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HOW FINE SEDIMENT IN RIVERBEDS IMPAIRS GROWTH AND SURVIVAL OF JUVENILE SALMONIDS

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Abstract. Although excessive loading of fine sediments into rivers is well known to degrade salmonid spawning habitat, its effects on rearing juveniles have been unclear. We experimentally manipulated fine bed sediment in a northern California river and examined responses of juvenile salmonids and the food webs supporting them. Increasing concentrations of deposited fine sediment decreased growth and survival of juvenile steelhead trout. These declines were associated with a shift in invertebrates toward burrowing taxa unavailable as prey and with increased steelhead activity and injury at higher levels of fine sediment. The linear relationship between deposited fine sediment and juvenile steelhead growth suggests that there is no threshold below which exacerbation of fine-sediment delivery and storage in gravel bedded rivers will be harmless, but also that any reduction could produce immediate benefits for salmonid restoration.

Key words: fine sediment; Oncorhynchus mykiss; *Pacific salmonids; parr; river food web; sedimentation; steelhead trout.*

INTRODUCTION

Throughout western North America, historically large populations of native anadromous salmonids are in severe decline or extinct. In the United States alone, 26 Evolutionarily Significant Units of Pacific salmonid are currently threatened or endangered (National Marine Fisheries Service 2003). These declines are in large part attributable to degradation of spawning and rearing habitat (Nehlsen et al. 1991, Frissell 1993), a major cause of which is increased loading and storage of fine sediments (Miller et al. 1989, Bisson et al. 1992, Waters 1995).

The storage of fine sediments (particle sizes <2 mm median diameter) in gravel-bedded rivers is normally a transient phenomenon, as sediments enter and leave river channels naturally. Without frequent resupply from upstream sources or termination of gravel mobilizing flows, fine sediment is carried downstream to lowland reaches or the sea. Yet anthropogenic activities have greatly increased the storage of fine sediment in rivers throughout the world. Where it comes to rest in river reaches, fine sediment can transform the topography and porosity of the gravel riverbed in ways that profoundly affect the emergent ecosystem, particularly during biologically active periods of seasonal low flow. It is during these periods of low flow that demographically critical juvenile rearing occurs for salmonids.

Despite scientific, political, and commercial motivation to quantify the relationship between fine-sediment loading and juvenile salmon production in river systems (and in particular, thresholds beyond which impairment occurs), no causal relationship has been established. Research on the influence of deposited fine sediment on juvenile salmonids has consisted primarily of laboratory work and correlative field studies comparing salmonid assemblages before and after or upstream and downstream of a fine-sediment influx, or among rivers with differing bed compositions. This work has suggested that fine-sediment deposition negatively impacts juvenile salmonids and the food webs supporting them (Crouse et al. 1981, Murphy and Hall 1981, Reeves et al. 1993), but field experimental support has been lacking. As a result, mechanisms by which these effects arise are also poorly understood. This is due in part to difficulty in isolating the impacts of fine sediment from other co-varying physical factors (e.g., flow velocity and turbulence, channel depth, plan form morphology) that can also influence salmonid performance.

Here we provide the results of an experiment designed to isolate the impact of fine sediment on a juvenile salmonid (*Oncorhynchus mykiss*) in its natural habitat. We manipulated fine bed sediment in replicate

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FIG. 1. Juvenile steelhead over 100%, 80%, and 0% embedded substrates (left to right).

channels in the South Fork Eel River, California (39°43′45″ N, 123°38′40″ W) and measured the growth and behavior of steelhead parr and the density and composition of aquatic invertebrate assemblages on which they prey.

