

Crevice as refugia for stream diatoms: Effect of crevice size on abraded substrates

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Abstract

This study explored the mechanisms by which crevices act as refugia for small algae during abrasive disturbances. Four substrates with different crevice features were subjected to three levels of abrasion in a stream-based experiment. Substrates were sand-grain caddisfly cases and three glass rod substrates that mimicked caddisfly cases in size and shape, as well as forming a gradient of larger crevices (i.e., smooth with no crevices, sanded with shallow pits, and scratched with deeper grooves). Substrates were subjected to no, low, or high abrasion levels during 18 d of incubation by pulling substrates through a sand–gravel mixture in floating enclosures that housed the experiment. Diatom density, relative biovolume, location in crevices, detritus accumulation, and filamentous algal density were compared among substrate types and abrasion levels. Across all abrasion levels, diatom and filamentous algal densities were higher on caddisfly cases than on all three glass rod substrates. Although abrasion greatly reduced overall diatom density, diatoms within crevices were largely protected. Crevice size influenced diatom size and composition. The small crevices of sanded rods contained primarily small diatoms of a single species (*Achnanthes minutissimum*), whereas the larger crevices of scratched rods and caddisfly cases contained a greater range of diatom size and, consequently, greater species diversity. Detritus accumulated in all crevices, and accumulation increased with level of abrasion. Diatom biovolume decreased and location in crevices increased with the level of abrasion on the less textured smooth and sanded glass rods. Abrasion level had little effect on algal assemblages on caddisfly cases. This study demonstrates that crevices can be important refugia from abrasive disturbances, and that the size of crevices relative to organismal size can influence the protective value of crevices.

Algae in stony streams and in rocky intertidal zones experience disturbance in association with water movement and grazing. Disturbances resulting from water movement include the effects of floods in streams (Fisher and Grimm 1988; Resh et al. 1988; Biggs and Close 1989), abrasion by waterborne objects, such as logs in intertidal zones (Dayton 1971; Sousa 1984), and siltation from mobilized bedload (Seapy and Litterer 1982; Power 1990). Grazers both consume and dislodge algae (Scrimgeour et al. 1991). These disturbances can and often reduce local algal populations in marine and freshwater habitats, yet both ecosystems are characterized by spatially dense, taxonomically diverse algal communities.

Small size may be advantageous in resisting the mechanical forces of waves (Koehl 1984), and perhaps consequently, organisms in marine intertidal zones are smaller than organisms in sheltered marine and terrestrial habitats (Denny et al. 1985). Likewise, stream algae are generally small, and the combination of small size and prostrate morphology increases resistance to loss from disturbances such as spate-induced floods (Blenkinsopp and Lock 1994; Peterson 1996) and grazing (Jacoby 1987; Steinman et al. 1987; Lamberti et al. 1989). Small size has the additional benefit of enabling organisms to fit within crevices. For brevity, the term crevices is used to denote recessed areas of surfaces, such as pits, scratches, cracks, and small spaces among sessile or-

ganisms. Crevices may provide refugia from grazers (Lubchenco 1983; Dudley and D'Antonio 1991; Figueiredo et al. 1996), from drag and abrasion associated with moving water (Norton 1983; Luttenton and Rada 1986) or with burrowing (Bergey and Resh 1994), and from desiccation during exposure to air (Gosselin and Chia 1995).

The refuge value of crevices has been commonly illustrated by comparisons of algal assemblages between rough and smooth substrata. Rougher stones develop higher densities of diatoms (Blinn et al. 1980; Antoine and Benson-Evans 1985) and macroalgae (Thirb and Benson-Evans 1983; Antoine and Benson-Evans 1985; Dudley and D'Antonio 1991) than smoother stones. Likewise, rougher artificial substrata develop higher chlorophyll *a* (Clifford et al. 1992) and macroalgal densities (Harlin and Lindbergh 1977; Dudley and D'Antonio 1991) than smoother artificial substrata. Because rough substrata include exposed ridges and transitional areas in addition to crevices (Johnson 1994), these results do not distinguish the role of crevices versus adjacent areas in promoting algal growth on rough substrata nor characterize conditions in which crevices are refugia.

McCoy and Bell (1991) present a useful framework for categorizing habitat structure for ecological studies. Their model contains three descriptive axes: heterogeneity (the diversity of different structural elements), complexity (the density of all structural elements), and scale (a size component). Structural elements include not only three-dimensional abiotic features such as crevices but biotic features such as algal filaments (e.g., Dodds 1991; Downes et al. 1998) or forest canopies. Within this model, studies of rough versus smooth substrates or of the effects of crevice size fall primarily into the scale axis, especially when the size of crevices relative to organism size is compared.

This study explored mechanisms by which crevices can be refugia by examining diatom-dominated assemblages

