Structures Linking Physical and Biological Processes in Headwater Streams of the Maybeso Watershed, Southeast Alaska

Mason D. Bryant, Takashi Gomi, and Jack J. Piccolo

Abstract: We focus on headwater streams originating in the mountainous terrain of northern temperate rain forests. These streams rapidly descend from gradients greater than 20% to less than 5% in U-shaped glacial valleys. We use a set of studies on headwater streams in southeast Alaska to define headwater stream catchments, link physical and biological processes, and describe their significance within watersheds. We separate headwater stream systems into four units that have distinct hydrologic and geomorphic processes that link terrestrial processes to aquatic systems. Headwater streams collect, process, and transport material downstream. Physical and biological processes in headwater streams are complex and closely tied to terrestrial processes. Steps and step pools formed by large wood are keystone structures that link physical processes to biological processes and increase channel complexity. Large and coarse wood debris dams form in-channel step structures and act as valves that regulate the downstream flow of material. A large amount of inorganic and organic sediment is stored in step structures, which may be biological hotspots in headwater streams. Step pools formed by large woody debris are critical habitat for Dolly Varden (*Salvelinus malma*), juvenile coho salmon (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*) in reaches with gradients from less than 4% to those greater than 10%. Landslides and debris flows are the dominant channel-altering processes in headwater streams and remove the step profile. Management activities that increase the number and frequency of channel disturbance events in headwater streams can have important and long-term consequences throughout a watershed. FOR. SCI. 53(2):371–383.

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HEADWATER STREAMS are small, but they are numerous. They may compose up to 80% of the length of a stream network (Schumn 1956, Shreve 1969), and their cumulative effect in a watershed can be substantial. Among other functions, they are an important source of inorganic and organic matter derived from terrestrial sources to larger downstream reaches in watersheds. The river continuum paradigm and its offsprings bring them into the larger context of watershed function (Vannote et al. 1980, Ward and Stanford 1983, Minshall et al. 1985). These paradigms provide the theoretical basis for many of the linkages between terrestrial and aquatic systems of headwater streams and downstream reaches.

Headwater streams are small, often difficult to recognize from the finest scales of topographic maps, and are poorly defined (Meyer and Wallace 2001, Benda et al. 2004). Furthermore, the steep channel reaches (greater than 10% in gradient) often do not support fish, and adjacent downstream sections that may support fish are frequently not recognized as fish streams because of their small size and high gradient (Bryant et al. 2004). As a result of their small size, perceived lack of fish, and vague definition, they are often overlooked or discounted in management plans that affect watersheds.

Until recently, physical and chemical processes have been the primary concern and subject of inquiry for headwater streams (Swanston 1967, Patric and Swanston 1968, Likens et al. 1977, Tripp and Poulin 1986, Benda 1990, Johnson et al. 2000). The influence of riparian vegetation and large wood in headwater streams was initially described by Heede (1972, 1985a) and Bilby and Likens (1980). Numerous other studies describe the physical and chemical process in headwater streams in Hubbard Brook and elsewhere (Bilby 1981). Fewer studies directly address stream biota in headwater streams, particularly those in mountainous terrain. Most of the few studies that address the biotic community are on invertebrates (Wallace et al. 1991, Piccolo and Wipfli 2002, Wipfli and Gregovich 2002, Herlihy et al. 2005). Amphibians have been identified as important residents of headwater streams (Wilkins and Peterson 2000, Cole et al. 2003, Lowe 2003). In some cases, they are endemic to headwater streams (Adams and Bury 2002). Most of the studies of fish populations in headwater streams are from low-gradient (less than 5%) streams (Lotrich 1973, Schlosser 1982, Labbe and Fausch 2000, Roni 2002). A few studies report on populations in higher gradient systems (Young 1996, Adams et al. 2000, Bryant et al. 2004). These disparate studies identify important components of headwater streams and their direct or indirect influence on downstream habitats.

Meyer and Wallace (2001) provide an overview of processes and environmental effects on headwater streams in

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lower-elevation watersheds in the southeastern United States. Gomi et al. (2002) provide an overview of some of the processes in high-gradient mountainous headwater streams commonly found along the North Pacific coast of North America. Our focus is on headwater streams originating in steep-gradient landscapes of temperate rain forests. These often occur in watersheds that support socially and economically important salmonids. Because headwater streams are small and closely connected to upland forests, they may be more susceptible to management practices in upslope forests. Furthermore, many of these small high-gradient streams support both anadromous and nonanadromous salmonids in their lower reaches.

We use a set of studies conducted in headwater streams in the Maybeso Experimental Watershed, southeast Alaska, to illustrate some of the connections between physical processes and biological components, including fish in high-gradient headwater streams (Gomi et al. 2001, Piccolo and Wipfli 2002, Wipfli and Gregovich 2002, Gomi et al. 2003, Gomi and Sidle 2003, Bryant et al. 2004). These studies cover three major components: (1) stream channel morphology and sediment dynamics, (2) organic and invertebrate drift, and (3) salmonid populations. The studies are listed in Figure 1, where they are associated with the general location and processes within the system. Large wood appears to be a "keystone" feature that influences many of the processes.

Our goal is to illustrate linkages between physical and biological processes in headwater streams of mountainous regions (gradients greater than 5%) in southeast Alaska and the Pacific Northwest. We use a case study watershed in southeast Alaska; however, the key processes that we identify can occur throughout the mountainous Pacific Northwest. To accomplish this goal, we define headwater stream characteristics, and summarize geomorphic and biological processes in headwater streams of mountainous regions (gradients greater than 5%; channel width less than 4 m). We demonstrate a qualitative model to illustrate linkages between physical and biological processes and potential responses to natural and anthropogenic disturbance.

