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ScienceDirect
Geomorphology 93 (2008) 267–287
GEOMORPHOLOGY
www.elsevier.com/locate/geomorph

Crayfish and fish as bioturbators of streambed sediments: Assessing joint effects of species with different mechanistic abilities

Bernhard Statzner *, Pierre Sagnes

CNRS - "Ecologie des Hydrosystèmes Fluviaux", Université Lyon 1, 69622 Villeurbanne Cedex, France

Received 5 December 2006; received in revised form 28 February 2007; accepted 28 February 2007
Available online 12 March 2007

Abstract

Many studies illustrate that bioturbating animal species individually affect aquatic sediments through diverse mechanistic abilities, whereas assessments of joint effects of such species on sediments are relatively rare. Such joint effects have implications for real systems, in which different bioturbators coexist, but are difficult to predict for two reasons. First, they can be additive (being the sum of the individual effects of each species) or they can be positive or negative interactive (being greater or smaller than the sum of the individual effects). Second, if interactive, they can depend on biotic interactions that affect the bioturbating activities of the species and/or they can depend on physical interactions among bioturbator-induced sediment modifications. Using experimental streams, we assessed such joint effects on gravel–sand sediments for flow and sediment conditions preferred by barbel (*Barbus barbus*) but also used by gudgeon (*Gobio gobio*) and, in a second experiment, for flow and sediment conditions preferred by both male crayfish (*Orconectes limosus*) and gudgeon. These species have different mechanistic abilities to affect gravel and/or sand in stream beds. In each experiment, we measured (i) the transport of gravel and sand at baseflow (during 12 experimental days); (ii) four sediment surface characteristics (after 12 d); and (iii) the critical shear stress (τ_c) causing incipient gravel and sand motion during experimental floods (after 12 d). Gudgeon contributed differently to the joint effects in the two experiments, which related to its individual weight, prevailing baseflow shear stress, sediment particle weight, and sediment mixture (availability of surface sand). Overall, the species pairs had predominantly negative interactive joint effects on the sediment variables assessed by us. Both a literature survey and observations during the experiments provided no evidence for direct biotic interactions between barbel and gudgeon or crayfish and gudgeon, so one would reasonably associate their negative interactive effects on the sediments with physical interactions among bioturbator-induced sediment surface modifications. Individually, each species reduced the percentage of sand in the surface layer and the surface algal cover to relatively low values so that the species pairs could not accomplish much greater joint effects on these variables, explaining their negative interactive effects on them. As algal cover particularly affected the τ_c for gravel and sand, the negative interactive effects of the animals on this surface variable chained toward the τ_c for the sediments, on which the species pairs also had negative interactive effects. Such chained negative interactive effects on sediment variables are seemingly a general pattern of joint bioturbator effects on aquatic sediments, *i.e.*, the many so far described single-species effects should be smaller than their sum if the species coexists in nature.

Keywords: Additive effects; Biogeomorphology; Bioerosion; Benthos; Gravel–sand bed; Interactive effects

1. Introduction

The interest of geomorphologists and ecologists in the impact of organisms on their physical environment is

* Corresponding author. Tel.: +33 4 7244 8034; fax: +33 4 7243 1141.
E-mail address: statzner@biomserv.univ-lyon1.fr (B. Statzner).

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doi:10.1016/j.geomorph.2007.02.019

steadily increasing, as recent special sections/issues on the subject in the journals *Geomorphology* and *BioScience* witness (see introductory articles by Viles and Naylor, 2002; Montgomery and Piégay, 2003; Urban and Daniels, 2006; Wright and Jones, 2006). Naturally, the focus of this interest often differs between these disciplines: geomorphologists are primarily concerned by the impact of organisms on landforms (Butler, 1995; Naylor et al., 2002), whereas ecologists are primarily concerned by their impact on the physical habitat conditions of other organisms than themselves (Jones et al., 1994; Moore et al., 2004) [but see Fisher et al. (2006) and Stallins (2006) for a recent integration of these differing interests within a common framework]. In both disciplines, however, a central question is how organisms modify the surface of solids and thereby affect the erodibility of these solids by wind or water (Carter and Viles, 2005; Brummer et al., 2006; Gutiérrez and Jones, 2006; Moore, 2006; Thomas and Dougill, 2007).

