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The matrix influences direct and indirect effects of an anthropogenic disturbance on marine organisms

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ABSTRACT

The magnitude and direction of direct and indirect effects of disturbances can be context-dependent, with the matrix (surrounding habitat) in which populations are embedded either mitigating or worsening the impacts of disturbances. Chemical disturbances are particularly harmful and can affect organisms directly or indirectly. We used bleach, a common stressor in marine systems, to test hypotheses about direct and indirect effects of anthropogenic disturbances on intertidal grazers and the influence of the surrounding macro-algal matrix on such effects. We manipulated the contaminant, food (biofilm) and surrounding macro-algal matrix. Fewer limpets were found in contaminated areas. Bleach had a strong direct negative effect on limpets and caused a reduction in biofilm food, indirectly affecting limpets. This effect was strongest in the presence of macro-algal matrix. Anthropogenic disturbances can have major consequences via direct and indirect effects on key interacting species. We showed that such effects are, however, context-dependent. Capsule: Pollution is a major driver of biodiversity declines. We show that direct and indirect effects of contaminants on organisms depend on the context in which they occur.

1. Introduction

Disturbances play a major role in the structure and dynamics of communities (Dayton, 1971; Pickett and White, 1985; Sousa, 2001) and their effects may be manifested directly and/or indirectly (Wootton, 1994). Disturbances directly influence organisms, for example, by killing them or by restricting their opportunities to feed or reproduce. By altering availability of resources, however, disturbances can influence interactions among organisms and other important ecological processes in complex ways, resulting in indirect effects (Menge, 1976; Underwood et al., 1983).

Anthropogenic disturbances, such as pollution, can alter (directly or indirectly) a regime of natural disturbance by affecting the resilience and/or stability of populations and assemblages to natural disturbances (reviewed by Underwood, 1989). As with natural disturbances, anthropogenic disturbances can affect organisms, populations or assemblages directly or indirectly, through various ecological processes and interactions (Fleeger et al., 2003; Underwood, 1989). Interactions among species play a central role in structuring the ecological and evolutionary patterns in many natural and human-impacted systems. It is therefore expected that anthropogenic disturbances on one or more species would also indirectly affect other species, particularly where the species primarily affected is involved in strong interactions. Further, because indirect effects may also offset or exacerbate direct effects (Fleeger et al., 2003; Wootton, 1994), the modes of action of anthropogenic disturbances need to be understood for the consequences of disturbances to be interpretable.

The direction and magnitude of direct and indirect effects of disturbances may, however, depend on the context in which they occur. The structure of surrounding habitats, or the 'matrix' in which organisms occur, can influence biodiversity, resource utilisation and dispersal (e.g. Crowe, 1996; Goodsell and Connell, 2008; Matias, 2013; Ricketts, 2001). Specifically, in terms of dispersal, the matrix can either act as a barrier, or it can provide suitable structure for organisms, facilitating their dispersal by allowing movement across habitats and subsequent colonisation into new habitats (Gascon et al., 1999; e.g. Johnson et al., 1992). Disturbances that modify the matrix can therefore have significant, indirect effects on mobile organisms (Goodsell and Connell, 2005; Syms and Jones, 2000).

Limpets are important structuring organisms on temperate rocky shores (e.g. Branch, 1981; Lubchenco and Gaines, 1981;

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Underwood, 1980). Their grazing modifies the ecological "state" of a shore (bare rock vs. macro-algal dominance), their removal leading to a marked shift in assemblages composition and their spatial variability (Hawkins, 1981; Hawkins and Hartnoll, 1983; Hawkins et al., 1992; Underwood, 2000; Underwood and Jernakoff, 1984). Microbial films (i.e. biofilms, including cyanobacteria, propagules of macro-algae, diatoms, etc.) are the main source of food of limpets (see reviews by Branch, 1981; Hawkins et al., 1992), although macro-algae, where available, are used by some species (Davies et al., 2007; Notman, 2011). In addition, macro-algae can influence the distribution and abundance of limpets on rocky shores (Moore et al., 2007), as well as their competitive interactions (Marzinelli et al., 2012), having positive or negative effects on these gastropods. Macro-algae can mitigate effects of stressors, providing habitat and food for the animals (Hartnoll and Hawkins, 1985). On the other hand, macro-algae can negatively affect limpets, by occupying the substratum, pre-emptively outcompeting them for space on which to live and by making them more susceptible to dislodgement when moving along the rocky shore because they have no hard substratum on which to attach (Underwood and Jernakoff, 1981). Disturbances affecting key components of these systems (i.e. limpets, micro-, and macro-algae) can therefore have strong direct effects, but also important indirect or cascading effects.

The threat posed by contaminants worldwide is large and increasing (Crain et al., 2008). Contaminants are linked to declines in global biodiversity (Grey et al., 1990; Johnston and Roberts, 2009) and reductions in ecosystem functioning (Johnston et al., in press). The strength of impacts of disturbances by contaminants is, however, likely to be context-dependent, i.e. influenced by the matrix in which disturbances occur (see above).