Study Sites: The Maybeso Experimental Watershed

Maybeso Experimental Watershed is located in the Tongass National Forest, Prince of Wales Island, Southeast Alaska (Figure 2). The drainage area of the Maybeso watershed is 39 km^2. The watershed is part of the temperate rainforest that extends along the north Pacific Coast from southeast Alaska to Oregon (Alaback 1991). The climate is cool and wet, with a mean annual temperature of 10°C and mean annual precipitation of 2,800 mm. The U-shaped glacial valley is covered by a varying thickness of glacial till that was formed during late Wisconsinan glacial advance (Swanston 1967). Depth of soil plus the thin veneer of glacial till ranges from 0.30 to 1.0 m. Forest vegetation is dominated by western hemlock *Tsuga heterophylla* [Raf.] Sarg.), Sitka spruce (*Pieces sitchensis* [Bong.] Carr.), western redcedar (*Thuja plicata* Donn), and red alder (*Alnus rubra* Bong.) (Alaback 1982). Pink (*Oncorhynchus gorbuscha* Walbaum), chum (*O. keta*, Walbaum) and coho salmon (*O. kisutch* Walbaum), cutthroat trout (*O. clarkii* Richardson), steelhead (*O. mykiss,* Walbaum), and Dolly Varden (*Salvelinus malma* Walbaum) are present throughout the main channel and tributaries (Bryant 1985). Other species include sculpins (*Cottus* sp) and threespine stickleback (*Gasterosteus aculeatus* Linnaeus). Juvenile coho salmon,

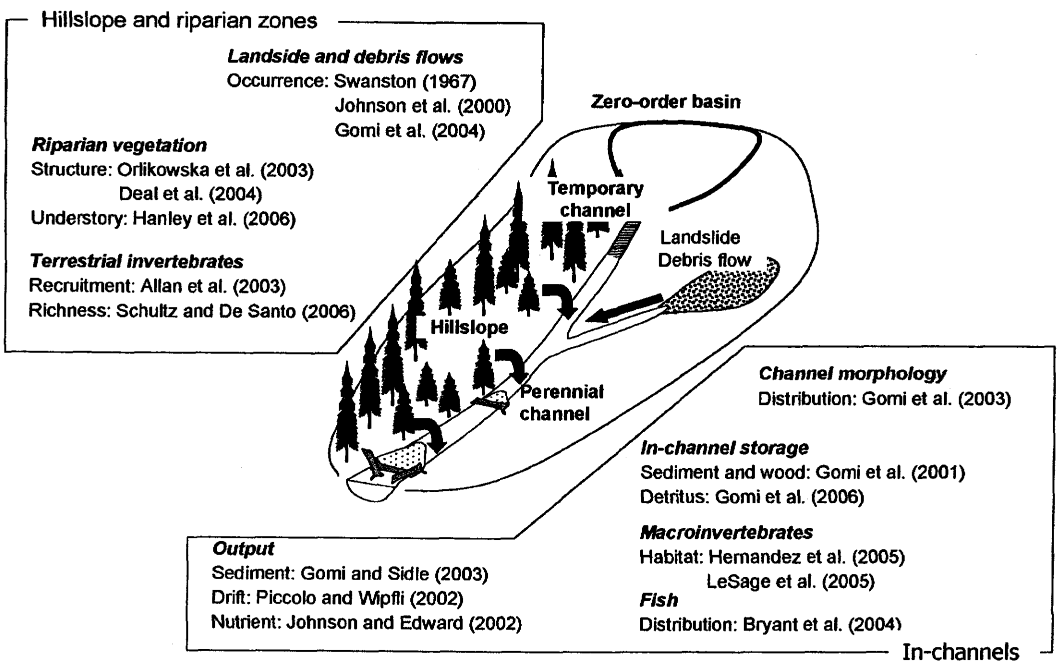

Figure 1. Schematic of a headwater stream network showing locations of major components of a headwater catchment and the studies related to the headwater streams of the Maybeso watershed.