METHODS

In June 2000, we constructed six 2 m long × 1 m wide channels in the downstream ends of each of four river pools distributed over a 3-km reach. The 24 channels consisted of vinyl flooring secured flush to the riverbed with rebar stakes and metal pipe, with walls protruding 15 cm above the water surface. Each channel was assigned to one of six fine-sediment loadings in a complete randomized block design. We filled each channel to a depth of 15 cm with pebbles, gravels, and cobbles collected from the adjacent riverbed and sifted through a 6-mm sieve. The size range of these coarse framework particles was 6–90 mm diameter. Median size class by weight was 22–32 mm diameter. The highest sediment loading treatment (''100% embeddedness'') received enough fine sediment so that only the upper surfaces of the coarse framework particles were visible. At this level, further additions of fine sediment would not alter the topography or porosity of the bed in a biologically meaningful manner. The other five treatments at each site received 80, 60, 40, 20, and 0% of that volume (Fig. 1). Fine sediment consisted of particles with diameter <2 mm. Median size class by weight was 0.60–1.18 mm diameter.

After allowing 25 d for invertebrate colonization and algal growth, we closed the upstream and downstream ends of each channel with 6-mm mesh walls that were permeable to invertebrate drift and smaller prey fishes but did not allow passage of juvenile steelhead. We seined steelhead parr from the river and measured and weighed each. We then stocked each channel with two parr (1 parr/m^2), approximating densities in the adjacent open habitat. At stocking, standard length ranged from 37 to 54 mm and mass from 0.65 to 2.53 g. The two fish in each channel were chosen to differ in length by 5–9 mm. Fish were confined for 46 d, during which time we conducted extensive behavioral observations. Observers approached the channels, remained motionless for 5 min, and then began 10-min continuous observation periods, in which swimming was distinguished from holding and sheltering behavior and all feeding movements and intraspecific interactions were recorded. A minimum of four such observations per experimental channel were conducted during the time fish were confined.

At experiment's end, all steelhead parr were measured, weighed, and released. Any fish that died over the course of the experiment were immediately replaced. Injury was inferred as the cause of death when a fish died after developing fin rot. We observed these infections on fish wounded during conspecific attacks. The infection whitened dorsal or caudal fins, spread from the fin into the body tissue, and resulted in death within 2 d. Analyses of growth included only steelhead that were enclosed in experimental channels for a minimum of 25 d. All growth measurements are reported on a per day basis.

We sampled the invertebrate community in each channel from sediment cores. Just prior to stocking steelhead in the channels and on the day after steelhead were removed, three circular cores (14 cm diameter) were taken from each channel and pooled. The sediment was elutriated to dislodge invertebrates, and all organisms were collected and stored in 70% ETOH. All organisms were classified to family and assigned to one of three broad functional groups (i.e., burrowing, armored, and vulnerable) based on life history traits influencing availability to steelhead fry. This information was gleaned from published reports (Merritt and Cummins 1996, Resh et al. 1997) and from direct field observation. Burrowing taxa included oligochaete worms, freshwater clams (Sphaeriidae), one genus of silt-encased Trichoptera (Sericostomatidae: Gumaga), one family of Megaloptera (Sialidae), two families of

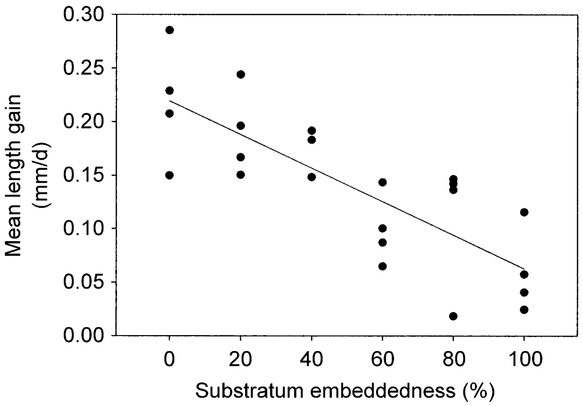

FIG. 2. Growth of juvenile steelhead trout in relation to direct manipulation of substratum embeddedness ($R^2 = 0.63$, $P < 0.0001$). Changes in growth in mass were similar ($R^2 = 0.59$, $P < 0.0001$). Analyses of relative growth, which accounts for differences in initial size, and of instantaneous growth rate produced similar linear patterns ($R^2 = 0.52$, $P = 0.0001$ and $R^2 = 0.53$, $P < 0.001$, respectively). One experimental channel with 40% substratum embeddedness contained no fish that survived the minimum 25 d and is thus excluded from the analysis.

