Ecology, 100(12), 2019, e02838

Climatic anomalies may create a long-lasting ecological phase shift by altering the reproduction of a foundation species

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Manuscript received 21 June 2019; revised 9 July 2019; accepted 11 July 2019. Corresponding Editor: John Pastor.

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Citation: Bevilacqua, S., G. Savonitto, M. Lipizer, P. Mancuso, S. Ciriaco, M. Srijemsi, and A. Falace. 2019. Climatic anomalies may create a long-lasting ecological phase shift by altering the reproduction of a foundation species. Ecology 100(12):e02838. 10.1002/ecy.2838

Key words: Algal forests; climate change; Cystoseira*; Fucales; heat waves; Mediterranean Sea; phenology.*

The resilience of ecological communities is often defined by one or a few species that have disproportionately important roles influencing many other species in the community. This is true for some areas of the Mediterranean Sea that are characterized by large brown fucoid algae of the genus *Cystoseira* that form dense underwater forests structurally similar to the giant kelps of the Pacific. While shorter than the giant kelp, *Cystoseira* species form dense underwater stands, contributing to the three-dimensional complexity of the seascape (Fig. 1). These canopy-forming seaweeds play a crucial role in primary production and nutrient cycling of temperate coastal ecosystems from the Mediterranean Sea to the Atlantic Ocean (Mineur et al. 2015) and act as “ecosystem engineers,” providing food, nursery, and shelter for a rich associated biota. Interacting human pressures are causing the widespread disappearance of these complex and productive species (Strain et al. 2014). As they are being replaced by simpler assemblages, biodiversity declines and ecosystem functions are altered (Falace et al. 2010, Sales et al. 2011). The natural recovery of these populations is hampered by their very limited dispersal ability (Capdevila et al. 2018).

In February 2019, during a routine survey within the Marine Protected Area of Strunjan (Slovenia) to monitor the vegetative and reproductive cycle of the fucoid *Cystoseira barbata* (Stackhouse) C. Agardh, we made a singular discovery. Even though they were in their winter resting phase, dozens of *C. barbata* thalli had reproductive structures (receptacles; Fig. 2a,b). In addition and even more amazing, the receptacles were also developing on adventitious branches, which are sterile by definition. Subsequent surveys revealed this unusual phenology in other areas as well, from Strunjan to the Marine Protected Area of Miramare (Italy), suggesting that this phenomenon spansned at least 50 km of rocky coast in the region. Like other congenerics, *C. barbata* has marked seasonal variations of vegetative growth. In the Northern Adriatic Sea, as temperature and photoperiod increase in early spring, branches usually start to develop from a perennial cauloid (Falace and Bressan 2006). Later, during late spring–early summer, the branches become fertile as they reach their maximum development. At the end of summer, upright branches are shed and the cauloid persists in a quiescent state during the fall–winter cold season.

During our study, instead of this normal life cycle, *C. barbata* was fertile almost 3 months earlier than usual, yielding mature receptacles (Fig. 3a) able to release zygotes and produce viable embryos (Fig. 3b). Interestingly, this early unexpected reproductive event followed a period of 2 yr where *C. barbata* was infertile in the Northern Adriatic Sea (personal observation of the authors).

Although drawing conclusions on the reasons behind the prolonged infertility of *C. barbata* and this mistimed reproductive event is still premature, there are some clues. After a period of relatively normal temperature from 2003 to 2013, there have been recurring episodes of exceptional warming in the cold season in the Northern Adriatic Sea during the last 6 yr (Appendix S1: Fig. S1). Immediately before the extraordinary reproductive event, in February 2019, a thermal anomaly of 2.65°C higher than the average during the last four decades has struck the whole basin. Near the Marine Protected Area of Strunjan, the coastal oceanographic buoy MAMBO-OGS (National Institute of Oceanography and Applied Geophysics) recorded a warming in the intermediate waters of about 1.5°C occurring in the middle of February and persisting for more than 1 month. This warming is 1 month prior to the average timing of warming during the first 10 yr (1999–2009) of measurements (Appendix S1: Fig. S2).