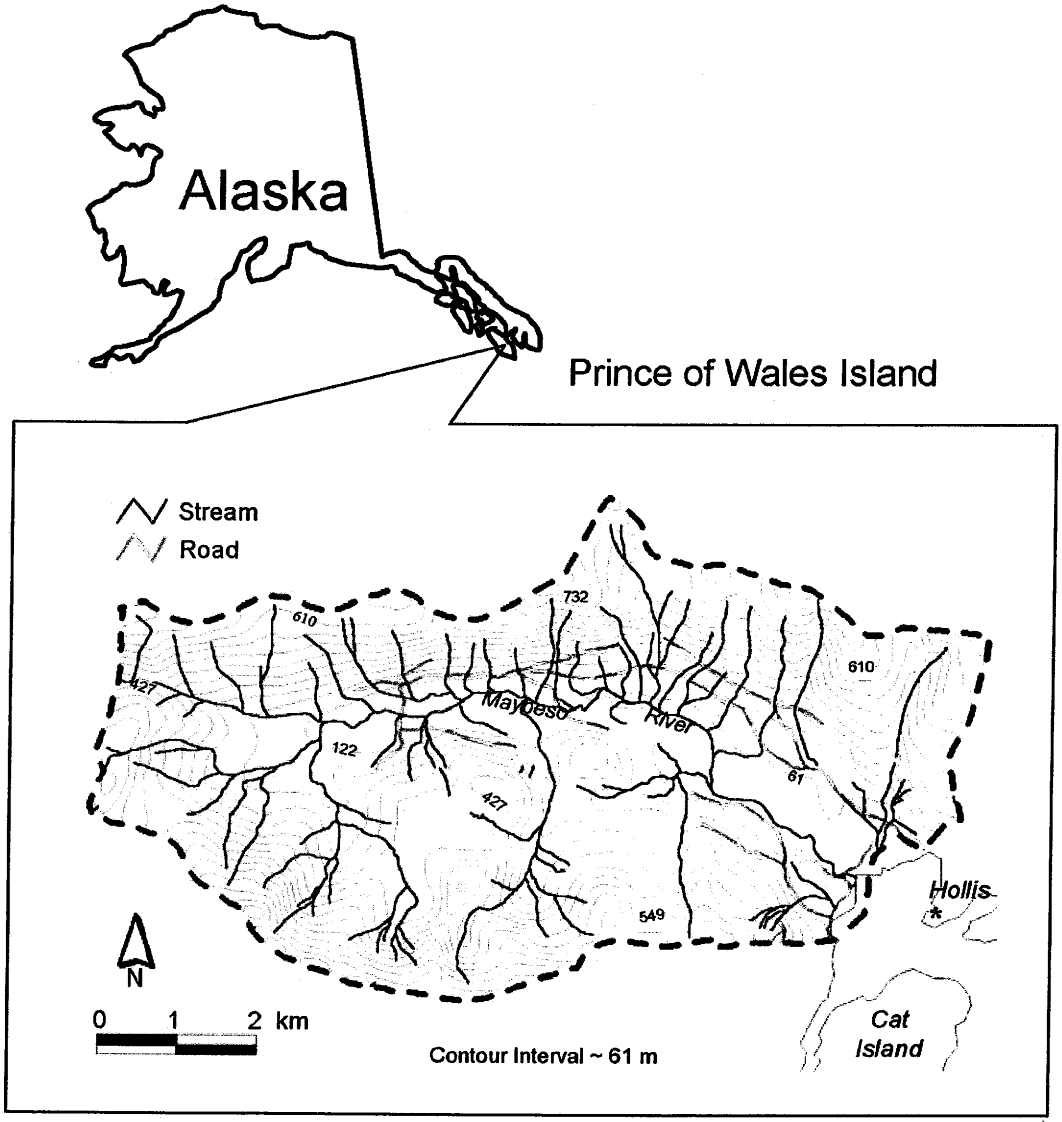

Figure 2. Location of Maybeso Experimental Watershed and the study sites of the headwater streams on Prince of Wales Island, southeast Alaska.

cutthroat trout, steelhead, and Dolly Varden were present in the headwater streams (Bryant et al. 2004).

The first large-scale logging in southeast Alaska started in 1953 in the Maybeso watershed. About 25% of the watershed (10 km^2), including riparian corridors along the mainstream and tributaries, was clearcut logged (Bryant 1980). New growth (less than 50 years old) Sitka spruce and western hemlock are the dominant tree species in most of the area that was logged. Landslides and mass movement events were common throughout the watershed following the cessation of major logging activity in 1960 and continue through the present. Landslides were more common in the logged area than in the unlogged area of Maybeso watershed based on the sequence of air photo observations from 1959 to 1996 (Gomi et al. 2004). Riparian vegetation was highly influenced by past disturbance regimes. Sitka alder rapidly revegetate riparian zones disturbed by landslides and debris flows (Deal et al. 2004, Orlikowska et al. 2004, Hanley et al. 2006).

Characteristics of a Headwater Stream

Benda et al. (2004) assert that there is no universally accepted definition of headwater streams. They point out that most are not readily apparent on topographic maps and are frequently not included in many GIS databases (Meyer and Wallace 2001, Gomi et al. 2002, Benda et al. 2005). The issue may be partially circumvented by considering them in the context of the headwater catchment. This may also be useful from an interdisciplinary perspective. A headwater stream from a hydrologic perspective can be different from that of an aquatic biologist. From the hydrologic perspective, headwater streams begin at the point where they begin to collect and direct water downstream. As water is retained in defined streambanks, headwater streams begin to support aquatic organisms and aquatic processes begin to become important. At this point, they enter the view of the aquatic ecologist. Further downstream, fish begin to appear and they become important to fishery managers and often more so to land managers.

The headwater catchment is separated into four units, hillslopes, zero-order basins, temporary channels, and perennial first- and second-order streams by Gomi et al. (2002) and illustrated in Figure 1. These also have distinct biological processes related to their physical processes (Figure 3). The upper most components and least well defined are the hillslope and zero-order basins, which generally have no channelized flow. Water is collected on hillslope and zero-order basins either through overland flow or subsurface flow; however, subsurface flow can be complex and depend on soil texture, soil depth, and preferential flow paths such as root channels (Sidle et al. 2000). The definition of zero-order basins as "unchannelized hollows with converging contour lines" is used by Gomi et al. (2002).

The next downstream unit is the temporary channel, the first unit with defined banks (Figure 3). These channels flow during wet periods and often for only a few days, typically during and after storm events. Perennial first- and second-order streams may arise from zero-order basins, temporary streams, seeps or springs, or from upwelling sources in karst topography. Depending on hydrologic conditions, surface flows may be intermittent or discontinuous during some periods.