Diptera (Ceratopogonidae and Tipulidae), and one family of Odonata (Gomphidae). Armored taxa included two families of snails (Planorbidae and Physidae), two families of stone-encased Trichoptera (Helicopsychidae and Limnephilidae), and wood-encased Limnephilidae over 10 mm in length. Vulnerable prey included three families of wood-encased Trichoptera under 10 mm in length (Lepidostomidae, Brachycentridae, and Limnephilidae), one family of free-living Trichoptera (Rhyacophilidae), four families of Ephemeroptera (Heptageniidae, Baetidae, Trichorythidae, and Leptophlebiidae), two families of Plecoptera (Perlidae and Chloroperlidae), three families of Coleoptera (Elmidae, Haliplidae, and Psephenidae), two families of Diptera (Blephariceridae and Chironomidae), and three families of Odonata (Aeshnidae, Lestidae, and Coenagrionidae). Individual insect dry biomass was determined based on length regressions published in the literature or generated in this study. Biomass of burrowing organisms was log transformed to meet assumptions of regression analysis.

RESULTS

Steelhead growth decreased steeply and roughly linearly with increasing fine-sediment concentration (Fig. 2). This result was consistent with the effects of sedimentation on the food supply available to steelhead. With increasing fine sediment, invertebrate assemblages shifted from available prey organisms (i.e., epibenthic grazers and predators) to unavailable burrowing taxa (Fig. 3), so that steelhead confined to channels with higher levels of sedimentation experienced lower food availability than those in less embedded channels.

In addition to reducing prey availability, deposited fine sediments increased steelhead activity. At higher levels of embeddedness, fine sediments filled spaces under and between coarse cobbles, producing a flat and featureless bed. As interstitial refuges and prey declined, steelhead spent less time sheltering behind or under cobbles and more time actively swimming (Fig. 4a). Steelhead also exhibited higher levels of intraspecific aggression, including attacks (Fig. 4b), as prey availability and visual separation between fish decreased with higher fine-sediment levels. This likely explains the increased incidence of at least one mortality event in more heavily embedded channels (logistic regression, $P < 0.05$, $n = 24$; Fig. 5).

DISCUSSION

Anadromous salmonids have a complex life history that exposes them to a wide range of threats across multiple life stages. As a commercially, culturally, and ecologically valuable group of animals, considerable research effort has been devoted to quantifying the impacts of these various threats (e.g., dams, fish farms, overharvesting, hatchery fish, invasive organisms, and river and estuarine pollution, degradation, and habitat loss) on wild salmon populations. It is widely known that salmonid stocks decline when land use increases fine-sediment delivery to gravel-bedded rivers (Bisson and Sedell 1984, Reeves et al. 1993, Waters 1995), but mechanistic understanding of the role of fine sediment

