 2a) was higher year-round in the native site
151 (Eilat) compared with its invasive site (Limassol; PERMANOVA, Pseudo-F =155.6, $p_{(perm)} =$
152 0.0001). This is not surprising since *Halophila stipulacea* is the dominant and often the only
153 seagrass species in Eilat ~~where (i.e. it is found)~~ growing in a monospecific meadows ~~(Fig. 1g;~~
154 Winters et al. 2017) while in Limassol, *H. stipulacea* has to compete with other native species
155 ~~and is usually (here it is found) growing in a mixed meadows (Fig. 1f).~~ ~~In the native population,~~
156 ~~the highest percent of *H. stipulacea* cover was found in the summer, for the native population,~~
157 while ~~in~~ the Cyprus ~~invasive~~ population, ~~percent of cover developed to a maximum relatively~~
158 ~~was highest~~ during autumn (Fig. 2a). This could be explained by two possible reasons, (1) the
159 invasive *H. stipulacea* could be limited by the fast-growing neighbouring Mediterranean
160 *Cymodocea nodosa* which reaches a maximum during the summer (Cancemi et al. 2002) and
161 (2) the much colder winter (~16°C) in Limassol than in Eilat (~21°C; Fig. 1h) might extend
162 the recovery time of the invasive plants before flowering takes place during the summer months
163 (Nguyen et al. 2018). As a result, we observed significant differences in season
164 (PERMANOVA, Pseudo-F =4.5192, $p_{(perm)} = 0.0041$) as well as the interaction between
165 seasons and sites (PERMANOVA, Pseudo-F =13.815, $p_{(perm)} = 0.0001$) in percent of cover.
166 ~~(Eilat vs. Limassol; PERMANOVA, Pseudo-F =4.5192, $p_{(perm)} = 0.0041$ and Pseudo-F~~
167 ~~=13.815, $p_{(perm)} = 0.0001$, respectively).~~

168 ~~It is interesting to see~~ ~~We also noticed~~ ~~note~~ that shoot density was ~~somehow~~ similar between both populations during spring, autumn
169 and winter ~~while but very different in the summer due to the~~ extremely higher shoot density in the
170 native population during summer time (Fig. 2b) that leads to the significant difference between
171 sites (Eilat vs. Limassol; PERMANOVA, Pseudo-F =4.979, $p_{[perm]} = 0.019$).

172 Results for the above-ground biomass (Fig. 2c) reflected what was found in the percent cover.
173 Above-ground dry biomass was significantly higher year-round in plants from Eilat compared
174 with their invasive counterparts (Fig. 2c, PERMANOVA, Pseudo-F =24.741, $p_{[perm]} =$
175 0.0001), with highest above-ground biomass found in Eilat during the summer, but in ~~October~~
176 ~~the autumn~~ for the Cyprus population.

177 In the invasive population, below-ground biomass (Fig. 2d) started to increase from the autumn
178 and reached the highest value during spring (PERMANOVA, Pseudo-F =2.4767, $p_{[perm]} =$
179 0.0261). This phenomenon corresponds with the hypothesis that the invasive plants were using
180 their below-ground energy to survive the cold Mediterranean winter (Figure 1h). The year-
181 round above- to below-ground biomass ratios in Eilat plants were much higher than that of
182 their Cyprus counterparts (never less than 0.7; Fig. 2e), indicating that relatively, in Eilat plants,
183 more biomass was being accumulated above-ground compared with the Cyprus population.
184 The significant interaction between sites and sampling seasons found for the above- to below-
185 ground biomass ratios (PERMANOVA, Pseudo-F =~~4.15882.565~~, $p_{[perm]} =$ ~~0.00420.0235~~)
186 confirms that both of these populations modified their above to below-ground biomass ratios
187 but at different seasons (Figure 2e). Above- to below-ground biomass ratios in invasive plants
188 were less than 0.5 most of the year (spring, summer, and winter) indicating that majority of the
189 biomass of these plants during most of the year was below ground. The accumulation of
190 underground biomass could potentially help these plants store energy in their “underground
191 storage” to better overcome the cold winter (Marín-Guirao et al. 2018). The year-round above-
192 to below-ground biomass ratios in Eilat plants were much higher than that of their Cyprus
193 counterparts (never less than 0.7), indicating that relatively, more biomass was being
194 accumulated above ground compared with the Cyprus population. Highest above- to below-
195 ground ratios were found in Cyprus in the autumn (close to 1.0) compared with maximal ratios
196 in the Eilat plants that were measured in the summer (close to 1.2).