Hydrologic processes including runoff processes from hillslopes and zero-order basins control flow response in channels, sediment transport, and occurrence of mass movement. The corresponding effect on channels also may be

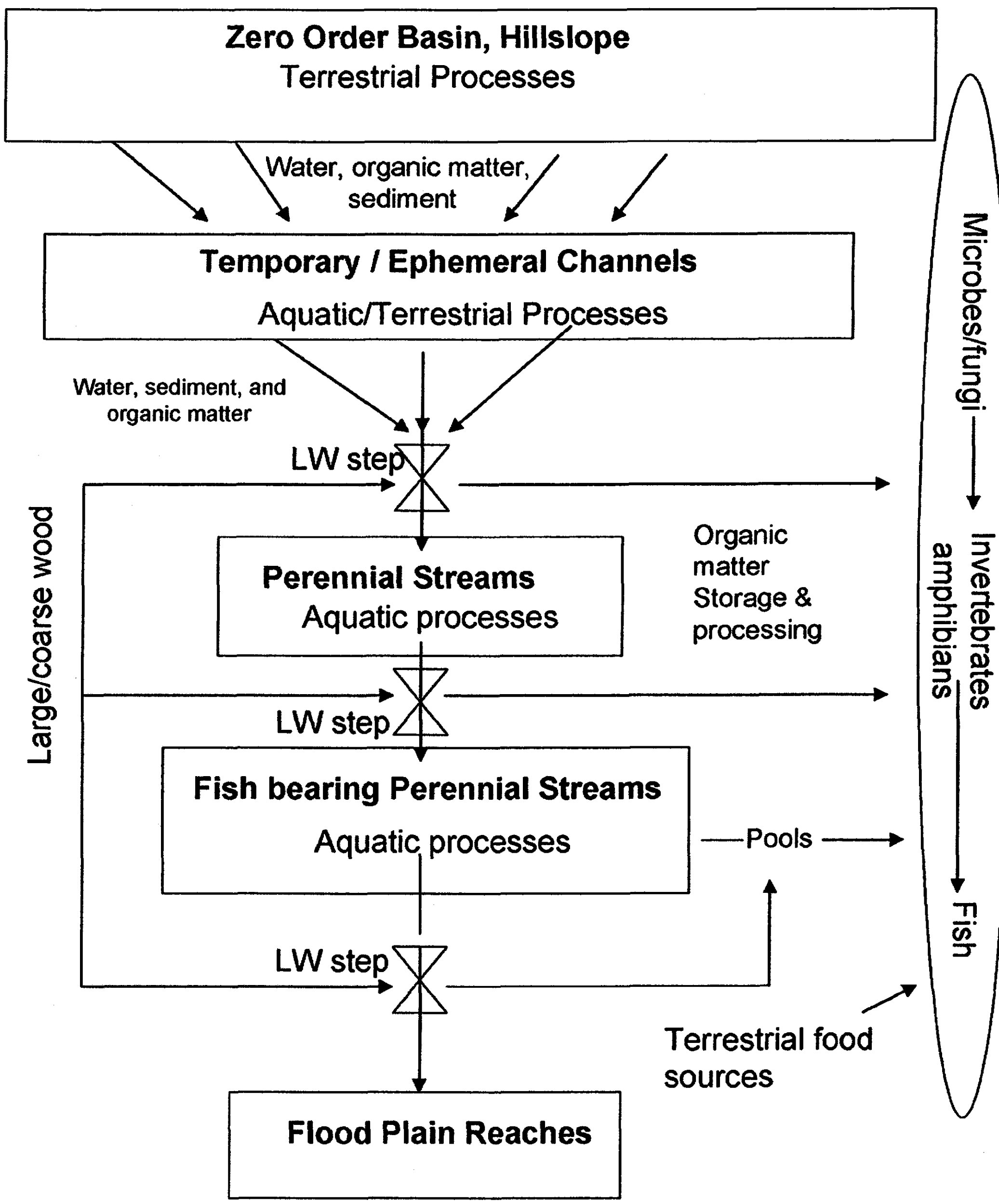

Figure 3. Model flow chart of processes and links in a headwater stream showing units, flow between units and inputs, large wood (LW) step valves (hour glasses), and links to biological processes.

magnified resulting in large scale events such as debris flows. Hydrologic events drive acute (short-term, large-scale events) and chronic (long-term small events and erosion) sediment movement. The quantity and frequency of sediment movement affects channel conditions and biological processes in headwater streams and in downstream reaches (Figure 1).

Biological processes in hillslopes and zero-order basins are terrestrial (Figure 3). Hillslope, zero-order channels, and temporary channels are conduits for terrestrial inputs into aquatic processes in perennial headwater streams. Aquatic processes begin in temporary channels with processing of organic detritus and some species of invertebrates that are not strongly dependent on surface water during the entire life cycles. The ecotone between the terrestrial and the aquatic zone of headwater streams is important for amphibians (Lowe 2003). Progar and Moldenke (2002) found higher density and biomass of invertebrates in temporary streams than in perennial streams; however, perennial streams had greater taxonomic diversity than temporary streams. Aquatic biological processes are fully developed in the perennial first- and second-order streams. The separation of these streams into reaches that support fish and those that do not support fish often has management significance, and in some instances is difficult to determine (Bryant et al. 2004). Furthermore, the point at which fish appear in a headwater stream may vary.

Because perennial headwater streams are small and have close links to the terrestrial ecosystem, the effects of disturbances in the surrounding forest may be more profound than in larger streams. Occurrence of landslides and debris flows is one of the more obvious effects. Less obvious effects may arise from modification of riparian vegetation and may include alterations in discharge regimes, riparian microclimate, radiation input and shade, sediment storage and transport, and large wood, organic material recruitment, and biological production.

