

Causes and ecological consequences of a climate-mediated disease

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ABSTRACT

As global climates change, the incidence and severity of diseases in natural ecosystems also appears to be increasing. This has been linked to increasingly stressful conditions, which can lead to more susceptible hosts and environmental effects on pathogen abundance and virulence. Recently, environmentally-mediated diseases have affected a diverse range of both terrestrial and marine organisms. The ecological impacts of diseases are likely to be more severe when they affect habitat-forming organisms like trees, corals and seaweeds, as any impacts could cascade throughout entire communities. In marine environments, organisms are exposed to persistently high densities of potentially pathogenic microorganisms, which can affect habitat-formers like corals and seagrasses. On temperate rocky reefs, the dominant habitat-formers are seaweeds. Here we review recent work on a chemically defended seaweed, and a bleaching phenomenon common in natural populations near Sydney, Australia. The prevalence of bleaching is positively correlated with water temperature and negatively correlated with concentrations of secondary metabolites in the alga, which are known to inhibit bacteria. Bleaching is associated with a shift in the composition of microbial communities on algal surfaces and can be induced via exposure to ambient seawater microbes and cultures of putative pathogens. Direct consequences of bleaching include reductions in algal growth and fecundity. Bleaching also has indirect ecological effects on the alga, with bleached individuals attracting higher densities of herbivores and preferential consumption of bleached tissues. This environmentally-mediated bleaching phenomenon appears to be the result of complex interactions between increasing ocean temperatures, host defences and pathogen virulence and has significant implications for this habitat-forming organism and the community it supports.

Key words: climate change, macroalgae, disease, pathogen, chemical defences, trophic interactions, sub-lethal effects

Introduction

As climates change and habitats are modified, disease is emerging as a major threat to biodiversity (Harvell *et al.* 2002). The rapid rates of current environmental change are unparalleled in recent history (Huntley 1991) and can cause physiological stress and overwhelm the capacity of many organisms to adapt (Chapin *et al.* 1993). Stressed organisms typically have depleted defences against natural enemies including pathogens and are thus more susceptible to disease (e.g. Banin *et al.* 2000; Raffel *et al.* 2006). Although many animals and plants can reduce stress by responding phenotypically (e.g. through behavioural or phenologically plastic responses), when conditions change rapidly, evolutionary adaptation may be difficult for organisms with long generation times. Besides affecting potential hosts, environmental change can also influence the abundance and virulence of pathogenic microorganisms (Lafferty 2009; Lafferty and Holt 2003), which, relative to macro-organisms, have shorter generation times (e.g.

Bell and Gonzalez 2009) and other mechanisms for rapid evolution, including horizontal gene transfer (Garcia-Vallve *et al.* 2000) and plasmid acquisition (Stephens and Murray 2001), in bacteria. These traits theoretically confer an evolutionary advantage under rapidly changing conditions, and as such, microorganisms (including bacteria) may be better equipped to deal with current rates of environmental change than most 'higher' organisms.

As a consequence of environmental influences on both hosts and pathogens, the frequency and severity of diseases in natural ecosystems appears to be increasing (Harvell *et al.* 1999). Disease has already affected diverse organisms, including marine mammals (Kennedy *et al.* 2000), amphibians (Pounds *et al.* 2006), trees (Eranen *et al.* 2009) and corals (Rosenberg and Ben-Haim 2002). Marine organisms may be particularly at risk of disease because seawater is an ideal medium for microbial dispersal and pathogen virulence (Ewald 1994) and contains persistently high densities of potentially

pathogenic microorganisms (Reinheimer 1992). In addition to warming, marine environments are also under threat from ocean acidification (Feely *et al.* 2004) and with higher proportions of global human populations living in coastal cities than at any time previous in history, other localised anthropogenic stressors, such as from pollution (Airoldi and Beck 2007).

The ecological consequences of disease can be catastrophic, resulting in mass mortalities of the affected organisms (e.g. Kennedy *et al.* 2000; Martin *et al.* 2002; Pounds *et al.* 2006). However, pathogens do not always kill their hosts but can instead have significant sub-lethal impacts on fitness and performance (e.g. Boots 2008; Gemmill and Read 1998). Lethal or otherwise, if disease affects ecosystem engineers like habitat-forming organisms or apex predators, it could have disproportionately important impacts on ecosystems, by altering trophic interactions throughout the food web of an ecosystem (Jackson 2001; Jackson *et al.* 2001). For example, the loss of reef-building corals due to bleaching, which can be disease-induced (Rosenberg *et al.* 2007) has impacts on fish assemblages (Bellwood *et al.* 2006; Booth and Beretta 2002) and benthic invertebrates associated with corals (Przeslawski *et al.* 2008).