197 Although found growing in similar depths, in terms of leaf surface area (Fig. 2f), native plants
198 were found to be significantly larger year-round than leaves from invasive plants
199 (PERMANOVA, Pseudo-F =123.21, $p_{[perm]} = 0.0001$). The fact that leaf area might be affected
200 by different environmental parameters at the different sites might be indicated by the
201 significant differences between seasons and a significant season×site interaction

202 (PERMANOVA, Pseudo-F = 12.103, $p_{[perm]}$ = 0.0001 and Pseudo-F = 7.7689, $p_{[perm]}$ = 0.0003,
203 respectively). Changes in leaf area may help *Halophila stipulacea* plants to optimize their
204 carbon balances. In Eilat where there are relatively small changes in water temperature
205 throughout the year (21-27°C; Fig. 1h), changes in leaf area reflect the seasonal changes in light
206 in this region (Winters et al. 2006). Minimal leaf areas in the Eilat's summer could indicate
207 photoacclimation to the intense irradiance experienced during this season, while maximal leaf
208 areas in the winter probably indicate attempts to compensate for the relatively low light in his
209 season. In contrast, in the invasive population, smaller leaves during spring and winter can
210 strengthen the ability of invasive *H. stipulacea* plants to cope better with the colder
211 temperatures experienced in this region (17-18°C), as compared with warmer waters of Eilat
212 (21°C). A similar mechanism has been demonstrated in terrestrial plants (Milford and Riley
213 1980). Indeed, results showed that the invasive plants increased their leaf size during autumn
214 ($2.09 \text{ cm}^2 \pm 0.14 \text{ SE}$, Fig. 2f), when water temperatures were more favourable. Shoot density
215 results (Fig. 2b) concur with the results from above-ground biomass and leaf surface area.
216 Invasive plants produced a similar number of shoots as native plants during the spring and
217 winter, but smaller leaf surface area year round (Fig. 2f) resulted in lower above-ground
218 biomass (Fig. 2d).
219 Furthermore, our results demonstrate some of the different morphology that might be
220 associated with the invasive characteristic of *Halophila stipulacea* in the Mediterranean ranges
221 via a higher percentage of apical shoots and longer internode distances. Having significantly
222 more apical shoots and longer internode distances (Fig. 2g,h; Eilat vs. Limassol,
223 PERMANOVA, Pseudo-F = 6.7344, $p_{[perm]}$ = 0.0178 and Pseudo-F = 15.74, $p_{[perm]}$ = 0.0015,
224 respectively) could contribute to the ability of the invasive plants to (i) rapidly occupy more
225 space and (ii) escape from un-favourable new environments. These ~~invasive~~ morphological
226 traits can potentially contribute to the invasiveness of *H. stipulacea* in the Mediterranean
227 (Gambi et al. 2009) and Caribbean Seas (Steiner and Willette 2015).
228 Although *Halophila stipulacea* was included in the "100 Worst Invasive Alien Species in the
229 Mediterranean" (Streftaris and Zenetos 2006), in this basin, evidence for its "invasive"
230 characteristics are scarce. In the Mediterranean, *H. stipulacea* has been continuously spreading
231 westwards and northwards (Lipkin 1975, Gambi et al. 2009, Sghaier et al. 2011) and was
232 experimentally predicted to spread throughout the whole Mediterranean Sea in the coming
233 future (Georgiou et al. 2006, Nguyen et al. *in review*). With the semi-enclosed Mediterranean
234 Sea becoming warmer and saltier (Bianchi and Morri 2003), it has been predicted that the

