

Abstract Disturbance frequency, intensity, and areal extent may influence the effects of disturbance on biological communities. Furthermore, these three factors may have interacting effects on biological diversity. We manipulated the frequency, intensity, and area of disturbance in a full-factorial design on artificial substrates and measured responses of benthic macroinvertebrates in a northern Vermont stream. Macroinvertebrate abundance was lower in all disturbance treatments than in the undisturbed control. As in most other studies in streams, species density (number of species/sample) was lower in disturbed treatments than in undisturbed controls. However, species density is very sensitive to total abundance of a sample, which is usually reduced by disturbance. We used a rarefaction method to compare species richness based on an equivalent number of individuals. In rarefied samples, species richness was higher in all eight disturbed treatments than in the undisturbed control, with significant increases in species richness for larger areas and greater intensities of disturbance. Increases in species richness in response to disturbance were consistent within patches, among patches with similar disturbance histories, and among patches with differing disturbance histories. These results provide some support for Huston's dynamic-equilibrium model but do not support the intermediate-disturbance hypothesis. Our analyses demonstrate that species richness and species density can generate opposite patterns of community response to disturbance. The interplay of abundance, species richness, and species density has been neglected in previous tests of disturbance models.

Key words Intermediate disturbance hypothesis · Dynamic equilibrium model · Stream invertebrate community · Rarefaction · Diversity

Introduction

The intensity, frequency, and area of disturbance may determine the abundance and species richness of an assemblage (Abugov 1982; Sousa 1985; Resh et al. 1988; Huston 1994; Townsend et al. 1997). Increasing disturbance intensity may remove more individuals, more species, and more of the food resources necessary for recolonization. If disturbance frequency is greater than the rate of competitive exclusion, diversity may be maintained at a high level (Huston 1979). Increasing the areal extent of disturbance removes more individuals, thus reducing the local pool of potential colonists. Although all three aspects of disturbance can affect species richness (Sousa 1985), little is known about their interactions (Death and Winterbourn 1995).

The intermediate-disturbance hypothesis (IDH; Connell 1978) continues to be an important hypothesis explaining the effects of ecological disturbance (Collins et al. 1995; Hiura 1995; Hacker and Gains 1997; Dial and Roughgarden 1998; Wilkinson 1999). The qualitative prediction that diversity should peak at an intermediate disturbance level has been tested in marine, freshwater, and

terrestrial systems.

rates of population growth, species diversity can peak at low, high, or intermediate levels of disturbance (Figs. 5, 6 in Huston 1994).

In contrast to the predictions of the IDH, disturbance in streams usually reduces invertebrate species richness (Lake 1990; Englund 1991; Matthaei et al. 1996, 1997; reviewed by Vinson and Hawkins 1998), although rapid recolonization may quickly restore diversity (Townsend and Hildrew 1976; Boulton et al. 1988; Lake and Schreiber 1991). Resh et al. (1988) and Reice et al. (1990) reviewed the role of disturbance in streams and concluded that the dynamic-equilibrium model (Huston 1979, 1994) is generally applicable to stream communities. In contrast, Lake (1990) suggested that Huston's model appears too simple to explain the structure of stream communities.

Whereas the IDH predicts that diversity will peak at some intermediate intensity or frequency of disturbance (Connell 1978; Collins and Glenn 1997), Huston's dynamic-equilibrium model predicts that the location of the diversity peak depends on the rates of population growth and competitive displacement in the community (Figs. 5, 6 in Huston 1994). Huston's (1994) model assumes that competitive exclusion occurs more rapidly when populations have high growth rates. At low rates of population growth and competitive displacement, maximum diversity is predicted at minimum disturbance frequency or intensity; at intermediate growth rates, diversity peaks at intermediate disturbance levels (as predicted by the IDH); at high growth rates, diversity peaks at maximum disturbance intensity or frequency (Huston 1994). Huston's model assumes that disturbance reduces population sizes and that competitive exclusion is more likely when populations are large. If the interval between disturbances is less than the time to competitive exclusion, then equilibrium conditions are never reached, competitive exclusion does not occur, and diversity is maintained at a high level (Huston 1979; Resh et al. 1988). The essential difference between Huston's (1994) model and the IDH is that the former predicts that the position of the diversity peak with respect to disturbance frequency depends on population growth rates.

Despite widespread interest in disturbance of stream assemblages, intensity, frequency, and area of disturbance have not been simultaneously manipulated in a controlled field experiment. In studies to date, frequency (Reice 1985; Robinson and Minshall 1986; Lake et al. 1989; Death 1996), intensity (Boulton et al. 1988; Rosser and Pearson 1995), and area of disturbance (Dudgeon 1991; Rosser and Pearson 1995) have all been manipulated separately. Accordingly, we know nothing of the potential interactions between these factors (Death and Winterbourn 1995).