On temperate rocky reefs, which fringe the southern half of the Australian coastline, seaweeds are the dominant habitat-forming organisms. Evidence of declines of kelp forests is emerging (e.g. Coleman *et al.* 2008; Connell *et al.* 2008; Edwards and Estes 2006; Steneck *et al.* 2002; Thibaut *et al.* 2005) from many parts of the world. If disease affects these macrophytes, any impacts have the potential to cascade through all trophic levels in the ecosystem. Large-scale die-offs have been observed in macroalgal systems and disease has been suggested as a potential cause of massive declines (40-100%) of the habitat-forming *Ecklonia radiata* in New Zealand (Cole and Babcock 1996), of *Laminaria religiosa* in Japan (Vairappan *et al.* 2001), and of coralline algae throughout the Pacific (Littler *et al.* 1995). However, these suggestions have been rarely confirmed or investigated further, and overall we have an extremely limited knowledge of the impact of disease on seaweeds.

We studied a bleaching disease that affects natural populations of an abundant, chemically-defended seaweed, *Delisea pulchra* in south-eastern Australia, a global-warming “hot-spot” (Ridgeway 2007). Large proportions of populations of *D. pulchra* are affected by a bleaching phenomenon (Campbell *et al.* 2011; Case *et al.* 2011), particularly when water temperatures are elevated. Here we provide a mini-