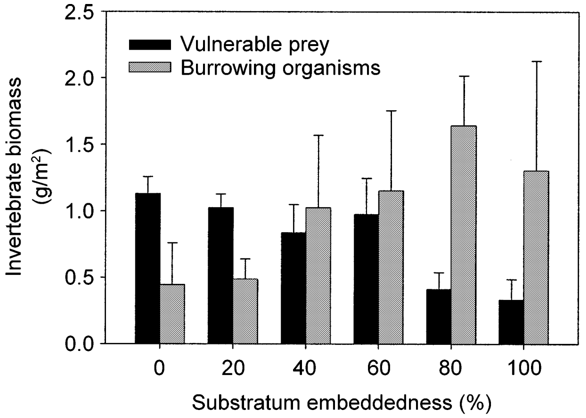

FIG. 3. Biomass of invertebrates from sediment core samples taken at the experiment's end (mean + 1 SE). There were significant linear relationships between fine sediment and the biomass of individual functional groups of invertebrates. As fine sediment increased (greater embeddedness), biomass of vulnerable prey declined ($R^2 = 0.42$, $P < 0.001$) and biomass of unavailable burrowing organisms increased ($R^2 = 0.23$, $P = 0.02$). A similar pattern was found in the prestocking samples taken on 30 June; there was a significant and negative relationship between fine sediment and vulnerable prey biomass ($R^2 = 0.35$, $P = 0.003$) and a significant and positive relationship between fine sediment and burrowing organism biomass ($R^2 = 0.37$, $P = 0.002$). Fine sediment had no influence on the biomass of armored grazers. Similar taxon-specific responses to fine sediment have been observed in other studies (Bjornn et al. 1977, Mebane 2001).

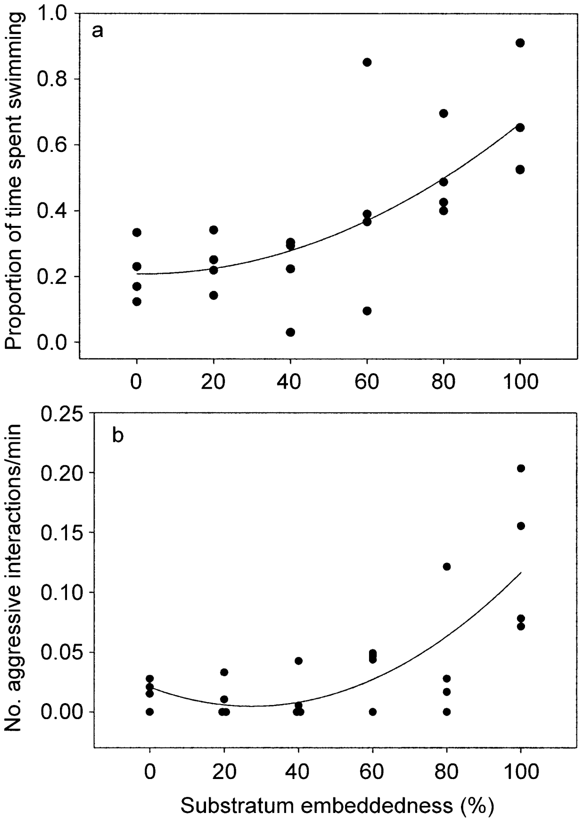

FIG. 4. Behavior of steelhead parr in experimental channels. Data represent mean values for each experimental channel. (a) Fish activity (swimming time) is represented by the best-fit line from a second-order polynomial regression ($R^2 = 0.45$, $P = 0.004$). The difference in activity between steelhead in 100% embeddedness channels and those in 0% embeddedness channels translates to a 47% higher energy expenditure, based on metabolic data for the same size class of sockeye salmon (*O. nerka*) under similar environmental conditions (Brett and Glass 1973), energy equivalents of animal oxygen consumption (Elliot and Davison 1975), and assuming a standard 12-h period of nightly inactivity. (b) Intraspecific aggression is represented by the best-fit line from a second-order polynomial regression ($R^2 = 0.56$, $P = 0.0002$).

in these declines has been restricted to the embryo stage.

When deposited in riverbeds, fine sediment can reduce survival of embryos and emergence of fry from redds (nests in the riverbed) by decreasing dissolved oxygen and water exchange and entrapping emerging fry (Chapman 1988). Survival of embryos may not, however, limit salmonid populations. Even where sediment influxes destroy many redds, higher survival rates from redds in suitable substrate in heterogeneous reaches could compensate for these losses (Magee et al. 1996). Fry and parr from successful redds must then contend with changes in rearing habitat imposed by fine sediment. Even fry hatched from redds in unimpacted tributaries and side channels are susceptible, as they ultimately rear in larger channels (Reiser and Bjornn 1979, Hackelroad and La Marr 1993), where larger drainage areas and lower gradients increase the likelihood of fine-sediment loading and storage. Steelhead trout may be particularly vulnerable, as they remain in natal streams up to two years longer than other anadromous salmonids. By confining juvenile steelhead over discreet patches of riverbed with experimentally imposed fine-sediment concentrations, we were able to investigate the mechanisms underlying previously observed patterns of salmonid declines in response to fine-sediment loading and storage.