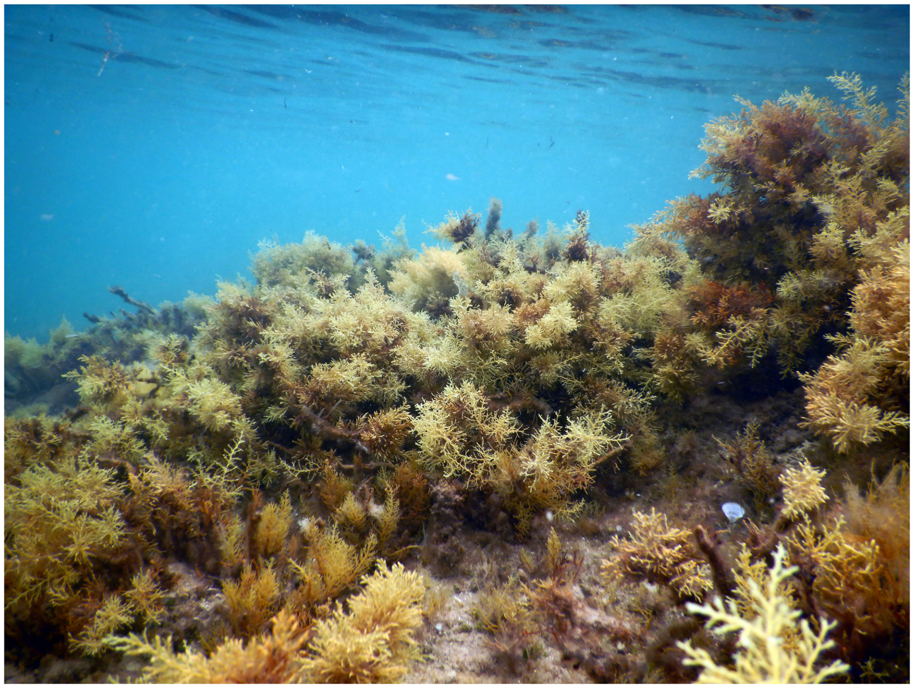

FIG. 1. Mediterranean underwater *Cystoseira* spp. forest.

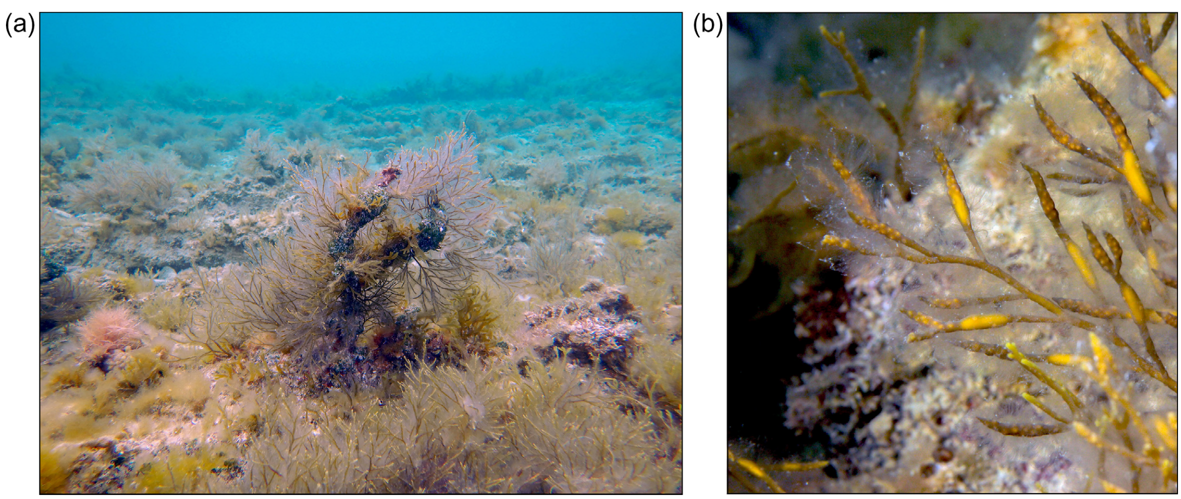

FIG. 2. (a) *Cystoseira barbata* winter habitus, with short primary and adventitious branches. (b) Branches with reproductive structures (receptacles).