235 ongoing tropicalization of the Mediterranean Sea might be causing declines in local
236 Mediterranean temperate seagrasses species (Jordà et al. 2012), while favouring the expansion
237 of the tropical invasive *H. stipulacea* (Georgiou et al. 2016, Gambi et al. 2009). Evidence for
238 the invasive characteristics of *H. stipulacea* in the Mediterranean includes observations by
239 Sghaier et al. (2014) that showed in Tunisia, that introduced *H. stipulacea* was taking over the
240 meadows of the local Mediterranean seagrass species (i.e. *Cymodocea nodosa*). Work by
241 Chiquillo et al. (*in prep.*) has recently experimentally shown that both in the Caribbean and the
242 Mediterranean Seas, *H. stipulacea* grows better with local native species than by itself, hinting
243 to the potential mechanism of *H. stipulacea*'s success in its new invasive habitats.

~~244 Indeed, the limited data available for year round population dynamics of *Halophila stipulacea*
245 within the Gulf of Aqaba, where it is considered the dominant and sometimes only (Winters et
246 al. 2017) seagrass species (Wahbeh 1988, Cardini et al. 2018) is worrying.~~

247 On the other hand, tropicalization (Bianchi and Morri 2003) of the Mediterranean invasive
248 habitats, accompanied by the recent doubling of the Suez Canal (Galil et al. 2015), could
249 potentially (i) facilitate the further spreading of *Halophila stipulacea*, (ii) enhance its ability to
250 outcompete local seagrass species (Sghaier et al. 2014) or (iii) broaden its stability to occupy
251 newly available habitat following predicted extirpation of local Mediterranean seagrass species
252 (Jordà et al. 2012). Although *H. stipulacea* has yet been on the main agenda of seagrass
253 research and monitoring efforts in Mediterranean waters, we emphasize that now is the time to
254 put more effort into studying and monitoring this seagrass species.

255 It is important to note that in this study, we used only one population from each basin and
256 visited each site only once per season. Considering the exponentially growing human pressures
257 on coastal areas, specifically in the crowded shores of Mediterranean and the northern GoA,
258 we highlight the need for coordinated monitoring (e.g. this study) and mapping efforts (e.g.
259 Winters et al. 2017) that will focus on recording changes over time and space in *Halophila*
260 *stipulacea* and associated communities in multiple sites both its native and invasive ranges. ~~In
261 addition to field based efforts, simulated mesocosm studies answering the question about the
262 future of the seagrass *H. stipulacea* both natively and invasively are incredibly crucial in an
263 era of rapid global change (Oliver et al. 2018).~~

264
265 **Funding:** This work was partially funded by a short term scientific mission (STSM) awarded
266 to GW and DK through COST Action CA15121 (Advancing marine conservation in the
267 European and contiguous seas = MarCons). We thank the Arava International Center for
268 Agriculture Training (AICAT) for giving Hung Manh Nguyen financial support during his

269 M.Sc. We thank the Manna Center Program for Food Safety & Security, at the School of
270 Plant Sciences and Food Security Faculty of Life Sciences Tel Aviv University (TAU) for
271 their ongoing support for the co-op between TAU and ADSSC. [We thank the Israeli Ministry](#)
272 [of Science and Technology \(MOST\) for their continued support of the ADSSC.](#)
273