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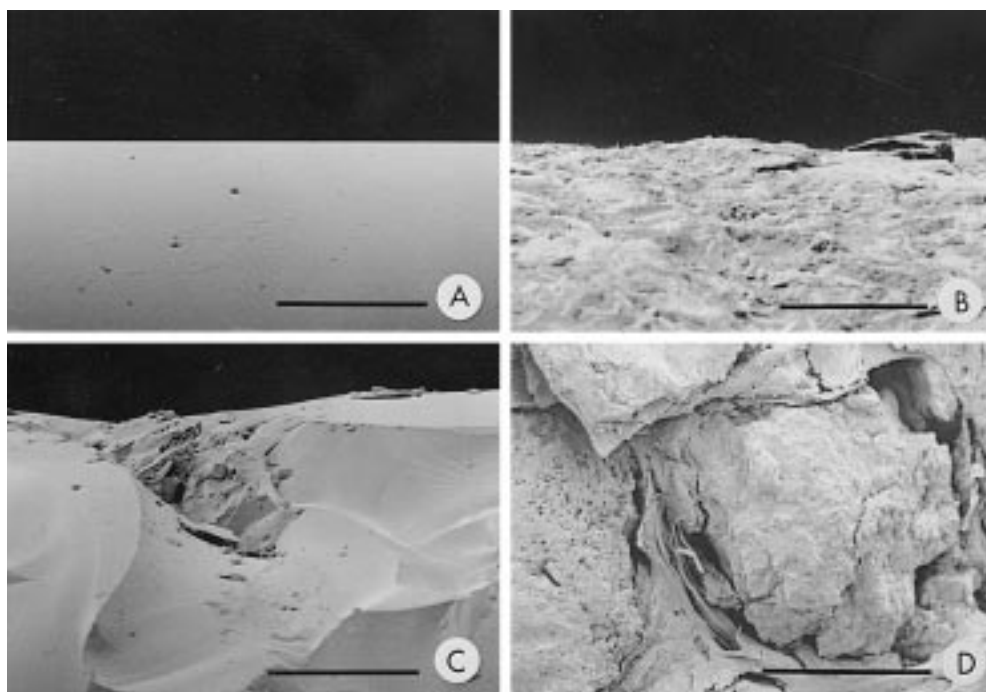


Fig. 1. Scanning electron photographs of the four substrate types prior to algal colonization. Lateral view of a smooth glass rod (A), a sanded glass rod with shallow crevices (B), and a scratched glass rod (C) with smooth areas between deep scratches; and top view of a case (D) of *Gumaga nigricula* with crevices containing silk between sand grains. Bars are 50 μm long.

within crevices of different sizes under different levels of disturbance. Their small size, high propagule pool, rapid colonization, and low mobility make diatoms ideal for exploring mechanisms of crevice refugia. I hypothesized that (1) crevices act as refugia for small algae, (2) crevices become poorer refugia as disturbance level increases, and (3) crevices initially become better refugia and then poorer refugia as crevice size increases.

Materials and methods

Field—The experiment was conducted in the South Fork of the Eel River at the University of California's Northern California Coast Range Preserve (Sonoma Co.). Because of the area's Mediterranean-like climate, stream flow was near base level and no rainfall occurred during the study (6–24 June). Water was 0.5–0.8 m deep and received direct sunlight for 6–7 h daily.

Algae were allowed to colonize four types of substrates that differed in texture (Fig. 1) under a regime of three levels of abrasion (=12 texture–abrasion combinations). Substrates included the sand-grain cases of the caddisfly *Gumaga nigricula* (McL.) (Insecta: Trichoptera), which has abundant crevices that protect diatoms against abrasive disturbance during burrowing (Bergey and Resh 1994). Although these cases are a convenient size for studying the conditions under which crevices can be refugia, their architectural complexity and mixed composition of silk and sand are confounding effects that reduce their usefulness. In addition to caddisfly cases, three substrate types were made from glass rods. Glass rods approximate the size

and shape of the caddisfly cases but have a simpler texture that mimics polished surfaces and can be scratched to mimic the pitted surfaces and crevices of stone substrates. Using empty cases and glass rods also eliminated the potentially confounding factors of nutrient interactions and grazing by case-inhabiting caddisflies. Glass rod segments (diameter = 0.3 cm, mean length = 1.6 cm) were smooth (unaltered), sanded (using no. 60 grit sandpaper that produced a pitted surface), or scratched (spirally cut with a glass scorer that produced deep, linear crevices) (Fig. 1). Dimensions of crevices in sanded rods averaged 28.0 μm wide and 5.3 μm deep and in scratched rods, 152.2 μm wide and 22.1 μm deep. Scratched rod crevices covered about 60% of the planar surface area of rods; noncrevice areas were smooth. Crevice dimensions of caddisfly cases were not measured because of difficulty in obtaining side views with scanning electron microscopy (SEM). Caddisfly cases were collected in Big Sulphur Creek (Sonoma Co., California) the previous year. Cases were treated with methanol during earlier chlorophyll extraction, stored dried, and then cleaned with 30% hydrogen peroxide to remove any algal remains before the experiment.

The experiment was housed in floating tubs. Tubs were plastic 0.47-liter freezer boxes with two sides replaced with 1-mm mesh, that excluded grazers. Tubs were floated with individual styrofoam collars and held in six racks (=blocks). Each tub contained about 2.5 cm of sand–gravel from the stream bank and had ca. 2 cm of water above the added substrate. Racks were positioned in two rows perpendicular to stream flow. Depth and water velocity were similar among rack locations.

Abrasion was simulated by pulling substrates through the sand-gravel mixture in the tubs, using a monofilament lead glued to one end of the substrates. Two levels of abrasion were applied, low (a daily abrasion path of 8 cm) and high (a daily abrasion path of 40 cm), as well as an unabrased control (no abrasion). Abrasion-based disturbance was used because it mimics the natural disturbance that algae growing on the cases of burrowing *Gumaga* experience daily in the field (Bergey and Resh 1994). The abrasion disturbance could be easily quantified and regularly reproduced.

Each of the 12 texture-abrasion combinations was replicated six times, and the resulting 72 replicates were randomly assigned to individual tubs, regardless of rack location. Replicates contained two of each of the substrates, one for electron microscopy and one for diatom counts. Substrates were placed in the tubs on 6 June, incubated for 18 d (with the appropriate abrasion treatment each day), and preserved in 5% formalin on 24 June. Substrates were labeled by tub location rather than treatment to reduce observer bias during data collection.

Laboratory—Substrates were prepared for SEM by passage through a graded ethanol series (25%, 50%, 75%, 80%, 95%, and 100%) and freon prior to air drying. Entire substrates were glued to aluminum SEM stubs with a carbon glue and sputter coated with platinum. Substrates were viewed with an ISI DS-130 scanning electron microscope. Polaroid photographs were taken of each substrate in a standard manner: 250 \times magnification at the location on the substrate closest to the center of the stub (about midlength along the glass rod or caddisfly case).

