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Disentangling settlement responses to nutrient-rich contaminants: Elevated nutrients impact marine invertebrate recruitment via water-borne and substrate-bound cues

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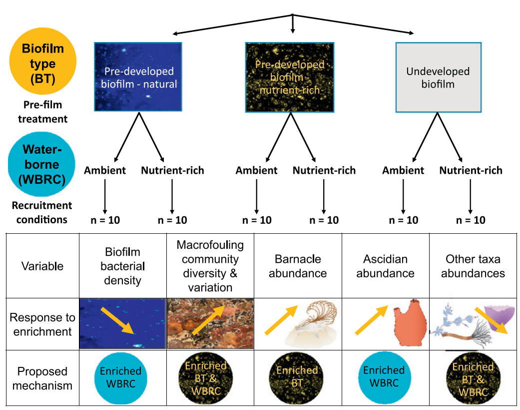
HIGHLIGHTS

- Nutrients from fertiliser affect biofilm and macrofouling communities.
- Nutrients affect invertebrate recruitment at community and taxonomic group levels.
- Water-borne nutrients increased ascidian and barnacle recruitment.
- Direct and indirect nutrient impacts could select for specific macrofouling groups.
- Excess nutrient inputs alter community structure and may affect ecosystem function.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic contaminants, including nutrient enrichment, frequently alter environmental conditions in marine systems and affect the development of communities on hard-substrata. Biofilms can influence the settlement of marine invertebrates and hence impact on the structure of fouling communities. Few studies have examined bacteria, invertebrates and nutrient-rich contaminants in concert, with none yet to examine the effects of nutrient-rich contaminants on both biofilms and the recruitment of sessile invertebrate communities in-situ to ascertain the mechanistic basis behind observed impacts. Biofilm treatments were allowed to develop under manipulated environmental conditions of either ambient or enriched nutrient levels. Enrichment conditions were elevated via slow-release fertiliser and invertebrate recruitment was prevented during initial biofilm development. Biofilm treatments (including a no film control) were then subject to either ambient or enriched water-borne nutrients (in a fully-factorial design) during a period of invertebrate colonisation in the field. Effects of nutrient-rich contaminants on invertebrate recruitment were observed as changes to community composition and the abundances of taxonomic groups. Communities on no biofilm control treatments differed from those with pre-developed biofilms. Naturally developed biofilms promoted recruitment by all organisms, except barnacles, which preferred nutrient-enriched biofilms. Water-borne nutrients increased the recruitment of ascidians and barnacles, but suppressed bryozoan, serpulid polychaete and sponge recruitment. The direct and indirect impacts observed on biofilm and invertebrate communities suggest that increasing nutrient levels via nutrient-rich

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contaminants will result in structural community shifts that may ultimately impact ecosystem functioning within estuaries.

1. Introduction

Identifying, deciphering and understanding the effects of contaminants on interacting biological components is one of the most important challenges facing environmental managers and scientists. Anthropogenic activities threaten many natural systems by increasing contaminant inputs (Borja et al., 2008) that induce a variety of responses in biological organisms (Folt et al., 1999; Johnston et al., 2015; Johnston and Roberts, 2009). This can impact on the diversity (Johnston and Roberts, 2009) within and function (Johnston et al., 2015) of a system. However, causal relationships between contaminants and biological components can be obscured by biotic and abiotic factors that mediate how organisms respond. There is therefore a need for experimental field-based contaminant impact assessments to test and disentangle causal relationships between contaminants and complex system or community effects.

Hard-substrate marine communities, including microbes and macrofouling invertebrates, represent a major component of marine biodiversity and are commonly used to assess contaminant impacts on estuaries. Developing community structure is regulated by recruitment, competition, and mortality (Gaines and Roughgarden, 1985; Lawes et al., 2016a; Minchinton and McKenzie, 2008), which can be affected by contaminants. For example, larval recruitment can be sensitive to contaminants (Johnston and Keough, 2000; Johnston and Keough, 2002; King et al., 2006), while ongoing community development reflects the time-integrated effects of contaminants on species interactions (Johnston and Keough, 2003). The structure of these communities is further influenced by biotic and abiotic factors, such as competition and temperature (Bracewell et al., 2017). Changes occurring in constituent populations are reflected by shifts within community structure (Attrill and Depledge, 1997; Lawes et al., 2016a; Lawes et al., 2017; Lawes et al., 2016b). As a result, experimentally manipulated invertebrate communities are excellent models to predict and identify responses that might be transferable to the ecosystem-level (Attrill and Depledge, 1997; Johnston and Keough, 2002).