Physical Processes

Occurrence of Mass Movement

The geomorphology of the headwater streams in the Maybeso watershed is strongly influenced by past management activities (Bryant 1980, Swanston and Marion 1991, Johnson et al. 2000, Gomi et al. 2001). Landslides and debris flows are the most common disturbance events in the channels. Occurrence of landslides and debris flows increased 5 to 15 years after clearcutting and many were related to roads (Bishop and Stevens 1964, Sidle 1985, Gomi et al. 2004). Debris flows transport sediment and large wood pieces into lower-gradient reaches where sediment is dispersed further downstream (Swanson et al. 1987, Gomi et al. 2004). Typically, landslides and debris flows remove both instream and nearby riparian wood from headwater stream channels and deposit them in lower-gradient reaches—transition zones—where they may form complex debris jams (Figure 4). Fine material is moved rapidly downstream into floodplain channels. The end result of a landslide in a headwater stream is a simplified channel with little or no ability to retain sediment. Red alder rapidly

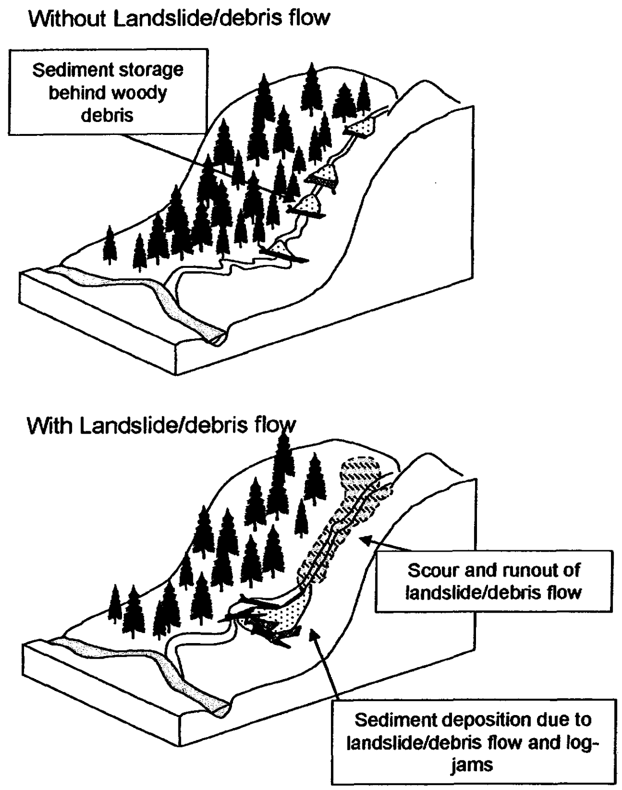

Figure 4. Illustration of headwater streams with and without landslides/debris flows (modified from Gomi et al. 2001).

revegetates disturbed riparian areas and is the dominant species along most slide paths. However, red alder does not provide the same stability as large conifers for sediment retention.

Effect of Large Wood in Channels

Steps and step pools formed by wood debris are keystone structures that link physical processes to biological processes. They regulate the downstream flow of material and increase channel complexity. Sediment—inorganic and organic—accumulates behind debris dams and step pools formed by wood debris (Bilby and Likens 1980, Bisson et al. 1987). Large wood pieces are the primary agent for sediment storage in high-gradient channels dominated by bedrock (Montgomery et al. 1996, Hassan et al. 2005). In the Maybeso watershed, sediment storage and wood debris were correlated (Gomi et al. 2001). However, debris dams are transitory structures that deteriorate over time and release sediment to downstream reaches. The rate of deterioration of dams and the amount of sediment released depends on a complex set of factors, many of which are related to management of riparian vegetation. In undisturbed reaches, collapse of individual debris dams may be relatively frequent, with small events releasing small amounts of sediment downstream a short distance to the next debris dam.

Smaller pieces of wood that are less stable in larger streams with greater power are retained and affect channel morphology in headwater streams (Bilby and Ward 1991a). Wood debris from 3 to 10 cm in diameter was an important pool forming agent in headwater streams in southeast

Alaska (Gomi et al. 2003). Similar effects were observed in Washington State by Jackson and Sturm (2002), who reported that small wood from 10 to 40 cm in diameter and smaller organic matter and colluvium composed more than 90% of the steps in forested streams in Washington coastal streams.

Landslides that run through headwater streams to lower-gradient transition zones effectively remove all of the "debris valves" in the stream. Typically, landslide and debris flows in high-gradient streams remove all large wood along the channel and often scour the channel to bedrock (Bovis et al. 1998, Hogan et al. 1998). In the Maybeso watershed, reaches with recent landslides had less wood and storage capacity (Gomi et al. 2001). Steps formed by wood and separated by short intervals will moderate the amount of material transported downstream, as well as reduce the distance that it moves downstream. These in-channel structures affect sediment transport along the channel because wood pieces provide channel roughness and mechanically trap sediment.

The distance between steps differed by management treatment and disturbance (Figure 5). Intervals were shorter in old-growth reaches and longer in reaches that had been exposed to landslides. Even in higher-gradient reaches, the interval between channel steps was less than 10 m. Shorter intervals between steps at higher gradients lead to greater complexity at higher gradients in reaches that have not been recently exposed to landslides or debris flows; furthermore, shorter steps increase storage capacity at higher gradients, resulting in greater channel complexity in higher-gradient reaches than in similar reaches without steps (Heed 1985b).

The interaction of large wood from riparian trees and sediment transforms channel profiles in headwater streams (Montgomery and Buffington 1997). When large wood is recruited into headwater channels the number of step structures increases. As the number of step structures increases, channel reaches change from cascade to step-step and step-pool (Gomi et al. 2003) (Figure 6). The step profile moves up the stream channel as steps are formed by large wood pieces. The size of riparian trees affects the size of wood-forming steps (Gomi et al. 2003). Steps in old-growth reaches were generally formed with larger pieces; however, pieces of legacy wood larger than the mean diameter of riparian trees were observed in second-growth conifer and alder-dominated channels.