Photographs were assessed for biovolume, spatial arrangement of algal assemblages, detrital accumulation on substrates, and density of filamentous algae. Photographs were compared within texture type (i.e., smooth, sanded, scratched, or cases), and the 18 photographs per texture type were ranked for each of the above characters (total biovolume, proportion of cells located in crevices, amount of detritus, and abundance of filamentous algae). Rank data were analyzed with Kruskal-Wallis tests, using α -values adjusted for the number of tests run on each set of photographs (e.g., $\alpha = 0.017$ or 0.05/three characters tested), followed by non-parametric Tukey-type multiple-comparison tests (Zar 1996).

The second substrate from each tub was oxidized with heated hydrogen peroxide and potassium dichromate in preparation for counting diatoms. This treatment effectively removed diatoms from the substrates and cleared the diatoms but also destroyed nondiatomaceous algae. Diatoms were the dominant algae on all of the substrates; the only other algae visible with SEM were filamentous green algae that were assessed with SEM. After diatom samples were rinsed with water, 1 ml of a glass bead (diameter = 5–20 μ m) suspension of known concentration was added to each of the 72 samples. Permanent slides were made with Hyrax mounting medium. Diatoms and glass beads were counted along random transects until at least 350 diatoms or 2,000 glass beads (in samples containing few diatoms) were counted. Counts of glass beads were used to calculate absolute diatom numbers (Battarbee and Kneen 1982). Because diatoms were oxidized prior to counting, counts include both living and dead individuals. Areas for diatom density calculations were mea-

Table 1. Two-way blocked ANOVA results of the effects of substrate type (sm = smooth, sa = sanded, or sc = scratched rods, or cs = caddisfly cases), abrasion regime (none, low, and high), and block (a–e denote the six racks) on total diatom density. A square-root transformation of the density data [$\sqrt{\text{density} + 0.5}$] was required to produce normality (Zar 1984). Treatments that did not differ significantly (Tukey test; $\alpha < 0.05$) are shown by joined overlying bars.

| Treatment | df | F | P | Treatments |
|----------------------------|----|--------|---------|----------------------|
| Substrate type (1) | 3 | 61.914 | <0.0001 | <u>sm sa sc cs</u> |
| Abrasion regime (2) | 2 | 17.302 | <0.0001 | None <u>Low High</u> |
| Interaction (1 \times 2) | 6 | 0.568 | 0.754 | |
| Block | 5 | 5.633 | 0.0003 | <u>a b c d e</u> |
| Error | 55 | | | |

sured using substrate dimensions, with no correction for differences in surface texture. Diatom densities were transformed and analyzed with a two-way blocked analysis of variance (ANOVA; substrate type and abrasion level were independent variables, rack location was the blocking variable) followed by Tukey multiple-comparison tests (Zar 1996). Dominant taxa in crevice and noncrevice areas were noted using SEM.

Results

Diatom densities were a magnitude higher on the caddisfly cases than on glass rods (Table 1, Fig. 2). This difference was also visually apparent with SEM. Despite the difference in density, dominant diatom taxa were very similar between caddisfly cases and glass rod substrates. Dominant diatoms were *Achnantheidium minutissimum*, *Epithemia sorex*, *Epithemia turgida*, and *Cocconeis placentula*. Caddisfly cases had more filamentous algae, especially the green alga *Cladophora glomerata*, than glass rods. Filamentous algae were present in 72.2% ($N = 18$) of the SEM photographs of caddisfly cases but only 1.9% ($N = 54$) of the photographs of glass rod substrates. Most filaments were short and unbranched and emerged from the crevices between the sand grains making up the case. The diatom *Cocconeis pediculus* was epiphytic on many *Cladophora* filaments.

Diatom densities on all four substrate types (smooth, sanded, and scratched rods; caddisfly cases) were lower under an abrasion regime than under the nonabrased regime (Table 1, Fig. 2). Density reduction under an abrasion regime was greater on the glass rod treatments (79–92% reduction from nonabrased densities; Fig. 2A) than on caddisfly cases (59% reduction; Fig. 2B). Increasing from a low to a high abrasion regime had little effect on diatom density. Diatom density also differed among racks, with one rack (e) having significantly higher diatom densities (Table 1).

Relative diatom biovolume was reduced by an abrasion regime on the less textured smooth rod and sanded rod substrates but not on the more textured scratched rods and caddisfly cases (Table 2, Fig. 3A). The large diatom *E. turgida*, which contributed much of the biovolume, was common on the unabrased smooth and sanded glass rods but not on these same substrates when abraded (cf. Fig. 4, A versus A' and

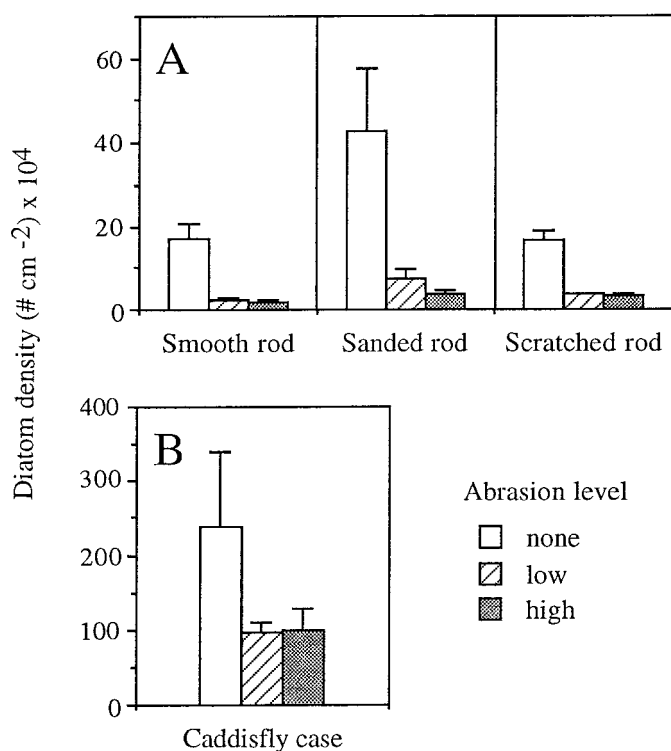


Fig. 2. Total diatom densities on the four substrates after 18 d of colonization. A = glass rod substrates; B = caddisfly cases. Note the differences in vertical scale between A and B. Statistical results are in Table 1; Error bars = +1 standard error (SE). Nontransformed density data shown for clarity.