274 Reference

- 275 1. Anderson, M., R.N. Gorley and R.K. Clarke. 2008. Permanova+ for primer: Guide to
276 software and statistical methods. Primer-E Limited. Plymouth, UK.
- 277 2. Beijbom, O., P.J. Edmunds, C. Roelfsema, J. Smith, D.I. Kline, B.P. Neal, M.J. Dunlap, V.
278 Moriarty, T.-Y. Fan and C.-J. Tan. 2015. Towards automated annotation of benthic survey
279 images: Variability of human experts and operational modes of automation. *PloS one*. 10:
280 e0130312.
- 281 3. Bianchi, C.N. and C. Morri. 2003. Global sea warming and “tropicalization” of the
282 Mediterranean Sea: biogeographic and ecological aspects. *Biogeographia*. 24: 319-327.
- 283 4. Cancemi, G., M.C. Buia and L. Mazzella. 2002. Structure and growth dynamics of
284 *Cymodocea nodosa* meadows. *Sci. Mar.* 66: 365-373.
- 285 5. Cardini, U., N. van Hoytema, V. Bednarz, M. Al-Rshaidat, and C. Wild. 2018. N₂ fixation
286 and primary productivity in a red sea *Halophila stipulacea* meadow exposed to seasonality.
287 *Limnol. Oceanogr.* 63: 786-798.
- 288 6. Chiquillo, K. L., P. Fong, D. A. Willette, G. Winters, E. Cruz-Rivera, M. I. Vasquez and P.
289 H. Barber. 2019. League of seagrasses: interspecific interactions between native versus
290 invasive seagrass shows a positive effect on the invasive, *Halophila stipulacea*. ASLO 2019
291 Aquatic Sciences meeting, 23 February – 2 March 2019, San Juan, Puerto Rico.
- 292 7. Costanza, R., R. de Groot, P. Sutton, S. Van der Ploeg, S.J. Anderson, I. Kubiszewski, S.
293 Farber and R.K. Turner. 2014. Changes in the global value of ecosystem services. *Global*
294 *Environ Chang.* 26:152-158.
- 295 8. Galil, Boero, F., M.L. Campbell, J.T. Carlton, E. Cook, S. Fraschetti, S. Gollasch, C.L.
296 Hewitt, A. Jelmert and E. Macpherson. 2015. ‘Double trouble’: the expansion of the Suez
297 Canal and marine bioinvasions in the Mediterranean Sea. *Biol. Invasions*. 17: 973-976.
- 298 9. Gambi, M.C., F. Barbieri and C.N. Bianchi. 2009. New record of the alien seagrass
299 *Halophila stipulacea* (Hydrocharitaceae) in the western Mediterranean: a further clue to
300 changing Mediterranean Sea biogeography. *Mar. Biol. Rec.* 2: e84.

