## Compounded perturbations in coastal areas: contrasting responses to nutrient enrichment and the regime of storm-related disturbance depend on life-history traits

lacopo Bertocci<sup>\*,1,2</sup>, Jorge A. Domínguez Godino<sup>1,3</sup>, Cristiano Freitas<sup>1</sup>, Monica Incera<sup>1,4</sup>, Ana Bio<sup>1</sup> and Rula Domínguez<sup>1,5</sup>

<sup>1</sup>CIIMAR/CIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Terminal de Cruzeiros do Porto de Leixões, Av. General Norton de Matos s/n, 4450-208 Matosinhos, Portugal; <sup>2</sup>Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy; <sup>3</sup>CCMAR, CIMAR-Laboratório Associado, Universidade do Algarve Gambelas, 8005-139 Faro, Portugal; <sup>4</sup>Centro Tecnológico del Mar – Fundación CETMAR, C/Eduardo Cabello, s/n E-36208, Bouzas, Vigo, Spain; and <sup>5</sup>Departamento de Ecoloxía e Bioloxía Animal, Faculdade de Ciencias do Mar, Universidade de Vigo, Vigo, Spain

## Summary

1. Natural systems are exposed to compounded perturbations, whose changes in temporal variance can be as important as those in mean intensity for shaping the structure of assemblages. Specifically, climate-related physical disturbances and nutrient inputs due to natural and/or anthropogenic activities occur concomitantly, but experimental tests of the simultaneous effects of changes in the regime of more than one perturbation are generally lacking. Filling this gap is the key to understand ecological responses of natural assemblages to climate-related change in the intensity and temporal patterning of physical disturbance combined with other global stressors.

**2.** Responses to factorial manipulations of nutrient enrichment, mean intensity and temporal variability in storm-like mechanical disturbance were examined, using benthic assemblages of tide-pools as model system.

**3.** Response variables were mean abundance values and temporal variances of taxa with different life-traits. Consistent negative effects of disturbance intensity were observed for the mean cover of long-living taxa (algal canopies and the polychaete *Sabellaria alveolata*), whose temporal fluctuations were also reduced by more severe mechanical stress. More resilient taxa (ephemeral algae, mostly green of the genus *Ulva*) increased under enriched conditions, particularly when low-intensity events were irregularly applied over time. Opposite effects of disturbance intensity depending on nutrient availability occurred on filamentous algae (e.g. red of the genus *Ceramium*). This was probably due to the fact that, although nutrient enrichment stimulated the abundance of both algal groups, when this condition was combined with relatively mild physical disturbance the competitively superior ephemeral green algae tended to become dominant over filamentous red algae. The same did not occur under high intensity of disturbance since it likely damaged large, foliose fronds of *Ulva*-like forms more than small, filamentous fronds of *Ceramium*-like forms. Grazers were positively affected by nutrients, likely responding indirectly to more food available.

**4.** A direct relationship between the mean abundance of most organisms and their temporal fluctuations was documented. However, all organisms persisted throughout the study, even under experimental conditions associated to the largest temporal variation in their abundance, likely due to their ability to resist to/quickly recover from, the applied perturbations. Therefore, in systems with great recovery abilities of dominant organisms (e.g. rocky intertidal, grasslands), effects of traits of the regime of disturbance and nutrient enrichment may

<sup>\*</sup>Correspondence author. E-mail: ibertocci@ciimar.up.pt