B versus B'). This same pattern occurred on the smooth intercrevice portions of the scratched rods. In contrast, *E. turgida* was common in the larger crevices of both unabraded and abraded scratched rods and caddisfly cases (cf. Fig. 4, C versus C' and D versus D').

Small diatoms such as *A. minutissimum* were found both in the shallow crevices and on the ridges between crevices on unabraded sanded rods (Fig. 4B). Large diatoms such as *E. turgida* were usually too big to fit into most of the small crevices. On sanded rods exposed to an abrasion regime (Fig. 4B'), large diatoms were rare, small diatoms were common, and nearly all diatoms were found within crevices.

Scratched rods were architecturally more complex than sanded rods and contained scratches with smaller subcrevices and smooth interscratch areas (Fig. 1). Smooth interscratch areas were like smooth rods with nearly all diatoms removed by abrasion. Diatom location in scratches was affected by abrasion level (Fig. 3B); abrasion reduced diatom establishment in the shallow edges of scratches. In contrast, diatom location in the subcrevices of scratches was unaffected by abrasion regime (Fig. 3B), and most diatoms were in subcrevices in all abrasion regimes (Fig. 4C and C'). Diatom location in the deep crevices of caddisfly cases was unaffected by abrasion regime (Fig. 3B).

The amount of detrital material on substrates was affected by the abrasion regime in most substrates (Fig. 3C). On smooth rods, bacteria and fungi were progressively less common as abrasion increased. The amorphous detritus that characterized the other substrates was absent on smooth rods (cf. Fig. 4B', C', and D' versus A'). On scratched rods and caddisfly cases, this amorphous detritus increased within scratches as abrasion increased (Fig. 3C and Fig. 4C versus C'). Smooth areas on scratched rods showed the same pattern as smooth rods, with bacteria evident on unabraded substrates and less abundant on abraded substrates (Fig. 4C versus C').

Discussion

Crevice as refugia—Crevices can be effective refugia for algae. Whereas diatoms were abundant on all surfaces of unabraded glass rods, diatoms were abundant only in the

Table 2. Statistical summary of Kruskal-Wallis tests for four community characteristics: diatom biovolume, location within crevices, amount of detritus, and abundance of filamentous algae. Tests were run separately within each substrate type (smooth rod, sanded rod, scratched rod, and caddisfly case). Critical P values are adjusted for multiple tests on the same set of photographs (e.g., critical P = 0.05/2 for two tests using smooth rod photographs).

| Character | Substrate | H | Critical P | P |
|--------------------------------|----------------|-------|------------|---------|
| Biovolume | Smooth rod | 13.16 | 0.025 | 0.0014* |
| | Sanded rod | 12.89 | 0.017 | 0.0016* |
| | Scratched rod | 1.77 | 0.013 | 0.41 |
| | Caddisfly case | 0.69 | 0.013 | 0.71 |
| Location in crevices | Sanded rod | 9.70 | 0.017 | 0.0078* |
| | Scratched rod | 12.60 | 0.013 | 0.0018* |
| | Caddisfly case | 1.46 | 0.013 | 0.48 |
| Location in subcrevices | Scratched rod | 2.05 | 0.013 | 0.36 |
| Amount of detritus | Smooth rod | 11.57 | 0.025 | 0.0031* |
| | Sanded rod | 6.04 | 0.017 | 0.049 |
| | Scratched rod | 10.73 | 0.013 | 0.0047* |
| | Caddisfly case | 10.23 | 0.013 | 0.0060* |
| Abundance of filamentous algae | Caddisfly case | 0.33 | 0.013 | 0.85 |

* Significant P values.