In addition, effects of disturbance may depend on precisely how diversity is quantified. Most ecologists have not disentangled the effects of abundance, species density (number of species/area; Simpson 1949), and species richness (number of species/number of individuals sampled; James and Wamer 1982; Downes et al. 1998). All

diversity and richness measures are influenced by sample size, and statistical procedures such as rarefaction (Simberloff 1978) are necessary for valid comparisons of samples (Gotelli and Graves 1996; Vinson and Hawkins 1996). This topic, and the related issue of using fixed counts versus standardized areas for evaluating benthic communities, has been the focus of recent debate in the freshwater ecology literature (Larsen and Herlihy 1998 and references therein). These issues are especially important in evaluating effects of disturbance, because disturbance reduces abundance.

The purpose of our study was to examine the impacts of physical disturbance on macroinvertebrates of a northern Vermont stream. We manipulated intensity, frequency, and area of physical disturbance on artificial substrates in a full-factorial design. Our disturbances mimicked natural substrate scouring events. We used a rarefaction technique (Gotelli and Entsminger 1999) to quantify effects of disturbance on macroinvertebrate abundance, species density, and species richness. Our experimental design enabled us to test for main effects and interactions between intensity, area, and frequency. We were also able to assess the effects of disturbance within and among patches, a recent source of controversy in the disturbance literature (Wilson 1994; Collins and Glenn 1997).

Materials and methods

Study site

We conducted this study in a third-order perennial reach of the La Platte River in Chittenden County, Vermont. Mean annual discharge for the 5 years prior to this study was $1.1 \text{ m}^3 \text{ s}^{-1}$ (Hammond et al. 1997). The channel gradient was low at the study site, and the maximum stream depth was 1 m under baseflow conditions. The stream bank was lightly wooded, with little canopy cover over the channel. Stream bed substrates included boulders, cobbles, gravel, and sand. This stream is highly prone to spring spates caused by snow melt and rain storms. Periodic spates following rain storms continue through fall (Fig. 1; data from Coakley et al.

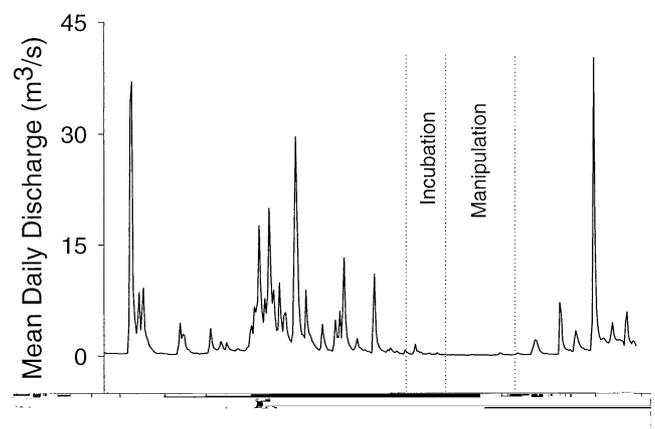


Fig. 1 Mean daily discharge of the LaPlatte River at the Shelburne Falls USGS gauging station (Coakley et al. 1997, 1998). The gauging station is approximately 5 km downstream from the study site. Incubation and manipulative periods are indicated

1997, 1998). The year we conducted this study was unusual, in that there were no large spates during the months of field work. During winter, the stream surface freezes, and ice buildup can be significant, although the stream continues to flow throughout the year.

Disturbance manipulations

We manipulated the frequency, intensity, and area of disturbance on artificial substrates and monitored the response of benthic invertebrate assemblages. We created two levels of each disturbance factor. The three disturbance factors (frequency, intensity, area) were applied in a full-factorial design, yielding eight treatments and an unmanipulated control. We replicated each treatment seven times and arrayed the replicates in the stream in a randomized-block design. Each block, consisting of nine treatments, was positioned across the width of the stream, and treatment position within blocks was assigned randomly. Treatments were not replicated within blocks. Patio stones within a block were separated by 15 cm, and blocks were separated by 50 cm.

We used the upper surfaces of rectangular cement patio stones (19.2×39.2×4 cm) as experimental substrates. Cement stones were chosen because they provided comparable texture to stream substrates. Treatments were applied only to the upper surfaces and, at the end of the treatment period, samples were taken from only the upper surfaces. Because the disturbances were applied during daylight hours, invertebrates that spend daylight hours on rock tops would be more strongly affected. We made no attempt to prevent colonization of the upper surfaces by invertebrates from the under surfaces or surrounding benthos. To allow for colonization by periphyton and invertebrates, we placed all of the patio stones in the stream on 29 July 1996, 27 days before initiating disturbances. We checked and repositioned the stones during the colonization period to ensure constant submersion.