- 301 10. Georgiou, D., A. Alexandre, J. Luis and R. Santos. 2016. Temperature is not a limiting
302 factor for the expansion of *Halophila stipulacea* throughout the Mediterranean Sea. *Mar.*
303 *Ecol. Prog. Ser.* 544: 159-167.
- 304 11. Jordà, G., N. Marbà and C.M. Duarte. 2012. Mediterranean seagrass vulnerable to regional
305 climate warming. *Nat. Clim. Change.* 2: 821-824.
- 306 12. Lamb, J.B., J.A. van de Water, D.G. Bourne, C. Altier, M.Y. Hein, E.A. Fiorenza, N. Abu,
307 J. Jompa and C.D. Harvell. 2017. Seagrass ecosystems reduce exposure to bacterial
308 pathogens of humans, fishes, and invertebrates. *Science.* 355:731-733.
- 309 13. Lima, F. P., D. S. Wethey. 2012. Three decades of high-resolution coastal sea surface
310 temperatures reveal more than warming. *Nat commun.* 3: 704.
- 311 14. Lipkin, Y. 1975. *Halophila stipulacea*, a review of a successful immigration. *Aquat. Bot. 1:*
312 203-215.
- 313 15. Marín-Guirao, L., J. Bernardeau-Esteller, R. García-Muñoz, A. Ramos, Y. Ontoria, J.
314 Romero, M. Pérez, J. Ruiz and G. Procaccini. 2018. Carbon economy of Mediterranean
315 seagrasses in response to thermal stress. *Mar. Pollut. Bull.* 135: 617-629.
- 316 16. Milford, G. and J. Riley. 1980. The effects of temperature on leaf growth of sugar beet
317 varieties. *Ann. Appl. Biol.* 94: 431-443.
- 318 17. Nguyen, H.M., P. Kleitou, D. Kletou, Y. Sapir and G. Winters. 2018. Differences in
319 flowering sex ratios between native and invasive populations of the seagrass *Halophila*
320 *stipulacea*. *Bot. Mar.* 61: 337-342.
- 321 18. Nguyen, H.M., N. S. Yadav, S. Barak, F. P. Lima, Y. Sapir and G. Winters. 2019. Responses
322 of invasive and native *Halophila stipulacea* populations to simulated climate change. *Environ Exper Front.*
323 *Mar. Sci. Bot.* In review.
- 324 19. Oliver, E.C., M.G. Donat, M.T. Burrows, P.J. Moore, D.A. Smale, L.V. Alexander, J.A.
325 Benthuisen, M. Feng, A.S. Gupta and A.J. Hobday. 2018. Longer and more frequent marine
326 heatwaves over the past century. *Nat. Commun.* 9: 1324.
- 327 20. Sghaier, Y.R., R. Zakhama-Sraieb, I. Benamer and F. Charfi-Cheikhrouha. 2011.
328 Occurrence of the seagrass *Halophila stipulacea* (Hydrocharitaceae) in the southern
329 Mediterranean Sea. *Bot. Mar.* 54: 575-582.
- 330 21. Sghaier, Y.R., R. Zakhama-Sraieb and F. Charfi-Cheikhrouha. 2014. Effects of the invasive
331 seagrass *Halophila stipulacea* on the native seagrass *Cymodocea nodosa*. *Proceedings of*
332 *the Fifth Mediterranean Symposium on Marine Vegetation. Portorož, Slovenia, 27-28*
333 *October 2014. pp.* 167-171.

334 [22.](#) Steiner, S. and D. Willette. 2015a. The expansion of *Halophila stipulacea*
335 (Hydrocharitaceae, Angiospermae) is changing the seagrass landscape in the
336 commonwealth of Dominica, Lesser Antilles. *Caribb. Nat.* 22: 1-19.

337 [23.](#) Steiner, S., and D. Willette. 2015b. [Dimming sand halos in Dominica and the expansion of](#)
338 [the invasive seagrass *Halophila stipulacea*. *Reef Encount.* 30: 43-45.](#)

339 ~~[22.](#)~~

340 meadows modify seawater carbon chemistry: implications for coral reefs impacted by ocean
341 acidification. *Environ Res Lett.* 7: 024026.

342 ~~[24-25.](#)~~ Vera, B., L. Collado-Vides, C. Moreno and B.I. van Tussenbroek. 2014. *Halophila*
343 *stipulacea* (Hydrocharitaceae): A recent introduction to the continental waters of Venezuela.
344 *Caribb. J. Sci.* 48: 66-70.

345 ~~[25-26.](#)~~ Wahbeh, M.I. 1988. Seasonal distribution and variation in the nutritional quality of
346 different fractions of two seagrass species from Aqaba (Red Sea), Jordan. *Aquat. Bot.* 32:
347 383-392.

348 ~~[26-27.](#)~~ Willette, D.A. and R.F. Ambrose. 2012. Effects of the invasive seagrass *Halophila*
349 *stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiota
350 communities in the Eastern Caribbean. *Aquat. Bot.* 103: 74-82.

351 ~~[27-28.](#)~~ Winters, G., D. Edelist, R. Shem-Tov, S. Beer and G. Rilov. 2017. A low cost field-
352 survey method for mapping seagrasses and their potential threats: an example from the
353 northern Gulf of Aqaba, Red Sea. *Aquat Conserv.* 27: 324-339.