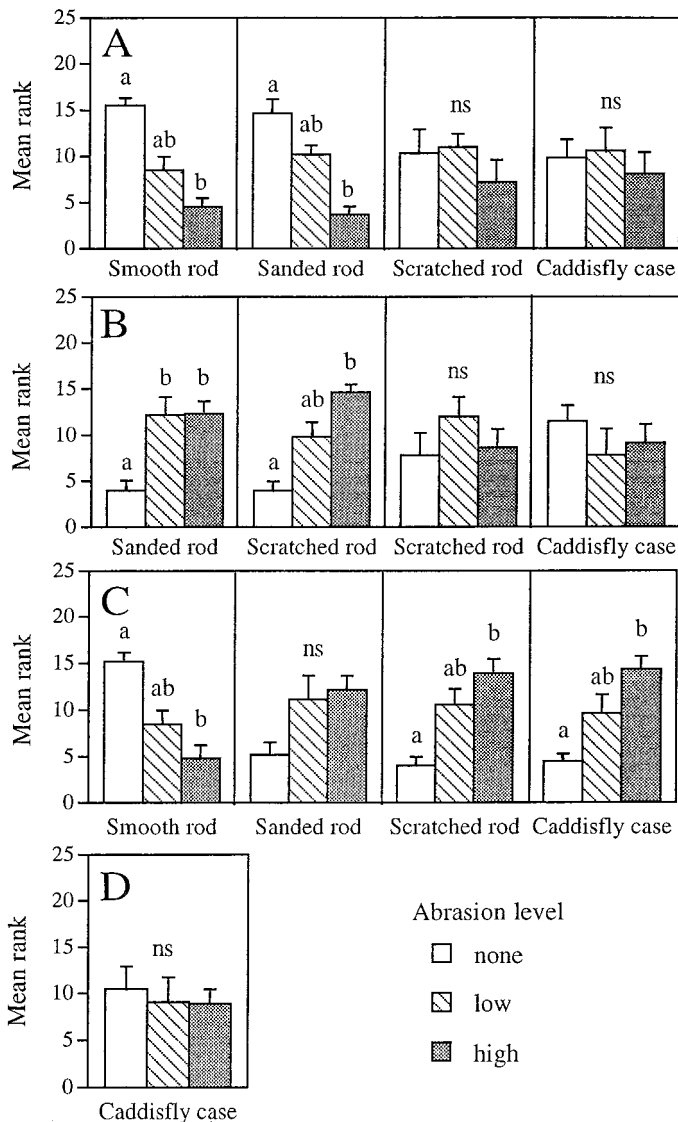


Fig. 3. Kruskal-Wallis rank and nonparametric Tukey test results for four community characteristics: (A) diatom biovolume, (B) location within crevices, (C) amount of detritus, and (D) abundance of filamentous algae. Tests were run separately within each substrate type (smooth rod, sanded rod, scratched rod, and caddisfly case). For B, location in the overall crevice (left) and within subcrevices (right) of scratched rods were considered separately. Test results are shown in Table 2. Significant differences among none, low, and high abrasion regimes (nonparametric Tukey test; $P < 0.05$, $N = 6$) indicated by different letters over bars; ns = not significant. Error bars = +1 SE.

crevices of abraded glass rods. Crevices that are refugia for algae include the artificial crevices in this study, and many natural crevices such as depressions in sand grains (Meadows and Anderson 1966; Miller et al. 1987) and rocks (Lubchenco 1983; Barnese et al. 1990), rough surfaces of coralline algae (Figueiredo et al. 1996), and crevices between the sand grains of caddisfly cases (Bergey and Resh 1994).

The protected area provided by crevices in most natural substrates is relatively small (Sanson et al. 1995); hence,

crevices are not refugia for entire populations of algae. However, the algae within crevices that survive disturbance may be ecologically important as a source of colonists (e.g., Harlin and Lindbergh 1977; Dudley and D'Antonio 1991). Thus for grazers, the slight reduction in potential grazing area due to crevices is unlikely to affect grazer production negatively and may benefit grazers by providing a propagule pool for consumption or recolonization of food resources.

Detrital accumulation within crevices was found in all three substrates with crevices. This accumulation of detritus within crevices indicates their depositional nature (Nowell and Jumars 1984; Davis and Barmuta 1989; Snelgrove et al. 1993) that may be linked to algal deposition in crevices (DeNicola and McIntire 1990; Douglas and Lake 1994). Higher algal immigration in crevices than noncrevice areas was not observed in this study perhaps because of filtering by the tub screens and the low water velocity within tubs.

Crevices are also frequently used by macroinvertebrates in both freshwater and marine habitats. Macroinvertebrates derive the same potential benefits from crevices as do algae (e.g., protection from predators, water flow, moving objects, and desiccation). Additionally, macroinvertebrates may use crevices in feeding, either by consuming algae (McGuinness and Underwood 1986; Douglas and Lake 1994; Gawne and Lake 1995; Downes et al. 1998) or macroinvertebrates (Kohn and Leviten 1976; Douglas and Lake 1994) within crevices. Crevices can be a base for mobile grazers or predators (Menge 1976, 1978; Witman 1985; Fairweather 1988) that feed primarily on exposed surfaces and return to crevices during periods of exposure to air or intense wave action. In contrast, some macroinvertebrates avoid crevices or rough surfaces because of interference with feeding (e.g., effectiveness of brushing/scraping mouthparts in heptageniid mayflies [Clifford et al. 1989, 1992] and filter-feeding in blackfly larvae [Downes et al. 1998]). Crevice use may vary with life-history stage.

Crevices are especially effective refugia on bare surfaces (e.g., Norton and Fetter 1981; Clifford et al. 1989; Harmsworth and Sleight 1993; Gawne and Lake 1995) that occur commonly in early succession or in harsh habitats. As communities age, crevices may become less important as organisms overgrow crevices and biogenic structures such as mosses, macroalgae, or invertebrates dominate (e.g., Dudley et al. 1986; Sebens 1991; Suren 1991; Dodds and Gudder 1992; Jacobi and Langevin 1996). Disturbances, such as scouring spates in streams or storms in rocky intertidal zones, can remove patches of biogenic structure and reset succession. On such cleaned surfaces, crevices may promote community development by harboring relict populations and promoting the successful establishment of colonizers. For example, diatom assemblages on *Gumaga* cases that have copious crevice areas survive spates better (Bergey 1992) and may recover faster than algae on rounded stream stones.

Effect of disturbance level—The increase in abrasive disturbance from no to high abrasion gave three distinct responses: none, a threshold, or an incremental response. No response to disturbance was seen in the abundance of filamentous algae and diatom biovolume and location on caddisfly cases. Direct impacts of abrasion on caddisfly cases were probably reduced by the depth of the crevices, protec-