As temperature is one of the main variables regulating reproductive and vegetative phenology in seaweeds (Eggert 2012), early and extreme episodes of warming could play a decisive role in triggering the survival of subsequent life stages. For example, the release of zygotes during early warm spells in winter could cause later mass mortality of embryos because of the unfavorable environmental conditions. To make matters worse, if the algae allocated much of their resources for unusual reproductive events, then they may not be able to become fertile during the normal season or to produce healthy propagules. Receptacles from *C. barbata* sampled in May 2019 released 10 times fewer zygotes than during the previous exceptional event in February 2019, and the subsequent growth of germlings from them differed consistently (Fig. 4). Intense reservoir depletion under reiterated reproductive efforts could also affect the vegetative phase of adults. Available data

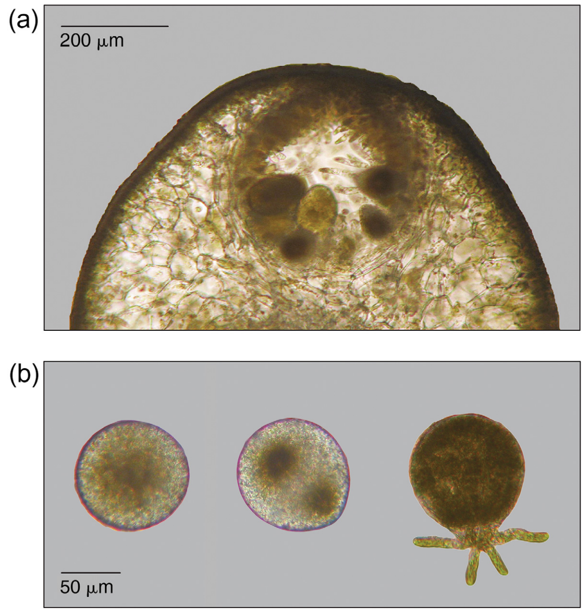

FIG. 3. (a) Transverse section of a receptacle with a fully mature conceptacle (gametes are fully developed and close to release). (b) Zygote and early life stages of *C. barbata* embryos.

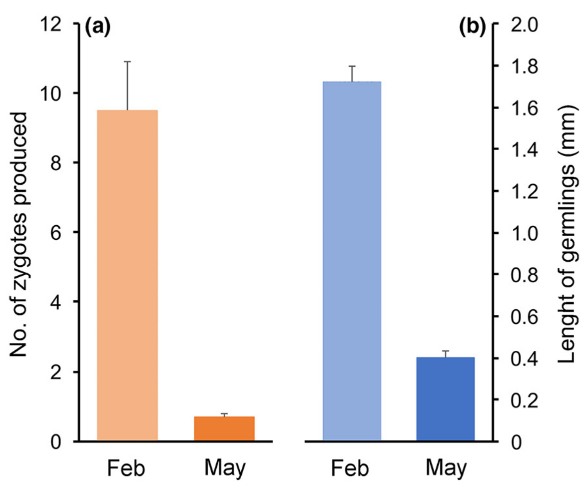

FIG. 4. (a) Mean (±SE) number of zygotes produced by receptacles (n = 33) collected in February and May 2019. (b) Mean (±SE) length of germlings after 4 weeks (n = 60) from cultured zygotes produced in the two periods.

corroborated this hypothesis, showing that the average length of *C. barbata* thalli in the study area greatly contracted during the last 15 yr, which coincided with an increased frequency of hot spells (Fig. 5).