Combining the action of physical factors with that of mobile animals in considerations of surface characteristics and the transport of solids generates a particularly complex scenario. The knowledge about physical factors complicating this scenario is steadily increasing (*e.g.*, Billi et al., 1992; Wilcock, 1998; Pyrce and Ashmore, 2003; MacKinnon et al., 2004; Pearce and Walker, 2005), and mobile animals complicate this scenario even more: they have diverse mechanistic abilities to modify solid surfaces and to increase or decrease the transport of solids, and these animal actions vary in space and time (*e.g.*, Butler, 1995; Statzner et al., 2003b; Butler, 2006). Thus, for a start, quantifications of such action of animals focused on separate single-species assessments of mammals (*e.g.*, Butler, 1995; Trimble and Mendel, 1995; Butler, 2006), salmonids and other fish groups (*e.g.*, Flecker, 1996; Montgomery et al., 1996; DeVries, 1997; Rennie and Millar, 2000; Gottesfeld et al., 2004), and many groups of marine invertebrates (*e.g.*, Fager, 1964; Eckman et al., 1981; Meadows et al., 1990; Willows et al., 1998; François et al., 1999; Botto and Iribarne, 2000; Katrak and Bird, 2003; Jackson et al., 2005; see also the review by Murray et al., 2002) or freshwater invertebrates (*e.g.*, McCall and Tevesz, 1982; Statzner et al., 1996; Parkyn et al., 1997; Statzner et al., 1999; 2000; Mermillod-Blondin et al., 2002; Creed and Reed, 2004; Usio and Townsend, 2004; Takao et al., 2006).

Obviously, these species live not alone and interactions with other species may modify their impact on solid surfaces. For example, North American bisons (or "buffalo") have geomorphic impacts through trampling and, through their grazing, they keep the vegetation sufficiently short so that the colonization by prairie-dogs is favoured; the latter have geomorphic impacts through burrowing in the soil and through this and other activities they favour bison grazing, thus causing a positive feedback of bison trampling (Butler, 2006). Therefore, particularly recent research on the impact of bioturbating aquatic animals on finer sediments expanded to studies of two or more species (Meadows and Tait, 1989; Mermillod-Blondin et al., 2004a,b; Zhang et al., 2004; Mermillod-Blondin et al., 2005; Boyer and Fong, 2005; Helms and Creed, 2005; Nogaro et al., 2006; O'Reilly et al., 2006).

A key question of most of these studies related to bioturbating effects of species mixtures in comparison with the individual effects of each species: are the joint effects of species additive, corresponding to the sum of the individual effects of each species, or are they positive or negative interactive, corresponding to more or less than the sum of the individual effects of each species? Obviously, an answer to this key question provides important information about the implications for real systems of the many so far available single-species assessments of bioturbators in the context of biodiversity effects on landform processes and habitat modifications. Correspondingly, the objective of this experimental study was to assess the joint effects of bioturbators of coarser streambed sediments in comparison with the individual effects of each species, using a North American crayfish introduced to Europe [*Orconectes limosus* (Raffinesque)] and two native European fish, barbel [*Barbus barbus* (L.)] and gudgeon [*Gobio gobio* (L.)].

2. Uncertainties of *a priori* hypotheses: effects of biotic species interactions on bioturbating activities or physical interactions among bioturbator-induced sediment modifications?

In designing experiments such as ours, a major concern is to synthesize the available knowledge on the relevant biological details of the test organisms, as this is a prerequisite for making *a priori* hypotheses. For example, the strength of biotic interactions between stream animals, such as in predator–prey relationships, depends on the similarity of the prevailing flow conditions with the different flow conditions preferred by a predator and its prey (Statzner and Borchardt, 1994). Thus, working at experimental flow conditions preferred by the predator would produce other results than working at flow conditions preferred by the prey. Likewise, working at experimental flow conditions preferred by a stream bioturbator would produce other