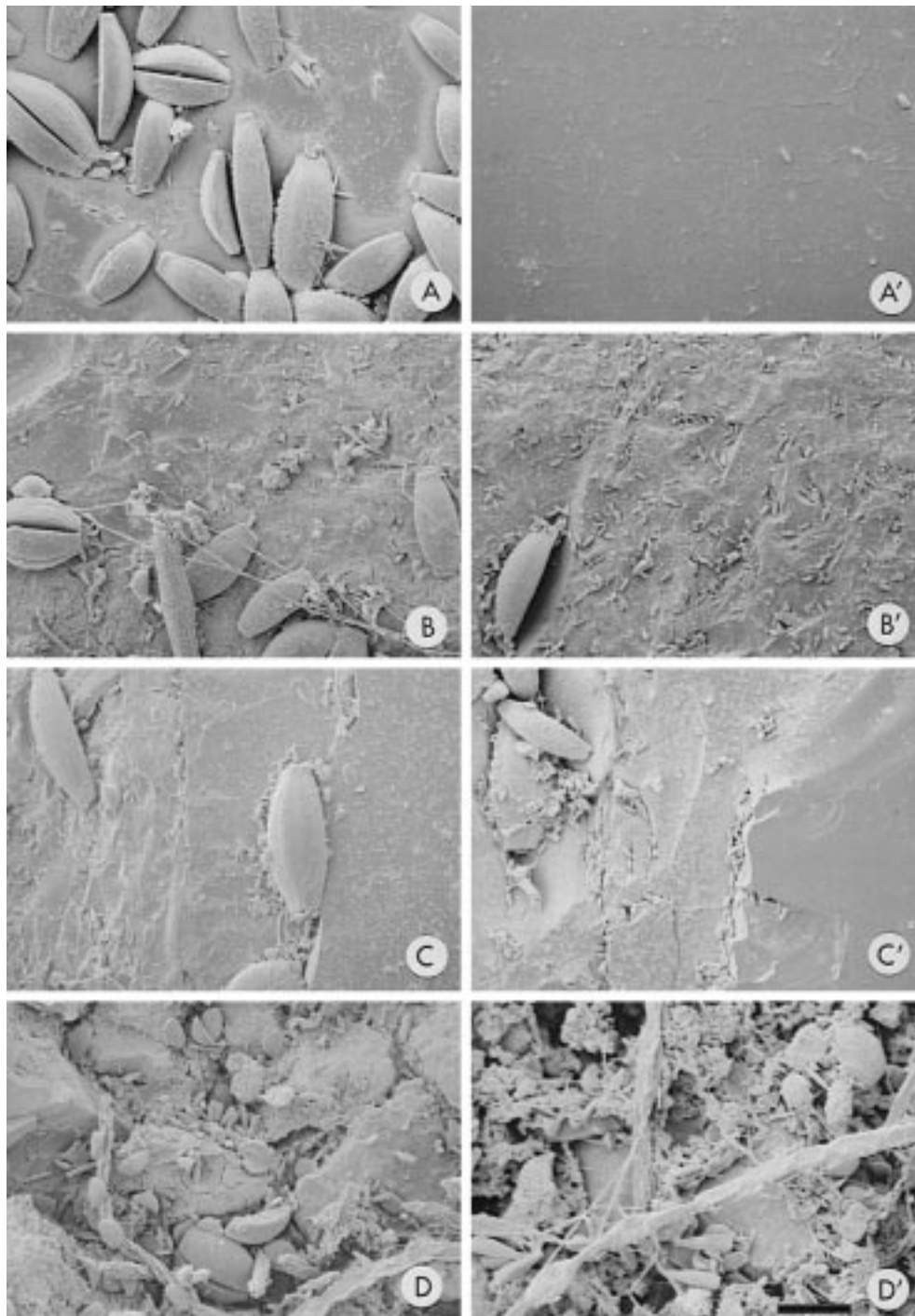


Fig. 4. Examples of diatom assemblages on the four substrate types with no abrasion (left column) and high abrasion (right column). (A–A') smooth glass rods, (B–B') sanded glass rods, (C–C') scratched glass rods, and (D–D') a caddisfly case. The bar in the lower right corner is 50 μm long.

tion of diatoms by emergent algal filaments during abrasion, and the tapered design of the cases (versus the cylindrical glass rods). In contrast, diatom density on all substrates showed a threshold response to the presence and absence of abrasion, whereas detrital content increased as abrasion level increased. This difference between threshold and incremen-

tal effects reflects the tremendous loss of diatoms outside of crevices due to disturbance versus more gradual accumulation of detritus within crevices as the disturbance level increased.

Effect of crevice size—This study supports the hypothesis that crevices may serve as refugia only under conditions in

which crevice and organism sizes are within a particular range. Small crevices contain young stages or small-sized taxa while moderate crevices are effective refugia for a larger organism size range and greater taxonomic diversity. Very large crevices are no longer effective refugia because disturbance agents (including predators) can affect intracrevise areas, even though subcrevices within them may be refugia. Other studies involving crevice size also support this hypothesis. Norton and Fetter (1981) describe the settlement patterns of germlings of the brown alga *Sargassum muticum* in flowing water in the laboratory. Settlement density increased with crevice size, peaked at the optimum crevice size, and decreased thereafter. The distribution of *Littorina* snails in crevices on exposed intertidal zones (Raffaelli and Hughes 1978) is such that small crevices contained small snails, whereas large crevices contained both large and small snails.

The effectiveness of crevice refugia may alter as organisms grow. As individual algae and invertebrates increase in size, they may no longer fit entirely within crevices and may be subject to predation (Keough and Downes 1982; Catesby and McKillup 1998) or other disturbances. Alternatively, these larger individuals may reach a size refuge and no longer be affected by the disturbance (Lubchenco 1983).

In both marine and freshwater habitats, much of the emphasis in studies of crevices has been to document the abundance and taxonomic richness of the organisms inside and outside of crevices, often as a function of increased surface area (e.g., Erman and Erman 1984; Dean and Connell 1987; Hart and Horwitz 1991; Douglas and Lake 1994; Robson and Barmuta 1998). Experimental studies dealing with the mechanisms by which crevices may be refugia and studies exploring the ecological role of crevices are much less common and are needed to increase our understanding of the overall role of crevices in disturbance ecology. Such mechanistic areas of study include documenting conditions inside versus outside of crevices, comparisons across levels and types of disturbances, and further investigation of size relationships among crevices, disturbance agents, and organisms. Larger scale ecological studies include the effects of crevices on the resistance and resilience of disturbed benthic communities and the role of relict populations inside crevices in influencing recovery trajectories.