Recruitment of marine invertebrates can be strongly influenced by biological settlement cues (Hadfield and Paul, 2001), which can be either water-borne (e.g. chemical cues in the water column) or substrate-bound (e.g. biological films). Many environmental and physico-chemical conditions contribute to cue efficacy (Kingsford et al., 2002) and can affect the induction or inhibition of larval recruitment. Environmental conditions are increasingly altered by fluxing anthropogenic inputs, such as the discharge of nutrient-rich contaminants, which can alter the physico-chemical characteristics within the water column (Elliott and Quintino, 2007) and also introduce novel compounds (Richardson and Ternes, 2014) into coastal systems. These contaminants can, directly or indirectly, affect community development through their effects on settlement cues (Minchinton and McKenzie, 2008). It is therefore important to understand how contaminants influence settlement cues and the consequent impact on larval recruitment and community dynamics. Deciphering the mechanistic basis behind these effects can inform the effective management of contaminants and coastal resources.

Water-borne cues are soluble compounds in the water column that trigger larval responses. They can induce larval settlement and indicate suitable habitat where post-settlement survival of larvae is maximised (Hadfield and Paul, 2001; Steinberg et al., 2002). Conversely, water-borne cues can also be inhibitory, such as those emitted by sessile organisms to deter other fouling organisms (Harder et al., 2004; Steinberg et al., 2002). While water-borne cues naturally exist within marine systems (Hadfield and Paul, 2001), laboratory studies have shown certain chemical compounds can artificially induce settlement behaviours in pelagic larvae (e.g. Degnan et al., 1997; Degnan and Johnson, 1999; Green et al., 2002; Jackson et al., 2002). Since novel compounds frequently enter coastal systems (Richardson and Ternes, 2014), they have the potential to alter environmental conditions and impact larval settlement, e.g. poor timing of settlement resulting in the colonisation of unsuitable substrates, or artificial signals may encourage the exploitation of new substrates. Such inappropriate induction of larval settlement, in turn, has the potential to affect the success or failure of larvae responsive to water-borne settlement mechanisms, and to impact the development of macrofouling invertebrate communities.

Substrate-bound cues are commonly associated with surfaces colonised by biological films (biofilms). Biofilms are microbial communities that rapidly colonise submerged surfaces comprising adsorbed macro-molecules, bacteria, diatoms and other microorganisms bound together by a matrix of extracellular polymers (EPS) (Dobretsov, 2009; Dobretsov et al., 2013; Wahl et al., 2012). Natural biofilms may strongly influence marine larval settlement via chemical cues emitted by predominantly by bacteria or groups of bacteria (Salta et al., 2013; Wieczorek and Todd, 1997) and differing cohorts of bacteria can produce different types of cues (Hadfield, 2011; Hadfield and Paul, 2001). Biofilms are sensitive to environmental conditions, including contaminant inputs, and changes in environmental conditions can impact bacterial community structure and subsequent recruitment (Dobretsov, 2009; Dobretsov et al., 2006). Given this sensitivity, the effect of anthropogenic contaminants on biofilms and the settlement cues they produce is an important area of research (Lawes et al., 2016b).

Estuarine and coastal systems are increasingly affected by nutrient-rich contamination as a result of urban and agricultural run-off, sewage and industrial activity (Kennish, 2002). Nutrient-rich contaminants have become a pertinent issue for coastal areas, with their input having the potential to alter the structure of microbial (Lawes et al., 2016b; Sun et al., 2012) and invertebrate communities (Courtenay et al., 2011; Lawes et al., 2016a; Lawes et al., 2017; Minchinton and McKenzie, 2008). In extreme cases, nutrient enrichment can stimulate productivity and oxygen consumption, causing eutrophication and hypoxia (Selman and Greenhalgh, 2009a). Nutrient-rich contaminants can also affect invertebrate settlement and colonisation. For example, enrichment via elevated nutrient levels have been positively correlated with barnacle and ascidian recruitment (Courtenay et al., 2011; Lawes et al., 2016a) and generally greater abundances and biomass of sessile invertebrates (Clark et al., 2015). Moreover, Courtenay et al. (2011) promote the use of barnacle abundance as an indicator of urban run-off and sewage contamination within estuaries. As coastal activities escalate, nutrient-rich contaminants are increasingly expected to enter estuarine systems, with consequent impacts on recruitment and associated ecological effects.

Qian and Dahms (2008) introduced a conceptual triangular framework to describe the interactive relationship between environmental conditions, biofilm bioactivity, and the mediation of larval recruitment. They further acknowledge that no studies link nutrient enrichment, biofilms, and colonisation in situ. Few studies have examined bacteria, invertebrates and nutrient-rich contamination in concert (Chiu et al., 2008). To our knowledge, this relationship has not been investigated under field conditions, so this field study aims to examine the effects of nutrient-rich contaminants from fertiliser on both biofilms and the recruitment of sessile invertebrate communities. We have previously developed biofilms under different nutrient regimes and this revealed