We used bleach as a model contaminant to test hypotheses about direct and indirect effects of chemical disturbances on natural populations and the importance of the context (i.e. the surrounding matrix of habitats) on such effects. Bleach (sodium hypochlorite) has been used for at least 100 years in households and is a common type of contaminant on coastal systems through runoffs and storm-water drains worldwide (Carballeira et al., 2012; Moreira et al., 2010). It has, therefore, the potential to affect rocky intertidal systems via a series of direct and indirect effects.

Bleach caused a reduction in the abundance of limpets (see Section 3). This could be the result of direct effects on these gastropods, due to the toxicity of the contaminant, or indirectly, via changes in the abundance or palatability of microalgae. We predicted, therefore, that if the observed decrease of limpets was due to an indirect effect of the chemical disturbance via changes in the abundance of microbial films, areas where films were manually reduced would show similar reductions in numbers of limpets as in areas exposed to the contaminant. In contrast, if bleach was directly affecting limpets, we predicted that contaminated areas would end up with fewer limpets than control areas, even where biofilms were in natural condition. Indirect effects on limpet survival via the reduction of food are likely to take longer to occur than direct effects. However, the lack of food would presumably cause greater foraging by limpets, resulting in an immediate response (e.g. Mackay and Underwood, 1977). If this is the case, the presence of the macro-algal matrix would, in turn, negatively affect the survival of these foraging limpets by making them more susceptible to dislodgement when searching for food (Underwood and Jernakoff, 1981). To examine any influence of the matrix, we also manipulated surrounding macro-algae. We predicted that effects of bleach on limpets would be greater in areas surrounded by macro-algae.

2. Methods

2.1. Effects of chemical disturbances on limpets

The experiment was done at two sites on a moderately exposed rocky shore in the Cape Banks Scientific Marine Research Area in Botany Bay, Sydney, Australia (33.59°S; 151.14°E). Assemblages were composed of barnacles, several species of limpets, such as *Cellana tramoserica* and *Patelloida* spp. and macro-algae, including the genera *Corallina*, *Cladophora*, *Enteromorpha,* and *Ectocarpus*. Twelve 30 cmx30 cm quadrats were haphazardly chosen in each site and assigned randomly to three treatments ($n=4$ per treatment per site): (i) addition of bleach: a solution of bleach (25 g l^{-1} in freshwater) was sprayed for 10 s, totalling approximately 100 ml per quadrat per application (i.e. approx. 2.5 g per quadrat); (ii) procedural control: freshwater was sprayed in the same manner as the contaminant, and (iii) unmanipulated. The contaminant "30s" (50 g l^{-1} sodium hypochlorite; 30s Limited, New Zealand) was prepared at a concentration of 1:1 biocide/fresh-water following the manufacturers instructions and was applied at 30–50 cm from the substratum using a manual pump sprayer (Garden Sprayer, Hills, Australia) with a Bent Lance and Nozzle (code BH220384). This design allowed us to simulate a pulse disturbance on rocky-shores, such as those caused by storm-water drains and sewage and cooling systems discharges. The contaminant and procedural control solutions were applied every two weeks from November 2006 until February 2007.

2.2. Direct vs. indirect effects

This experiment was done at one site at Cape Banks. Eight plots of 1.1×1.1 m^2 were haphazardly marked in an area of the shore exposed only by low Spring tides, avoiding areas with rock pools or big crevices that could have affected distribution and movement of limpets and may have caused bias in the study. In 4 of the plots, all macro-algae were removed using scrapers. In the remaining 4 plots, macro-algae (mainly turf-forming algae) were left undisturbed. In 2 plots of each type (i.e. with or without macro-algal matrix), bleach was sprayed throughout the plot for 10 s as described above, once limpets were added (see below). In each plot, 4 quadrats of 14 cmx14 cm were marked. In plots with macro-algae, these quadrats were carefully scraped to remove macro-algae prior to the application of bleach. Quadrats were at least 30 cm apart and at least 20 cm from the edges of the plots. Biofilm was then reduced in two of the quadrats inside each plot by applying hydrochloric acid (330 g l^{-1}) twice. The experimental design consisted, therefore, of replicated plots with three orthogonal factors: $+/-$ macro-algal matrix (M), $+/-$ contaminant (C) and $+/-$ biofilm (B). Plots were nested in the combinations of macro-algae and contaminant.

To test whether the application of acid did actually reduce the amount of biofilm inside the quadrats, amounts were measured using a Diving PAM (Pulse Amplitude Modulated, WALZ, Germany) on the last day of each experiment. This technique is rapid, non-invasive and non-destructive (Consalvey et al., 2005). PAM measurements were taken from quadrats with or without biofilm and bleach ($n=8$). Before each measurement, the sampled areas were dark-adapted for 15 min. The measurements used in this study were F_o, the minimal fluorescent yield and F_v/F_m, which measure the maximal light utilisation efficiency measured in the dark. PAM has been considered a good method to evaluate the effects of contaminants on *chlorophyll-a* (Juneau et al., 2007). In addition, a linear relationship between F_o and *chlorophyll-a* has been established in situ and in the laboratory (Serodio et al., 1997, 2001), with increased *chlorophyll-a* causing increased intensity of the fluorescence signal (Consalvey et al., 2005). Photosynthetic