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## Ocean acidification as a driver of community simplification via the collapse of higher-order and rise of lower-order consumers

S. Vizzini<sup>1,2</sup>, B. Martínez-Crego<sup>3</sup>, C. Andolina<sup>1,4</sup>, A. Massa-Gallucci<sup>5</sup>, S. D. Connell<sup>6</sup> & M. C. Gambi<sup>5</sup>

Increasing oceanic uptake of CO<sub>2</sub> is predicted to drive ecological change as both a resource (i.e. CO<sub>2</sub> enrichment on primary producers) and stressor (i.e. lower pH on consumers). We use the natural ecological complexity of a CO<sub>2</sub> vent (i.e. a seagrass system) to assess the potential validity of conceptual models developed from laboratory and mesocosm research. Our observations suggest that the stressor-effect of CO<sub>2</sub> enrichment combined with its resource-effect drives simplified food web structure of lower trophic diversity and shorter length. The transfer of CO<sub>2</sub> enrichment from plants to herbivores through consumption (apparent resource-effect) was not compensated by predation, because carnivores failed to contain herbivore outbreaks. Instead, these higher-order consumers collapsed (apparent stressor-effect on carnivores) suggesting limited trophic propagation to predator populations. The dominance of primary producers and their lower-order consumers along with the loss of carnivores reflects the duality of intensifying ocean acidification acting both as resource-effect (i.e. bottom-up control) and stressor-effect (i.e. top-down control) to simplify community and trophic structure and function. This shifting balance between the propagation of resource enrichment and its consumption across trophic levels provides new insights into how the trophic dynamics might stabilize against or propagate future environmental change.

As a consequence of increasing CO<sub>2</sub> emissions in the atmosphere, oceanic uptake of CO<sub>2</sub> is predicted to rise progressively<sup>1,2</sup> with concomitant changes to pH and carbonate chemistry affecting marine organisms<sup>3,4</sup> and their ecosystem functions<sup>4</sup>. In recent recognition of the potential extent of this change, there has been a sudden increase in ecological research concerning ocean acidification (OA). Initially, research focused on CO<sub>2</sub> enrichment in laboratory and mesocosm experiments (e.g. ref. 5), progressing from physiological and morphological responses of individual species through community<sup>6,7</sup> and ecosystem<sup>8</sup> level responses. Conceptual models anticipate that near future concentrations of CO<sub>2</sub> may be severe for calcifying organisms (i.e. OA acts as a stressor), while boosting growth and photosynthesis in fleshy algae and seagrasses (i.e. CO<sub>2</sub> acts as a resource)<sup>4,6,9</sup>. As a result, major ecosystem disruption has been almost universally inferred at high CO<sub>2</sub><sup>3</sup>, although this assumption remains largely untested<sup>10</sup>.

The assessment of processes that propagate or buffer change is challenging in simplified laboratory and mesocosm research. Recent focus has incorporated natural systems where volcanic CO<sub>2</sub> emissions naturally acidify coastal waters<sup>9,11–15</sup>. A relatively large number of studies at the Castello Aragonese CO<sub>2</sub> vent of Ischia Island (Italy, Tyrrhenian Sea) have begun to shed light on the long-term biological and ecological responses along pH gradients at varying levels of biological hierarchy, from species-specific responses<sup>16–18</sup> to patterns of motile invertebrates<sup>19,20</sup> and macroalgae assemblages<sup>21</sup>. Of increasing interest from the global study of CO<sub>2</sub> vents has been the reported increase in the abundance of non-calcifying macroalgae that boost herbivore biomass<sup>9,22,23</sup>, suggesting

<sup>1</sup>Department of Earth and Marine Sciences, University of Palermo, Palermo, Italy. <sup>2</sup>CoNISMa, Roma, Italy. <sup>3</sup>Centre of Marine Sciences (CCMAR), Faro, Portugal. <sup>4</sup>Department of Environmental Sciences, Informatics and Statistics, DAIS, University Ca' Foscari, Venice, Italy. <sup>5</sup>Stazione Zoologica Anton Dohrn, Department of Integrative Marine Ecology, Villa Dohrn Benthic Ecology Center (Ischia), Naples, Italy. <sup>6</sup>Southern Seas Ecology Laboratories, School of Biological Sciences & Environment Institute, University of Adelaide, South Australia, Australia. Correspondence and requests for materials should be addressed to S.V. (email: [salvatrice.vizzini@unipa.it](mailto:salvatrice.vizzini@unipa.it))