Disturbances were initiated on 28 August 1996 and maintained until 10 October 1996. Spates are less frequent during this time than during spring and summer, but they do occur year-round. We applied the experimental disturbances with a frequency of either once or twice weekly. We chose these frequencies because other stream assemblages typically recover fully from disturbances within 8–30 days (Boulton et al. 1988; Lake and Schreiber 1991). Weekly disturbances are common in this stream, and even higher frequencies of spates are not unusual (Fig. 1). When we collected the macroinvertebrates from the substrates, the high-frequency treatments had been disturbed 4 days previously whereas the low-frequency treatments had been disturbed 7 days earlier. Thus, the high-frequency treatments could also be thought of as ‘young’ or recently disturbed patches and the low-frequency treatments as relatively ‘old.’

We used a wire scrubbing brush to simulate intense disturbance and a paintbrush to simulate mild disturbance. The intense disturbance removed sediment, insects such as *Hydropsyche* sp. and *Antocha* sp., filamentous algae, and many of the diatoms. The mild disturbance removed sediment and some insects, but left much of the filamentous algae intact.

Disturbances were applied to 50% or 100% of the surface area. The 50% disturbances were applied to four randomly selected circular patches, with each patch representing 12.5% of the total area. For each disturbance, we randomly assigned the location of the four patches on a substrate. This created patches of mixed age, or time since disturbance. The 50% area disturbances were designed to simulate creation of a disturbed area adjacent to an undisturbed area. Small-scale patchiness of this sort can result when stones are

ing the high-intensity disturbance had lower abundance than treatments receiving the low-intensity disturbance (Fig. 2). Abundance in the 100% area disturbance was

species richness response, species density was lower in disturbed treatments than in undisturbed controls

ness was higher in all of our disturbance treatments than in undisturbed controls (Fig. 3). This pattern is predicted by Huston's (1979, 1994) dynamic-equilibrium model when the species populations are growing rapidly and have high rates of competitive exclusion (Figs. 5, 6c in Huston 1994). Although we did not assess competitive interactions in our experiment, other studies have documented competition among species in the genera *Hydropsyche*, *Simulium* (Hemphill and Cooper 1983), and *Leucotrichia* (McAuliffe 1984; Hart 1985), all of which were present at our site. Resh et al. (1988) and Reice et al. (1990) also concluded that the dynamic-equilibrium model (Huston 1979) is generally applicable to stream communities, although they did not clearly state which of Huston's (1994) specific hypotheses were supported.

The increased richness we observed following disturbance is in sharp contrast to the results of most stream experiments (Table 4). In most other studies, experimental disturbance decreased species density and was followed by a rapid recovery to control levels or predisturbance levels (but see Engl 9 Ocfc 9 0 072ecies density by4-

dance of organisms is central to many definitions of ecological disturbance (Connell 1979; Sousa 1985; Townsend and Hildrew 1994). Although the abundance of some individual taxa can increase following disturbance (Levey 1988; Englund 1991; Wootton et al. 1996), total abundance of the community is typically reduced (Death 1996; Pringle and Hamazaki 1997).

Although definitions of intensity and frequency of disturbance are not consistent in the literature (White and

bance events, the number of macroinvertebrates available to colonize disturbed patches would still be reduced. Our disturbance manipulations are better suited to model the effects of patch scale disturbances.

Species richness versus species density

Should assemblages be compared on the basis of species density (number of species per unit area or sampling effort) or species richness (number of species per a standardized number of individuals)? Most ecologists have measured species density, even though they often call it species richness. Species density is a natural choice because it follows from the sensible practice of using standardized samples of equivalent area or sampling effort. However, because more abundant samples will tend to have more species, differences in species density among samples of differing abundance must be viewed as potential sampling artifacts unless a rarefaction technique provides evidence to the contrary. Rarefaction of our data confirms that decreases in species density after disturbance can in large part be explained by changes in abundance.

Furthermore, measures of species richness may be preferable because most ecological models describe changes in abundance or species richness, not changes in density or species density. In particular, 'classical' ecological models that are based on ordinary differential equations (e.g., Wootton 1998) usually do not contain terms for area or density. Instead, these models are built on per capita interaction effects of one population or species on another. To test these models, we think it is more relevant to use species richness than species density, which is affected by both species richness and abundance.

- Doeg TJ, Lake PS, Marchant R (1989) Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. *Aust J Ecol* 14:207–220
- Dole-Olivier MJ, Marmonier P, Beffy JL (1997) Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biol* 37:257–276
- Downes BJ, Lake PS, Schreiber SG, Glaister A (1998) Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecol Monogr* 68:237–257
- Dudgeon D (1991) An experimental study of abiotic disturbance effects on community structure and function in a tropical stream. *Arch Hydrobiol* 122:403–420
- Englund G (1991) Effects of disturbance on stream moss and invertebrate community structure. *J North Am Benthol Soc* 10:143–153
- Gotelli NJ, Entsminger GL (1999) *EcoSim: Null models software for ecology*, Version 5.0. Acquired Intelligence Inc & Kesey-Bear, Burlington, VT <http://homepages.together.net/~gentsmin/ecosim.htm>