Ecological Indicators 89 (2018) 74–83

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Effects of salinity and flow interactions on macroinvertebrate traits in temporary streams

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ARTICLE INFO

Keywords:
Flow
Salinity
Interaction
Temporary streams
Trait
Macroinvertebrate

ABSTRACT

Increasing salinity in freshwater ecosystems is globally widespread, especially, in arid and semi-arid regions, and can co-occur with flow intermittency, particularly in temporary streams. Both these stressors are known to affect macroinvertebrate traits individually, but their interactive effects have not been previously considered. There are inconsistencies reported in the literature regarding the response of particular traits to flow or salinity, and accordingly, we hypothesized that interactive effects between these two stressors may underlie inconsistencies in the literature. We used multivariate and univariate approaches to investigate the effects of salinity and flow interactions on macroinvertebrate traits using 13 years of data sampled across multiple sites in South Australia, the driest state in the driest inhabited continent in the world. Ovoviviparity, multivoltinism, aerial respiration and strong fliers were favoured as salinity increased, while medium-high physiological sensitivity to salinity and respiration via gills decreased. During low flows, holometaboly, univoltinism, high rheophily, cool eurythermality, streamlined body shape and gill respiration decreased, while aerial respiration and fliers and high crawling rate increased. Interestingly, traits with inconsistent responses (e.g. burrowing, tegument respiration and collector-gathering traits) in the literature were associated with interactions between flow and salinity in our study. These traits showed a similar interaction, by being least abundant in streams with high salinity and low flows, and low salinity and high flows. The interactions seem to be driven by the differential response of different taxa with the same trait category being abundant in different parts of the interaction plot. Our findings suggest that, in addition to differences in methodological and analytical approaches, interactions may also underlie inconsistencies in trait responses to flow and salinity. Finally, to foster the operative use of traits to resolve the effects of multiple stressors on ecosystems, there is the need for a better mechanistic understanding of how specific stressors (e.g. flow and salinity) act as trait filters, potentially through the use of experiments, to ensure that each of the stressors is strong enough to produce clear trait responses.

1. Introduction

Flow intermittency and salinity characterise temporary streams and, when studied separately, are held to be major drivers of aquatic communities in dry environments (Williams, 2002). Surprisingly, few studies address the combined or interactive effects of these stressors despite their known, separate effects on biodiversity and functioning of aquatic ecosystems (Moreno et al., 2010), including nutrients and water cycling (Arscott et al., 2010; Herbert et al., 2015). Furthermore, the generality of applying the results of many flow and salinity studies on aquatic invertebrates to other regions is limited by the biogeographic variability in taxonomic composition (McGill et al., 2006). Thus, comparable approaches, incorporating flow and salinity simultaneously, across study regions are essential to understand the effects of salinity and flow. In this study, we address this critical knowledge gap by tackling the individual and interactive effects of salinity and flow on macroinvertebrate traits across a large spatio-temporal scale in South Australia.

The effect of increased salinity (Schroder et al., 2015) and flow intermittency (Palmer et al., 2015) have traditionally been assessed

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https://doi.org/10.1016/j.ecolind.2018.01.036
Received 4 April 2017; Received in revised form 19 January 2018; Accepted 21 January 2018
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using taxonomically-based methods (macroinvertebrate identities, abundance and distribution), but comparisons and generalisations are difficult because different taxa occupy similar ecological niches in different biogeographic regions (Poff et al., 2006). Furthermore, taxonomically-based methods are often limited in their ability to distinguish mechanisms of impact (Townsend et al., 1997) and thus, are unable to distinguish the importance of different stressors or effects of multiple stressors (Wooster et al., 2012). In contrast, biological traits can provide a mechanistic understanding of stressor impacts (McGill et al., 2006), and therefore have the potential to identify the importance of different co-occurring stressors that influence different aspects of the environment (Statzner and Bêche, 2010). Therefore, macroinvertebrate traits have been proposed as an alternative approach to use (McGill et al., 2006). This potential for traits to be for traits to be used to identify the effects of multiple stressors (e.g. flow and salinity) on freshwater ecosystems may be useful because managers of these systems typically have multiple restoration options, and need decision support tools to make well-informed decisions about budget allocations for particular restoration measures (Niemi and McDonald, 2004).