The decreases in steelhead growth and survival we observed with increasing fine-sediment deposition were associated with lower prey availability and higher activity, aggression, and risk of injury. Declines in growth rates lower survival of salmonids and other fishes (Werner and Gilliam 1984, Walters and Korman 1999). Larger body size confers higher survival of over-wintering (Quinn and Peterson 1996) and smolting (Ward and Slaney 1988, Yamamoto et al. 1999) juvenile salmonids. Recent demographic models indicate that these juveniles may be the best age classes to target for effective conservation measures. Even modest reductions in juvenile mortality (i.e., 6–11%) are predicted to reverse population declines in Snake River chinook salmon (*Oncorhynchus tshawytscha*), regardless of adult dam passage success and egg survival (Kareiva et al. 2000). Differences in growth and survival imposed by fine sediment could therefore have important population-level impacts.

The flux of fine sediment into and out of river systems, while a natural process, has been greatly exacerbated by humans. Land uses that increase erosion, particularly road construction (Burns 1972, Megahan and Kidd 1972, Beschta 1978, Reid et al. 1981), increase fine-sediment loading, while flow regulation and diversion diminish transport and removal. The steep dissected terrain and weak parent material of drainages along California's North Coast make rivers of this region particularly vulnerable to land-management prac-

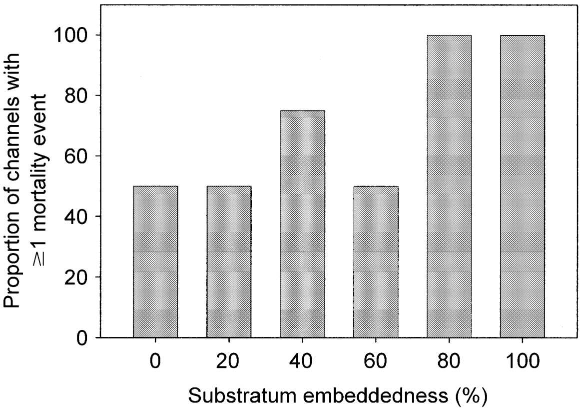

FIG. 5. Steelhead mortality in experimental channels, in relation to fine sediment.

tices that increase erosion. Increased storage of fines dramatically alters river ecosystems. This state is transient over geomorphic time scales, as fine-sediment pulses move down through steeper, gravel-bedded portions of drainage networks and eventually are discharged into lowland floodplains, estuaries, and the sea. In addition, certain steep microhabitats may not retain fine sediments even in rivers receiving heavy loading. In this sense, the river is potentially self-cleaning. If land uses that increase loading or decrease transport of fine sediments continue unabated, however, areas of formerly suitable juvenile rearing habitat may be lost from the riverbed long enough to cause irreversible population declines in resident salmonids. This concern is particularly important for juvenile salmonids, whose territoriality limits their ability to crowd into shrinking areas of good habitat.

Many states and countries throughout the world have regulations directed at fine-sediment management, intended in part to protect native and introduced salmon. None of these regulations derives from known quantitative relationships between the amount of loaded or stored fine sediment and the performance of salmonids in the receiving river. In particular, it is not known whether there might be an acceptable level of increase in fine-sediment loading that causes no damage to salmonids or the ecosystems supporting them. Nearly all sediment management regulations, however, make this reasonable assumption (U.S. EPA 1999).

Our experiment demonstrates that fine-sediment deposition, even at low concentrations, can decrease growth and survival of juvenile salmonids. We find no threshold below which fine-sediment addition is harmless. These results suggest that any augmentation of fine-sediment deposition in steelhead bearing rivers in this region will further impair this potentially population-limiting life stage, while land management practices that decrease fine-sediment loading or storage in channels may benefit salmonid populations.

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