Landslides and debris flows remove wood and sediment from headwater channels (Hassan et al. 2005). In the Maybeso watershed, landslides occurred in many headwater streams during a short period of time and often recurred in the same stream over a period of 40 years. Channels exposed to more recent slides had fewer large wood pieces than other channels, but regeneration of alder in the riparian zones of headwater streams in the Maybeso watershed increased the number of wood pieces in headwater channels (Gomi et al. 2001). Steps formed by conifer large wood were replaced by smaller alder pieces. Wood debris from

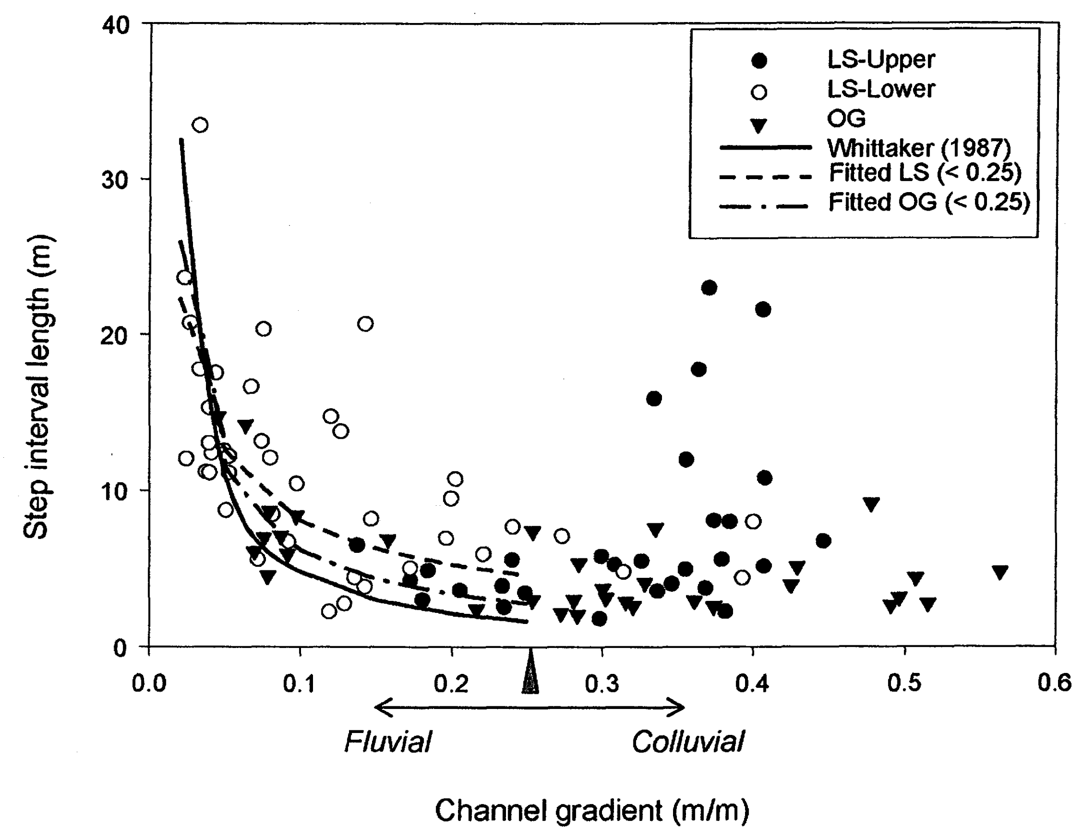

Figure 5. The relationship between channel gradient and step interval in headwater streams with old-growth riparian forest (OG) and channels affected by mass movement (LS) in the headwater streams of the Maybeso Creek (after Gomi et al. 2003).

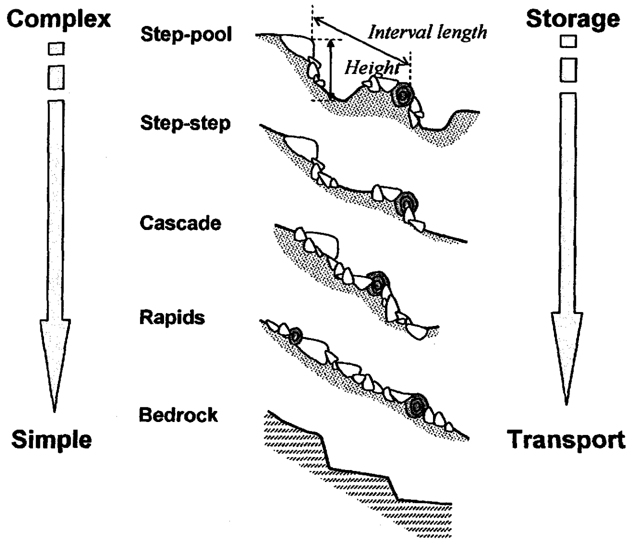

Figure 6. Illustration of channel reach classifications associated with large wood debris and boulders in headwater channels and their effect on sediment storage and transport and stream channel morphology (modified from Gomi et al. 2003).

alder has a much shorter residence time than large conifer pieces (Harmon et al. 1986). As steps formed by alder replace steps formed by conifers, debris dams may fail more frequently, reducing storage time and increasing the amount of downstream transport of organic and inorganic material. Sediment will be released in smaller increments and among fewer headwater streams with large wood recruited from large conifers in riparian zones.