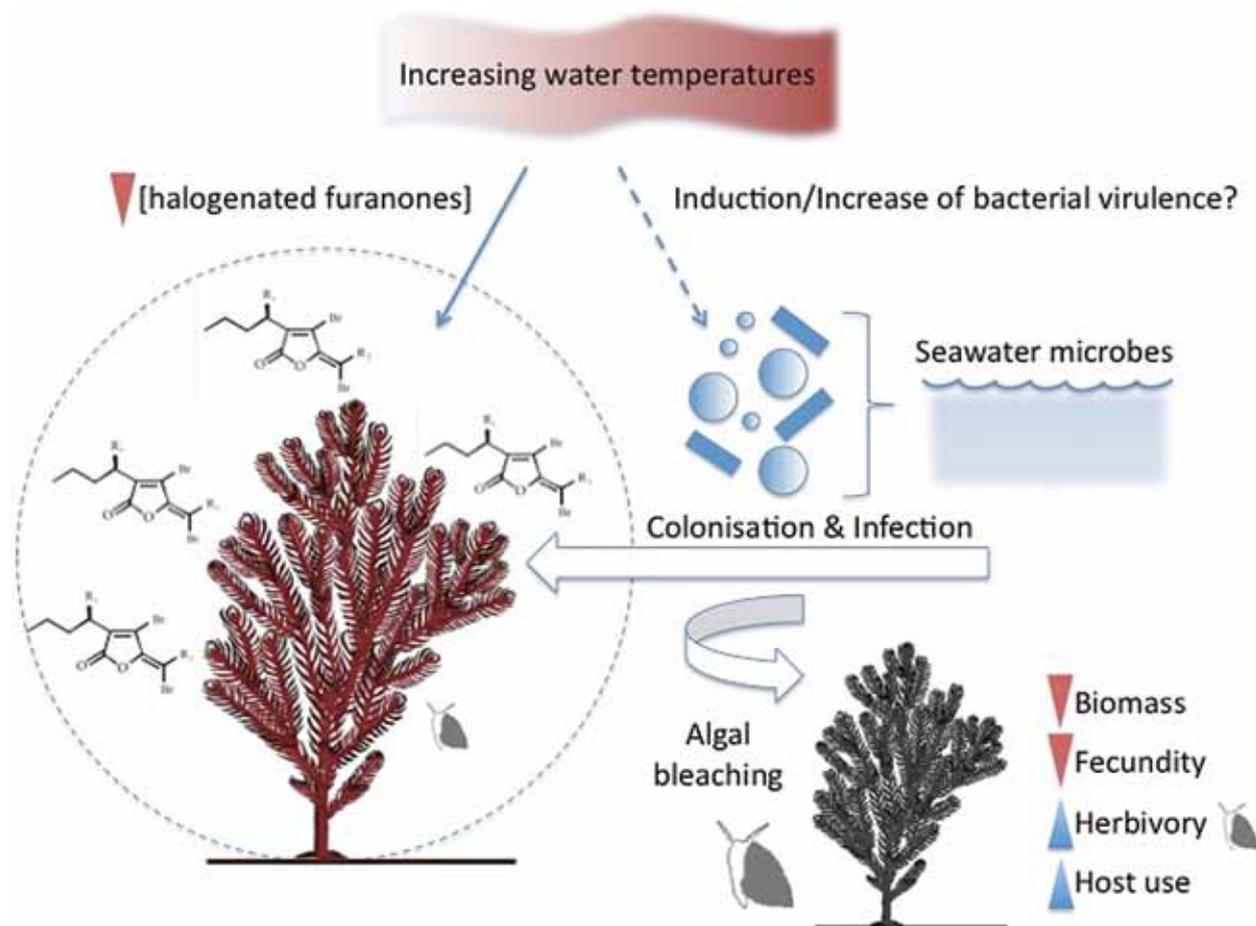


Figure 1. A conceptual model of the causes and ecological consequences of bleaching in *Delisea pulchra*: Environmental stressors cause a decrease in concentrations of halogenated furanones. This facilitates a shift in microbial communities associated with the algal surface and abiotic conditions may also induce or increase bacterial virulence. Pathogens colonise and infect *D. pulchra* and cause algal bleaching. Bleached algae are smaller and less fecund than healthy conspecifics and are also more likely to be consumed and used as a host by locally abundant herbivores.

review of recent work investigating algal bleaching and the interacting roles of bacterial pathogens, environmental variables and algal chemical defences. We also summarise a recent study into the consequences of bleaching on the survival and performance of *D. pulchra* and its interactions with locally abundant herbivores. Understanding the environmental and biological reasons behind declines of habitat-forming organisms such as seaweeds is essential for the management of these important natural resources and the ecosystems they support, particularly as environments continue to undergo rapid change.

Algal bleaching: links to warming oceans, pathogens and chemical defences

Over several years of monitoring populations of *D. pulchra* at two locations in 'deep' (7-10 m) and 'shallow' (1-4 m) water habitats, we found that the prevalence of bleaching in this seaweed was positively related to water temperature but not solar radiation, particularly in shallow waters, where temperatures were typically 1-2 °C warmer than at depth. The lack of correlation between the incidence of bleaching and light levels suggested that this phenomenon was not photo-bleaching, which has been observed in other algae (e.g. Scrosati and DeWreede 1998; Valentine and Johnson 2004). In fact, the patterns of bleaching suggested that bleaching was not the direct result of temperature, light or any other environmental variables. Both within populations and individuals, bleaching was non-uniform and patchy and not primarily at distal tips, suggesting that other, more complex mechanisms were involved in *D. pulchra*'s bleaching.

This seaweed produces secondary metabolites known as halogenated furanones (De Nys *et al.* 1993) and these compounds deter or inhibit many natural enemies including herbivores (e.g. Williamson *et al.* 2004; Wright *et al.* 2004; Wright *et al.* 2000) and bacterial pathogens (Manfield *et al.* 2001). The production of these compounds is energetically costly to the alga (Dworjanyn *et al.* 2006) and so it is likely that in suboptimal environments, algae may be less chemically-defended than when conditions are ideal. Over three years, levels of halogenated furanones were lowest when bleaching was most prevalent (Campbell *et al.* 2011). Similarly, bleached individuals had much lower levels of furanones than healthy conspecifics and the reduction in chemical defences was evident across the entire thalli of bleached algae, (e.g. not limited to visibly bleached sections, Campbell *et al.* 2011). Thus, algae were less well defended from pathogens during periods when bleaching was most common.

Interactions between plants, algae and their natural enemies are often chemically-mediated (Alexander 1992; Biere *et al.* 2004; Engel *et al.* 2002; Hay 1991; Steinberg *et al.* 2002). To establish whether halogenated furanones can protect *D. pulchra* from bleaching, we experimentally inhibited the production of these chemical defences in cultured sporelings (Case *et al.* 2011; Dworjanyn *et al.* 2006) and exposed them to natural seawater in the field. In this series of experiments, undefended sporelings

bleached significantly more than defended conspecifics, demonstrating that furanones play a protective role against bleaching in *D. pulchra* (Campbell *et al.* 2011). In natural populations of *D. pulchra*, concentrations of halogenated furanones are highly variable (Campbell *et al.* 2011; Wright *et al.* 2000) and so our ability to manipulate them provides a powerful tool with which the importance of chemical defences can be directly tested experimentally, and these were the first experiments to do so *in situ* for any seaweed.