References

- ANTOINE, S. E., AND K. BENSON-EVANS. 1985. Colonisation rates of benthic algae on four different rock substrata in the River Ithon, Mid Wales, U.K. *Limnologia* **16**: 307–313.
- BARNESE, L. E., R. L. LOWE, AND R. D. HUNTER. 1990. Comparative grazing efficiency of pulmonate and pseudobranch snails. *J. North Am. Benthol. Soc.* **9**: 35–44.
- BATTARBEE, R. W., AND M. J. KNEEN. 1982. The use of electronically counted microspheres in absolute diatom analysis. *Limnol. Oceanogr.* **27**: 184–188.
- BERGEY, E. A. 1992. Biotic and abiotic influences on benthic algal populations in California Coast Range streams. Ph.D. thesis, Univ. California-Berkeley.
- , AND V. H. RESH. 1994. Effects of burrowing by a stream caddisfly on case-associated algae. *J. North Am. Benthol. Soc.* **13**: 379–390.
- BIGGS, B. J. F., AND M. E. CLOSE. 1989. Periphyton biomass dynamics in gravel bed rivers: The relative effects of flows and nutrients. *Freshwater Biol.* **22**: 209–231.
- BLENKINSOPP, S. A., AND M. A. LOCK. 1994. The impact of storm-flow on river biofilm architecture. *J. Phycol.* **30**: 807–818.
- BLINN, D. W., A. FREDERICKSEN, AND V. KORTE. 1980. Colonization rates and community structure of diatoms on three different rock substrata in a lotic system. *Br. Phycol. J.* **15**: 303–310.
- CATESBY, S. M., AND S. C. MCKILLUP. 1998. The importance of crevices to the intertidal snail *Littoraria articulata* (Philippi) in a tropical mangrove forest. *Hydrobiologia* **367**: 131–138.
- CLIFFORD, H. F., R. J. CASEY, AND K. A. SAFFRAN. 1992. Short-term colonization of rough and smooth tiles by benthic macroinvertebrates and algae (chlorophyll *a*) in two streams. *J. North Am. Benthol. Soc.* **11**: 304–315.
- , V. GOTCEITAS, AND R. J. CASEY. 1989. Roughness and color of artificial substratum particles as possible factors in colonization of stream invertebrates. *Hydrobiologia* **175**: 89–95.
- DAVIS, J. A., AND L. A. BARMUTA. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biol.* **21**: 271–282.
- DAYTON, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**: 351–389.
- DEAN, R. L., AND J. H. CONNELL. 1987. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. *J. Exp. Mar. Biol. Ecol.* **109**: 217–247.
- DENICOLA, D. M., AND C. D. MCINTIRE. 1990. Effects of substrate relief on the distribution of periphyton in laboratory streams. I. *Hydrology. J. Phycol.* **26**: 624–633.
- DENNY, M. W., T. L. DANIEL, AND M. A. R. KOEHL. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**: 69–102.
- DODDS, W. K. 1991. Micro-environmental characteristics of filamentous algal communities in flowing freshwaters. *Freshwater Biol.* **25**: 199–209.
- , AND D. A. GUDDER. 1992. The ecology of *Cladophora*. *J. Phycol.* **28**: 415–427.
- DOUGLAS, M., AND P. S. LAKE. 1994. Species richness of stream stones: An investigation of the mechanisms generating the species-area relationship. *Oikos* **69**: 387–396.
- DOWNES, B. J., P. S. LAKE, E. S. G. SCHREIBER, AND A. GLAISTER. 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecol. Monogr.* **68**: 237–257.
- DUDLEY, T. L., S. D. COOPER, AND N. HEMPHILL. 1986. Effects of macroalgae on a stream invertebrate community. *J. North Am. Benthol. Soc.* **5**: 93–106.
- , AND C. M. D'ANTONIO. 1991. The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology* **72**: 297–309.
- ERMAN, D. C., AND N. A. ERMAN. 1984. The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia* **108**: 75–82.
- FAIRWEATHER, P. G. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Aust. J. Ecol.* **13**: 401–409.
- FIGUEIREDO, M. A. D. O., J. M. KAIN, AND T. A. NORTON. 1996. Biotic interactions in the colonization of crustose coralline algae by epiphytes. *J. Exp. Mar. Biol. Ecol.* **199**: 303–318.
- FISHER, S. G., AND N. B. GRIMM. 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verh. Int. Verein. Limnol.* **23**: 1183–1189.
- GAWNE, B., AND P. S. LAKE. 1995. Effects of microspatial com-