In the Mediterranean Sea, direct habitat destruction, pollution, and overgrazing by sea urchins and herbivorous fish are acknowledged as the main drivers of disappearing algal forests, with climate change representing an emerging threat to these ecosystems (Blanfuné et al. 2019). Our observations and preliminary assessments highlighted potential disruptive effects of winter hot spells on reproductive timing, recruitment, and adult survival that could severely affect the persistence of *Cystoseira* populations. However, most reproductive anomalies, like the one we had the chance to observe and report here, are likely to remain unnoticed because of the widespread preference of surveying macroalgae in late spring or summer. Thus, the contribution of climate change and related extreme events, such as heat waves, to the ongoing decline of *Cystoseira* canopies could have been largely overlooked.

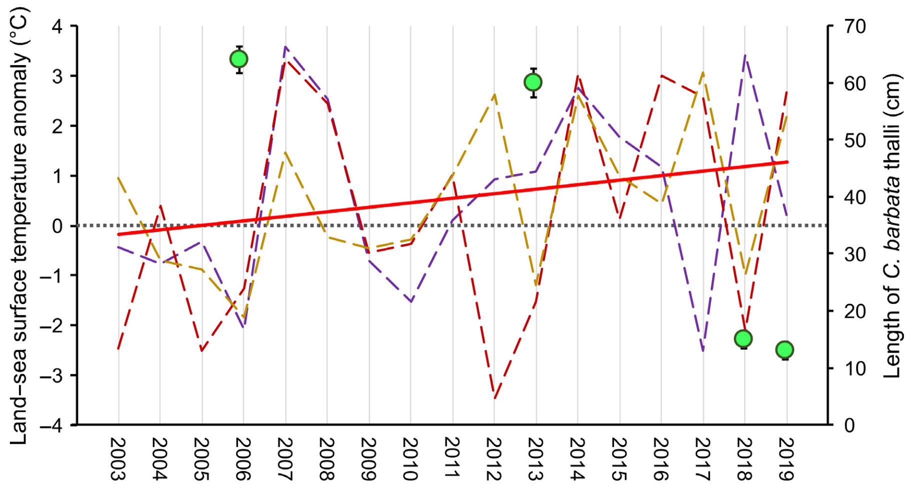

FIG. 5. (Left axis) Land–sea surface temperature anomalies (dashed lines) in the northern Adriatic Sea recorded in January (violet), February (red), and March (gold) in different years from 2003 to 2019. The solid red line indicates the overall trend in temperature increase. Anomalies were based on the average temperature since 1981 (black dotted line); data retrieved from https://www.ncdc.noaa.gov/cag; see supporting information for further details. (Right axis) Mean (±SE) length of *C. barbata* thalli (green circles) from Strunjan in 2006, 2013, 2018, and 2019 late spring ($n = 35$).

Because extreme climate episodes are increasing in intensity and frequency, implementing coordinated initiatives connecting centers for climate alerts and algologists may shed light on how these phenomena impact population dynamics of *Cystoseira* species, and help current attempts to restore algal forests. The ex situ restoration of *Cystoseira* requires three main steps, including the collection of fertile apices in healthy populations, the setup of mesocosms for controlled reproduction and generation of juveniles, and the implant of juveniles in the restoration sites (Falace et al. 2018). Understanding how climate unpredictability can affect the physiology and phenology of *Cystoseira* species is, therefore, crucial. Networks of early warning against extreme events might allow restoration ecologists to be in right place at the right time, in order to monitor phenological responses of *Cystoseira*, collect premature zygotes that can be cultured under controlled conditions and used for implantation, or select lineages with higher plasticity to temperature extremes, increasing the chance for successful restoration actions of these valuable marine habitat formers.

ACKNOWLEDGMENTS

We really thank John Pastor and Paul Dayton for their invaluable suggestions and constructive comments that greatly improved our manuscript.

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