The condition of downstream reaches depends on processes that occur in headwater streams. The quantity and quality of the substrate in downstream floodplain reaches is determined largely by material recruited from headwater reaches (Everest et al. 1987). Sediment from upstream sources is a necessary component for downstream biological processes that include microbial activity, invertebrate production, and spawning habitat for fish. Adverse effects to biological process arise when the quantity and the quality (i.e., size) of sediment changes (Everest et al. 1987). The loss of steps and step pools has short-term (acute) and long-term (chronic) effects on downstream reaches. The acute effects are those commonly associated with landslides that include scour and deposition of a large amount of material in a short period of time. The chronic effects are relatively small but occur over decades. Small amounts of sediment move downstream even during small precipitation events. When chronic events occur over a large segment of the watershed, such as in the Maybeso Creek watershed, the effects on floodplain processes are cumulative and can be substantial.

Biological Processes

Organic Matter Storage and Transport

Headwater streams are small and have proportionally greater exposure to terrestrial processes than larger floodplain reaches. In closed canopy forested headwater streams, biological processes are supported by allochthonous production (England and Rosemond 2004, Richardson et al. 2005). Removal of riparian trees increases solar radiation and summer temperature in headwater streams (Moore et al. 2005). Where riparian harvest has occurred, primary production can influence production (Kiffney and Bull 2000). However, increasing amounts of fine sediment may limit invertebrate biomass (Kiffney and Bull 2000). In an experimental treatment, food was a limiting factor for invertebrates in headwater streams (Richardson 1991). Litterfall, the primary food source, was seasonal and was related to riparian canopy coverage and tree species (Richardson 1992a). Increased retention of organic material, particularly deciduous leaf litter in small debris dams and pools, will provide greater access to organic material for processing and production.

In the Maybeso watershed, riparian stand conditions related to timber harvest and mass movement increased the amount of fine wood pieces and detritus accumulations (Gomi et al. 2001). Large conifers removed during timber harvest were replaced by red alder and wood recruitment was converted to mostly broken dead stems from small-diameter trees (diameter less than 3 cm), branches, and leaves. Recruitment of large and small wood from alder may increase biological productivity because alder and fine materials can be processed more quickly than larger pieces of wood from conifers (Richardson 1992b).

In upland reaches frequently affected by mass movement, red alder provides a large amount of leaves and small branches. Most of this material enters the stream during the fall, which also coincides with the period of greatest rainfall in southeast Alaska. Significant differences were not observed for ash free dry mass (AFDM) among canopy type for the streams in the Maybeso watershed (Piccolo and Wipfli 2002), but samples were not collected during the fall when peak rainfall occurs. The export and retention of detritus largely depends on physical characteristics of headwater streams, which were not measured in this study (e.g., discharge, roughness, and channel morphology) (Bilby and Ward 1991b, Kiffney et al. 2000, Gomi and Sidle 2003). In the streams of the Maybeso watershed, channel steps formed by large wood pieces and boulders decreased local channel gradient (less than 2 m long) and physically trapped organic matter in headwater channels. Increased retention of organic material, particularly deciduous leaf litter in small debris dams and pools, will provide greater access for processing and production.

Invertebrates

The invertebrate community is a complex and important part of the biological community of headwater streams and in the headwater stream reaches in the Maybeso watershed, a substantial number of invertebrates were captured in downstream traps (Piccolo and Wipfli 2002). Wood pieces supported higher density of macroinvertebrates in headwater channels, particularly those with riparian red alder (Hernandez et al. 2005). Greater biomass and more diverse functional groups of macroinvertebrates were captured in driftnets from alder-dominated headwater streams (Musslewhite and Wipfli 2004, Hernandez et al. 2005). Higher mean taxa richness and biomass were observed in advanced decayed wood pieces than other wood pieces (LeSage et al. 2005).

The diverse invertebrate community generally reflects a detritus-based food web (e.g., Haggerty et al. 2002, Cole et al. 2003) and alder provides a higher-quality food source for most macroinvertebrates (Volk et al. 2003). Understory vegetation biomass and species in headwater riparian zones are typically greater in mixed alder stands (Hanley et al. 2006), and mixed alder stands support more terrestrial invertebrate biomass (Schultz and De Santo 2006). Also, nitrate concentrations were higher in streams with greater than 20% mixed red alder of riparian forest (Johnson and Edwards 2002). This may elevate primary production in headwater channels. Higher numbers of invertebrates observed in drift samples from the reaches with young-growth alder riparian vegetation than in old-growth, clearcut, and young-growth conifer were attributed to canopy cover by Musselwhite and Wipfli (2004), Hernandez et al. (2005), and LeSage et al. (2005), but differences appeared in the channel morphology (Gomi et al. 2003). Higher numbers of invertebrates captured in the drift nets may be associated the low storage capacity in the alder-dominated reaches.

The young-growth alder reaches that had been scoured by debris flows had relatively fewer steps and smaller wood pieces. All of these effects serve to decrease retention and increase movement of material through the system, which would increase the amount of drift, confounding the effects of alder riparian stands on the absolute amount of drifting organic matter and macroinvertebrates. Greater percentages of scrapers were found in drift samples from alder riparian zones, whereas higher percentages of gatherers were found in old-growth and clearcut channels (Hernandez et al. 2005). Such differences may reflect riparian conditions in alder-dominated reaches that may increase primary production (see Kiffney and Bull 2000). Greater proportions of gatherer guilds might be expected in locations that retain organic material such as steps and step pools.

The contribution of invertebrates to downstream fish populations has been suggested as an important function of headwater streams (Wipfli and Gregovich 2002). However, invertebrate drift was related to discharge, with the highest amount of drift occurring during periods of high discharge when they would not be readily available to foraging fish. Although the direct use of invertebrates from headwater streams by downstream fish is speculative, a large amount of organic material enters downstream food webs that support fish populations, and alterations that decrease upstream production can influence trophic process that rely on detrital inputs (Vannote et al. 1980, Wallace et al. 1991).