- plexity on a herbivore–epilithon interaction in an Australian upland stream. *Freshwater Biol.* **33**: 557–565.
- GOSSELIN, L. A., AND F. CHIA. 1995. Distribution and dispersal of early juvenile snails: Effectiveness of intertidal microhabitats as refuges and food sources. *Mar. Ecol. Prog. Ser.* **128**: 213–223.
- HARLIN, M. M., AND J. M. LINDBERGH. 1977. Selection of substrata by seaweeds: Optimal surface relief. *Mar. Biol.* **40**: 33–40.
- HARMSWORTH, G. C., AND M. A. SLEIGH. 1993. Colonization of non-living surfaces in streams by peritrich ciliates. *Eur. J. Protistol.* **29**: 294–301.
- HART, D. D., AND R. J. HORWITZ. 1991. Habitat diversity and the species–area relationship: Alternative models and tests, p. 47–68. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky [eds.], *Habitat structure: The physical arrangement of objects in space*. Chapman and Hall.
- JACOBI, C. M., AND R. LANGEVIN. 1996. Habitat geometry of benthic substrata: Effects on arrival and settlement of mobile epifauna. *J. Exp. Mar. Biol. Ecol.* **206**: 39–54.
- JACOBY, J. M. 1987. Alterations in periphyton characteristics due to grazing in a Cascade foothill stream. *Freshwater Biol.* **18**: 495–508.
- JOHNSON, L. E. 1994. Enhanced settlement on microtopographical high points by the intertidal red alga *Halosaccion glandiforme*. *Limnol. Oceanogr.* **39**: 1893–1902.
- KEOUGH, M. J., AND B. J. DOWNES. 1982. Recruitment of marine invertebrates: The role of active larval choices and early mortality. *Oecologia* **54**: 348–352.
- KOEHL, M. A. R. 1984. How do benthic organisms withstand moving water? *Am. Zool.* **24**: 57–70.
- KOHN, A. J., AND P. J. LEVITEN. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* **25**: 199–210.
- LAMBERTI, G. A., S. V. GREGORY, L. R. ASHKENAS, A. D. STEINMAN, AND C. D. MCINTIRE. 1989. Productive capacity of periphyton as a determinant of plant–herbivore interactions in streams. *Ecology* **70**: 1840–1856.
- LUBCHENCO, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* **64**: 1116–1123.
- LUTTENTON, M. R., AND R. G. RADA. 1986. Effects of disturbance on epiphytic community architecture. *J. Phycol.* **22**: 320–326.
- MCCOY, E. D., AND S. S. BELL. 1991. Habitat structure: The evolution and diversification of a complex topic, p. 3–27. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky [eds.], *Habitat structure: The physical arrangement of objects in space*. Chapman and Hall.
- MCGUINNESS, K. A., AND A. J. UNDERWOOD. 1986. Habitat structure and the nature of communities on intertidal boulders. *J. Exp. Mar. Biol. Ecol.* **104**: 97–123.
- MEADOWS, P. S., AND J. G. ANDERSON. 1966. Micro-organisms attached to marine and freshwater sand grains. *Nature* **212**: 1059–1060.
- MENGE, B. A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* **46**: 355–393.
- . 1978. Predation intensity in a rocky intertidal community: Relation between predator foraging activity and environmental harshness. *Oecologia* **34**: 1–16.
- MILLER, A. R., R. L. LOWE, AND J. T. ROTENBERRY. 1987. Succession of diatom communities on sand grains. *J. Ecol.* **75**: 693–709.
- NORTON, T. A. 1983. The resistance to dislodgment of *Sargassum muticum* germlings under defined hydrodynamic conditions. *J. Mar. Biol. Assoc. U.K.* **63**: 181–193.
- , AND R. FETTER. 1981. The settlement of *Sargassum muticum* propagules in stationary and flowing water. *J. Mar. Biol. Assoc. U.K.* **61**: 929–940.
- NOWELL, A. R. M., AND P. A. JUMARS. 1984. Flow environments of aquatic benthos. *Annu. Rev. Ecol. Syst.* **15**: 303–328.
- PETERSON, C. G. 1996. Response of benthic algal communities to natural physical disturbance, p. 375–402. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe [eds.], *Algal ecology: Freshwater benthic ecosystems*. Academic.
- POWER, M. E. 1990. Resource enhancement by indirect effects of grazers: Armored catfish, algae, and sediment. *Ecology* **71**: 897–904.
- RAFFAELLI, D. G., AND R. N. HUGHES. 1978. The effects of crevice size and availability on populations of *Littorina rudis* and *Littorina neritoides*. *J. Anim. Ecol.* **47**: 71–83.
- RESH, V. H., AND OTHERS. 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* **7**: 433–455.
- ROBSON, B. J., AND L. A. BARMUTA. 1998. The effect of two scales of habitat architecture on benthic grazing in a river. *Freshwater Biol.* **39**: 207–220.
- SANSON, G. D., R. STOLK, AND B. J. DOWNES. 1995. A new method for characterizing surface roughness and available space in biological systems. *Funct. Ecol.* **9**: 127–135.
- SCRIMGEOUR, G. J., J. M. CULP, M. L. BOTHWELL, F. J. WRONA, AND M. H. MCKEE. 1991. Mechanisms of algal patch depletion: Importance of consumptive and non-consumptive losses in mayfly–diatom systems. *Oecologia* **85**: 343–348.
- SEAPY, R. R., AND M. M. LITTLER. 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Mar. Biol.* **71**: 87–96.
- SEBENS, K. P. 1991. Habitat structure and community dynamics in marine benthic systems, p. 211–234. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky [eds.], *Habitat structure: The physical arrangement of objects in space*. Chapman and Hall.
- SNELGROVE, P. V. R., C. A. BUTMAN, AND J. P. GRASSLE. 1993. Hydrodynamic enhancement of larval settlement in the bivalve *Mulinia lateralis* (Say) and the polychaete *Capitella* sp. I in microdepositional environments. *J. Exp. Mar. Biol. Ecol.* **168**: 71–109.
- SOUSA, W. P. 1984. Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. *Ecology* **65**: 1918–1935.
- STEINMAN, A. D., C. D. MCINTIRE, S. V. GREGORY, G. A. LAMBERTI, AND L. R. ASHKENAS. 1987. Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. *J. North Am. Benthol. Soc.* **6**: 175–188.
- SUREN, A. M. 1991. Bryophytes as habitat for New Zealand stream invertebrates. *Freshwater Biol.* **26**: 399–418.
- THIRB, H. H., AND K. BENSON-EVANS. 1983. Studies on the life cycle of *Lemanea* using natural and artificial substrates. *Hydrobiologia* **98**: 119–124.
- WITMAN, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecol. Monogr.* **55**: 421–445.
- ZAR, J. H. 1996. *Biostatistical analysis*, 3rd ed. Prentice-Hall.

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