Global Change Biology

Global Change Biology (2015) **21**, 1381–1382, doi: 10.1111/gcb.12772

LETTER

The devil in the detail: harmful seaweeds are not harmful to everyone

MADS S. THOMSEN[1,2] and THOMAS WERNBERG[2,3]

[1]*Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag, Christchurch 4800, New Zealand,* [2]*UWA Oceans Institute and School of Plant Biology, University of Western Australia, Hackett Drive, Crawley, WA 6009, Australia,* [3]*Australian Institute of Marine Science, 39 Fairway, Crawley, WA 6009, Australia*

In a stimulating paper, Lyons *et al.* (2014) reported results from meta-analyses on effects of bloom-forming seaweeds on ecosystem properties, emphasizing the importance of these impacts in coastal ecosystems. The main conclusions were that (i) effects of seaweeds were *'highly variable'* and (ii) marine invertebrates were *'particularly sensitive to blooms, suffering reductions in their abundance, species richness, and diversity'*. However, Lyons *et al.* did not test in detail what ecological mechanisms might have caused variable effects, for example by linking effect sizes to functional (Thomsen *et al.*, 2014) or neutral (e.g., abundance in space and time) (Powell *et al.*, 2011) attributes of independent and dependent variables. We reanalyzed Lyons *et al.*'s data on invertebrate effects (cf. online Table S1) and show that (i) their data pooling canceled out important contrasting effects that only become evident when ecological functions of the independent (seaweeds) and dependent (invertebrates habitat affinity) variables were matched; and (ii) an additional test of density-dependency suggests that effects on invertebrates increase with increasing seaweed abundances.

First we tested if effect sizes differed when invertebrates were sampled primarily below the seaweed (mainly infauna) or also included the seaweed structure itself (mainly epifauna) (Gribben *et al.*, 2013). We hypothesized that hypoxic sediments, smothered filter-feeding and interception of propagules would inhibit the fauna below the seaweed (Gamenick *et al.*, 1996), whereas provisioning of 3-dimensional habitat, food and protection against predation and stress would facilitate epifauna (e.g., through direct facilitation or in habitat cascades, Byers *et al.*, 2012; Thomsen *et al.*, 2010). Our analysis supported the functional-matching hypothesis; experiments that only sampled the infauna had a significant negative effect whereas experiments that also sampled the seaweed structure had a significant positive effect (Fig. 1a; $Q_{\text{total}} = 63.59$, df = 26, $P < 0.001$). Second, we tested if effect sizes were density-dependent. We hypothesized that effects on (mainly) epifauna would increase with increasing abundance of seaweeds because more seaweeds provide more 3-dimensional habitat, food and protection against predation and stress. Our analysis supported the density hypothesis; all four experiments that tested if seaweed density affected epifauna found more invertebrates in the 'high' than 'low' seaweed treatments (cf. online Table S1, footnote 2 for details). A formal analysis, calculating the percent difference in invertebrate abundances between the high and low seaweed treatments, showed that 176% more invertebrates were found in the high compared to the low seaweed levels (Fig. 1b).

Our analysis demonstrated that bloom-forming seaweeds can under certain conditions, like other habitat-forming species, contribute to biodiversity and ecological function. A key implication is that coastal managers should expect both opposing (but partly predictable) effects of bloom-forming seaweeds on local organisms and processes (Gribben *et al.*, 2013) as well as density-dependency and therefore potentially also threshold-responses and tipping points (Andersen *et al.*, 2009). We finally conclude that meta-analyses that

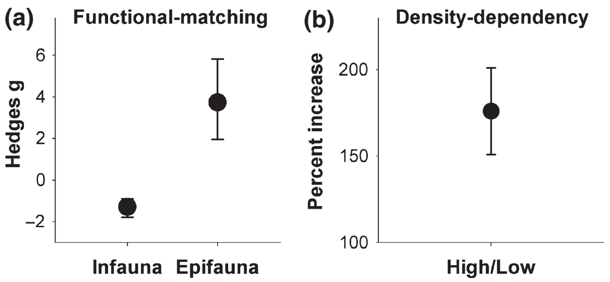

Fig. 1 Meta-analyses testing hypotheses of functional-matching (a) and density-dependency (b), showing Hedges g effect sizes with 95% bias-corrected confidence limits. (a) Bloom-forming seaweeds had negative effects on fauna sampled 'Below' the seaweed (mainly infauna, $n = 18$) but positive effects on fauna from samples that 'Included' the seaweed structure itself (mainly epifauna; $n = 9$). (b) Abundances of fauna from samples that included the seaweed structure were 176% higher in 'High' compared to 'Low' seaweed treatments ($n = 4$). See online Table S1 for details.

Correspondence: Mads S. Thomsen, tel. +64 3 364 2987, fax +64 3 364 2590, e-mail: mads.solgaard.thomsen@gmail.com

target specific ecological hypotheses promotes more nuanced conclusions about effect sizes.

Acknowledgements

MST was supported by the Marsden Fund of New Zealand and TW by the Australian Research Council.

References

Andersen T, Carstensen J, Hernandez-Garzia E, Duarte CM (2009) Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology and Evolution*, **24**, 49–57.

Byers J, Gribben P, Yeager C, Sotka E (2012) Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. *Biological Invasions*, **14**, 2587–2600.

Gamenick I, Jahn A, Vopel K, Giere O (1996) Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonisation studies and tolerance experiments. *Marine Ecology Progress Series*, **14**, 73–85.

Gribben PE, Byers JE, Wright JT, Glasby TM (2013) Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. *Oikos*, **122**, 816–824.

Lyons DA, Arvanitidis C, Blight AJ *et al.* (2014) Macroalgal blooms alter community structure and primary productivity in marine ecosystems. *Global Change Biology*, **20**, 2712–2724.

Powell KI, Chase JM, Knight TM (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany*, **98**, 539–548.

Thomsen Ms, Wernberg T, Altieri Ah *et al.* (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology*, **50**, 158–175.

Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Marine Ecology Progress Series*, **495**, 39–47.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Hedge's g effect sizes used in the analyses for functional matching and density dependency (extracted from Figure S3.5 in 1). To ensure causality between seaweeds and responses, only manipulative experiments were included. Effect sizes (ES#) 1–18 and 19–27 were classified as samples collected 'below the seaweed' or 'including the seaweed structure itself', respectively. Meta-analyses were conducted in Meta-win 2.0 following the procedures of Thomsen *et al.* (2); i.e., we interpreted factorial and nested experiments as multiple independent experiments, compared the most extreme contrast from multiple-density experiments, calculated bias-corrected confidence limits, and ran unweighted analyses. See footnotes for further details.