Given concurrent observations of bleaching and furanone depletion and the experimentally demonstrated protective role of halogenated furanones against bleaching, we hypothesised that bleaching may be the result of an opportunistic bacterial infection in susceptible (furanone-depleted) algae. In marine ecosystems, the early stages of disease are often associated with shifts in microbial consortia associated with the surfaces of host organisms (e.g. Frias-Lopez *et al.* 2002; Pantos *et al.* 2003). We thus characterised surface-associated microbial communities (SAMCs) on algal surfaces using PCR-based DNA fingerprinting techniques and found that bleached algae supported very different SAMCs than healthy conspecifics. This pattern was consistent across locations and depths and throughout all years of the study (Campbell *et al.* 2011). Notably, within bleached thalli, unbleached sections adjacent to visibly bleached parts of thalli represented a 'transition community' that was not statistically different to 'bleached' or 'healthy' SAMCs (Campbell *et al.* 2011). These results suggested that microbial communities associated with the surface of *D. pulchra* shifted in response to furanone depletion in algal tissues (which occurred thallus-wide), prior to visible bleaching. Without further experimental manipulations, it is difficult to elucidate whether the microbial community shifts we observed occurred prior to or in response to bleaching. However, our concurrent observations of depleted furanones on adjacent unbleached tissues supporting 'transition' microbial communities suggest, albeit correlatively, that visible bleaching occurs after microbial communities change.

To test this idea and the hypothesis that bleaching is a temperature-mediated bacterial infection that can be prevented by algal chemical defences, we exposed defended (furanone-containing) and undefended (furanone-depleted) sporelings to water temperatures representing low (19-20 °C) and high (25-26 °C) summer temperatures and to high and low bacterial abundances. We found that sporelings maintained in natural seawater with ambient microbes bleached more frequently and severely than conspecifics maintained in sterile artificial seawater and that this was more severe in sporelings lacking halogenated furanones than defended algae. This work supported that of Case *et al.*, (2011), who showed that furanone-depleted sporelings were more susceptible to biofilm formation and bleaching at high temperatures when inoculated with a specific bacterium isolated from *D. pulchra in situ*. These results are consistent with the premise that bleaching in *D. pulchra* is the result of a bacterial infection(s) and that this putative disease is more common and severe when water temperatures are elevated. This work also

provokes questions that should be the focus of future work addressing bleaching in this chemically defended seaweed, regarding the mechanistic relationships between increasing water temperatures and (i) the production or maintenance of halogenated furanones by *D. pulchra* and (ii) the induction or enhancement of bacterial virulence.

More broadly, the effects of increased temperatures on algal chemical defences are not well understood. The limited information available comes from studies on the effects of warming on terrestrial plant defences and suggests that effects are likely to be plant and compound specific (reviewed by Bidart-Bouzat and Imeh-Nathaniel 2008). More is known about the effects of warming on bacterial survival, growth, dispersal and virulence (Klinkert and Narberhaus 2009), with many pathogens having temperature-regulated virulence traits (Bally and Garrabou 2007; Banin *et al.* 2000; Konkel and Tilly 2000). In general, the environment can strongly influence microorganisms (Lafferty 2009; Lafferty and Holt 2003) and a significant shift in prevailing environmental conditions can even induce virulence in previously innocuous microorganisms (e.g. Vergeer and den Hartog 1994). Such effects are likely to be species-specific and more investigation into how predicted environmental change may influence chemically-mediated host-pathogen interactions is required, particularly when important ecosystem engineers are involved.

Consequences of bleaching

In order to assess the consequences of bleaching on affected *Delisea pulchra* individuals, we tagged several hundred healthy algae in early spring (before widespread bleaching was observed) and monitored them approximately fortnightly for six months (Campbell 2011). Algae in deep and shallow waters at two locations were tagged. We recorded algal survivorship and performance, the latter by monitoring condition (i.e. whether or not they bleached) and estimating biomass (Campbell 2011). Bleaching did not have any consistent or negative effects on algal survival, but had important effects on algal biomass, with bleached algae being smaller at the end of the season than conspecifics that had remained healthy throughout. This suggests that either bleached algae grew more slowly than healthy conspecifics and/or that bleached thalli suffered breakage throughout the study. In addition, bleaching may also have important negative impacts on the reproductive success of affected individuals, an impact observed in other host-pathogen interactions (Burdon 1987; Myers and Kuken 1995; Sait *et al.* 1994). Since biomass is positively related to fecundity in *D. pulchra* (Campbell 2011) a reduction in biomass will have a negative effect on reproductive output, as with many other seaweeds (e.g. Graham 2002; Santos and Duarte 1996). Moreover, any increased thallus breakage in bleached algae will also lead to the loss of distal tips, where reproductive structures are located.