Many studies have examined relationships between flow and macroinvertebrate traits (e.g. Bêche and Resh, 2007; Chessman, 2015; Walters, 2011), but fewer have examined relationships with salinity (e.g. Díaz et al., 2008; Szöcs et al., 2014). For flow, the most commonly documented patterns are that high flows favour traits such as slower maturation, high rheophily, low thermophily, holometaboly, lack of body armouring (not sclerotized) and filter feeding (e.g. Bêche and Resh, 2007; Chessman, 2015; Walters, 2011). Increased salinity promotes predators, multivoltinism, aerial respiration, aerial dispersal and ovoviviparity (e.g. Díaz et al., 2008; Szöcs et al., 2014). However, some traits are equivocal or show inconsistent responses between studies. For instance, during low flows, Brooks et al. (2011) found an increase in the prevalence of tegument (cutaneous) respiring taxa, while Bonada et al. (2007) reported the opposite response. Similarly, Walters (2011) found that low flows promoted burrowers, while Bonada et al. (2007) found fewer burrowers under low flows. During increased salinity, Vidal-Abarca et al. (2013) found an increase in the prevalence of tegument respiration while Szöcs et al. (2014) reported the opposite response. It is possible that such inconsistencies may reflect interactions between flow and salinity as these two stressors are commonly linked. For example, the major environmental impact of flow intermittency can include decreased flow permanence, increased sediment deposition, increased water temperatures, low dissolved oxygen and loss of some habitats (Dewson et al., 2007), while impacts of salinization include increased temperature, low dissolved oxygen and loss of riparian habitats (Schroder et al., 2015). Thus, these two types of stressors have similar environmental impacts: both are expected to increase water temperature, decrease habitat complexity and reduce dissolve oxygen content, which suggests that their effects could potentially interact. Importantly, there have been no studies focussing on the relationships of both salinity and flow with traits, especially across multiple catchments.

One of the reasons for a paucity of studies simultaneously addressing effects of salinity and flow on invertebrate traits, especially in dry environments, is that flow is often inversely correlated with salinity (Brock et al., 2005). To better understand the combined effect of salinity and flow on macroinvertebrate traits, it is therefore necessary to study a full range of both factors. Such information is critical for identifying how both factors shape the structure and functioning of aquatic communities in dry environments.

Our study area in southern South Australia constitutes a gradient from Mediterranean through to arid, warm temperate climates, with flow conditions ranging from permanent to ephemeral. Temporary streams are abundant (Laut et al., 1977) and include a variety of combinations of flow and salinity. Aquatic invertebrates in this region have been exceptionally well sampled (13 sites, sampled bi-annually for 13 years) and thus present an ideal data set to test the response of traits to salinity and flow.

Here we aim to identify the effects of salinity, flow and the interactions between them on the trait structure of macroinvertebrate communities. Based on the literature we surveyed, we expected high flows to favour traits such as univoltinism, holometaboly and high rheophily (e.g. Bêche and Resh, 2007; Chessman, 2015; Walters, 2011), while increased salinity was expected to promote predators, ovoviviparity and multivoltinism (e.g. Díaz et al., 2008; Szöcs et al., 2014). We also hypothesised that interactions between salinity and flow could explain some of the contradictory patterns observed in the trait literature regarding how some traits (e.g. tegument respiration, burrowing and collector-gathering) respond to flow and salinity separately.

2. Methods

2.1. Study area and macroinvertebrate sampling

Our study sites were distributed on Kangaroo Island (Rocky River), Fleurieu Peninsula (Finniss, Marne and Bremer Rivers), throughout the Mount Lofty Ranges (MLR) [Western MLR: Hindmarsh, Torrens, North Para, Myponga and Light Rivers, First and Scott Creeks], the Mid-North of South Australia (Hill River) and the Southern Flinders Ranges (Kanyaka Creek) [Fig. A1 in Supporting Information]. Flows in these streams are largely driven by groundwater, which over long time-scales have accumulated marine-derived salts (Herczeg et al., 2001).

The macroinvertebrate samples used in our analysis form part of the Australian Rivers Assessment System (AusRivAS) (Davies, 2000) of which South Australia has been part since 1994. The database includes a substantial, standardised record of benthic macroinvertebrates and a large number of environmental variables. Annual sampling was conducted in two seasons (autumn and spring) to avoid dried-out summer periods and low macroinvertebrate activity during winter. We used data collected for 13 years from 1994 to 2007 (excluding 1996 owing to a hiatus in funding).

Macroinvertebrates were collected using the same AusRivAS protocols which consisted of sampling approximately 5 m^2 area of pool habitats within each 100 m study site using a 250 μm mesh triangular dip net. Sampling involved vigorously kicking the substrate and sweeping the net over a total bank length of 10 m using sequential short sweeping movements at right angles to the bank and, sweeping under overhanging or emergent vegetation (Davies, 2000). Collected macroinvertebrates were preserved in ethanol on site, transported to the laboratory, and subsampled (where a minimum of 10% of the sample was counted and identified using dissecting and compound microscopes), and the residue scanned for rare taxa (Davies, 2000; Simpson and Norris, 2000). This approach ensured observer bias was minimised when counting individuals compared to alternative live-pick approaches included in the AusRivAS protocols, and it also provided an accurate estimate of the abundance of cryptic taxa. Taxa were identified to the lowest taxonomic level, given available keys, life-history stage and condition. This was most often to genus or species level. Voucher specimens of all taxa were retained as a reference collection at the South Australia Museum and Australian Water Quality Centre (AWQC).

2.2. Traits

We used 75 biological traits grouped into four categories (life history, mobility, ecology and morphology) to describe the functional composition of invertebrate communities (Supporting Information Table A2). Trait values were assigned at family level (except for the Chironomidae, where traits were assigned at subfamily level) using the trait databases of Poff et al. (2006) and Schäfer et al. (2011). Where South Australian taxa were not covered in these sources, we utilised expert opinion from taxonomists and information from *Identification and Ecology of Australian Freshwater Invertebrates* (http://www.mdfrc.org.au/bugguide/, accessed January 2016). The trait databases from

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