In general, host organisms can display multiple mechanisms to resist, recover from or tolerate diseases

(Boots 2008; Kover and Schaal 2002; Medel 2001). Terrestrial plants and algae can respond locally to pathogen attack by producing reactive oxygen species known as the hypersensitive response (Dring 2006; Lamb and Dixon 1997). Many seaweeds also have other constitutive and inducible chemical defences against natural enemies (Schnitzler *et al.* 2001; Sotka *et al.* 2002; Steinberg *et al.* 1997). In this host-pathogen system, *D. pulchra* may resist bacterial bleaching by producing halogenated furanones (Campbell *et al.* 2011, subject to revision). The production of halogenated furanones is heritable and potentially selected for by herbivores (Wright *et al.* 2004), but can also be energetically costly (Dworjanyn *et al.* 2006). As such, the absence of negative effects of bleaching on survivorship in *D. pulchra* suggests that this seaweed may have multiple mechanisms in place, initially to resist bleaching pathogens, and later, to tolerate bleaching when it does occur (although, with significant performance, and possibly also fitness costs; Campbell 2011).

As an ecosystem engineer, *D. pulchra* provides a food source and habitat for many other organisms, so we further aimed to examine whether bleaching had any impact on its interactions with locally abundant herbivores (Campbell 2011). To first assess whether bleaching affects *D. pulchra*'s role as a habitat-former, we destructively sampled thirty replicate bleached and healthy algae from two locations and quantified the abundance of three common herbivores (the gastropod *Phasianotrochus eximius*, the urchin *Holopneustes purpurascens* and the sea hare *Aplysia parvula*) known to inhabit and consume the alga (Rogers *et al.* 2003; Williamson *et al.* 2004; Wright *et al.* 2004; Wright *et al.* 2000). Bleached algae supported significantly higher abundances of herbivores than healthy conspecifics and this pattern was observed at both locations, suggesting that these mesoherbivores may preferentially choose bleached algae as hosts instead of healthy individuals (Campbell 2011).

To investigate whether bleaching affects consumption of *D. pulchra*, we offered these herbivores (*P. eximius*, *H. purpurascens* and *A. parvula*) a choice between bleached and healthy algal tissue and measured algal mass loss. Herbivores generally showed a strong preference for bleached tissue over healthy tissue (Campbell 2011). This work provided experimental evidence of an environmentally-mediated putative disease influencing trophic interactions (both host use and consumption) between a marine alga and its herbivores. It also raised some interesting questions about the potential role of herbivores in the development and spread of bleaching in this seaweed. Consumers can act as transmission vectors or pathogen reservoirs for infectious diseases (e.g. Sussman *et al.* 2003) and damage inflicted by herbivores can facilitate disease by providing infection sites (Borer *et al.* 2009). Indeed, an entire suite of plant defences have evolved to manage herbivory wounds (Ross *et al.* 2006; Ruuhola and Yang 2006) and this would be an interesting avenue of future research into the bacterial bleaching of *D. pulchra*.

Conclusions

Bleaching in this chemically-defended seaweed appears to be the result of interactions between environmental variables, the production of chemical defences and microbial pathogens. This work highlights the complex ways in which environmental change can influence organisms, populations and communities and emphasises the need to understand the mechanisms by which climate change or other anthropogenic disturbances can impact ecosystems. In this case, bleaching did not have negative impacts on algal survival, however it did have significant sub-lethal performance consequences for affected individuals and

also influenced *D. pulchra*'s role in the ecosystem, both as habitat and food. Further research into how environmentally-mediated changes in one organism may affect its interactions with others would be valuable, particularly when habitat-formers, which have a disproportionate importance in ecosystems, are involved. Finally, given the apparent increase of diseases in natural systems (Harvell *et al.*, 2002), investigations into the effects of changing climates on organisms and ecosystems need to consider the potential influence of microorganisms, especially as environments become more stressful and many macro-organisms more susceptible to attack.

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