Although the function of debris dams as nodes of invertebrate production was not examined by the invertebrate studies in the headwater streams of the Maybeso watershed, studies from other locations suggest that coarse wood debris dams retain organic and inorganic sediment that would support increased invertebrate production in the headwater streams of the Maybeso watershed (Bilby and Likens 1980, Bilby 1981, Palmer et al. 1996, Muotka and Laasonen 2002). In combination with high nutrient inputs from alder in the riparian zone, coarse wood debris dams can be patches of high biological activity. When taken in the context of the nutrient spiraling paradigm, steps formed by coarse wood "tighten" nutrient spirals that increase biological activity, including invertebrate production and regulation of (i.e., function as valves) downstream movement of organic matter and invertebrates into reaches with fish.

Fish Habitat and Distribution

Fish, and particularly salmonids, are often not considered part of the biological community of headwater streams, and management practices are often oriented toward downstream effects. The downstream effects of headwater streams that affect ecological processes that relate to fish in lower-gradient streams are important (Power and Dietrich 2002), but salmonids are present in headwater streams when habitat is available (Bryant et al. 2004). The perception that salmonids are not found in headwater streams may be based partly on definitions used for headwater streams that may categorically exclude fish, but more often it is based on the perception that fish are not found in higher-gradient reaches (greater than 10%) and lack of sampling effort for fish. In some instances, the absence of salmonids may be due to land management effects in the watershed, such as unidentified blocks to fish passage.

In the streams of the Maybeso watershed, salmonids were found in reaches with gradients that exceeded 15%, where habitat was accessible (Bryant et al. 2004). Juvenile coho salmon and Dolly Varden were present in headwater streams from steep to low-gradient reaches (Figure 7). Steelhead and cutthroat trout were found in some, but not all, headwater streams in the watershed. As stream gradient increased, the proportion of Dolly Varden in the stream reach increased (Figure 7). Juvenile coho salmon composed more than 50% of the fish captured in the low-gradient reaches (less than 5%). In the high-gradient reaches (greater than 7%), Dolly Varden composed more than 90% of the total fish caught (Figure 7). Dolly Varden juveniles and anadromous Dolly Varden were found in reaches with gradients greater than 15%. Cutthroat trout and steelhead occurred in reaches with gradients that exceeded 12%. Anadromous Dolly Varden in spawning condition were

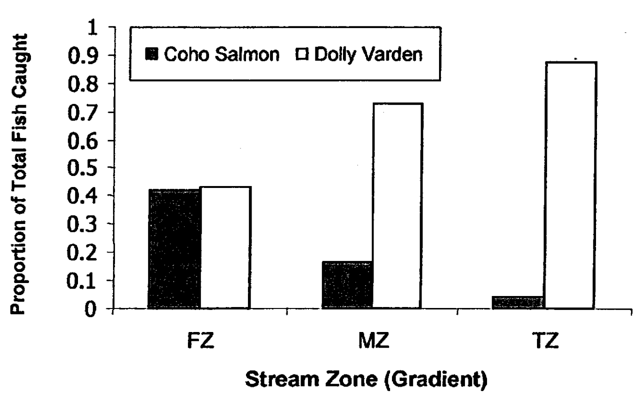

Figure 7. Proportion of Dolly Varden and juvenile coho salmon captured in low gradient (FZ less than 4%), moderate gradient (MZ greater than 4% to less than 7%), and high gradient (TZ greater than or equal to 7%) zones in the headwater streams of the Maybeso Creek study area (modified from Bryant et al. 2004).

observed in step pools in the highest reaches accessible to fish.

The critical component for all species in the high-gradient reaches was the presence of step pools formed by large wood. In the higher-gradient reaches (greater than 7%), water depth was a limiting factor and pools and most pools that provided sufficient depth for fish were formed by wood debris. The high-gradient reaches where fish were captured were characterized by step-pool profiles; however, as gradient increased pools became shallower and sparser (Bryant et al. 2004). Upstream barriers were either falls (greater than 2 m) or long, shallow chutes and bedrock riffles. The lack of upstream habitat for fish in these streams was generally defined by the absence of step pools formed by large and coarse wood.

Discussion

In forested watersheds, steps and step pools formed by large wood are "keystone" structures that link physical processes to biological processes in headwater streams. Steps formed by large wood increase retention time of sediment and increase biological activity (Meyer and Wallace 2001). Newbold et al. (1981) use the concept of nutrient spiraling to describe the utilization and downstream movement of nutrients in a stream food web. A tighter spiral (i.e., the coils are closer together) implies greater "recycling" of nutrients and organic material, and hence greater productive capacity per unit of stream reach. Channel step structures act as valves for transport of material to downstream reaches that store organic and inorganic sediments.

The same processes that control nutrient spiraling regulate the movement of inorganic sediment. Large wood dams create channel roughness that retains inorganic sediment and reduces transport distances for fine and coarse particulate matter in small streams (Brookshire and Dwire 2003, MacFarlane and Wohl 2003). Retention of sediment—fine and coarse—is important to processes within headwater reaches, but it also has downstream consequences. Stream substrate in floodplain reaches deposited from upstream sources is an important element in the productivity of floodplain reaches (Everest et al. 1987). However, timing and frequency of recruitment are important, and too much during a short time period will overwhelm floodplain processes with adverse effects on salmonid productivity (Everest et al. 1987, Reeves et al. 1995, Benda et al. 2004). Steps formed by large wood function as valves that control the frequency and quantity of sediment movement into floodplain reaches streams. In the absence of mass failures, these "valves" open a few at a time as the steps fail throughout the watershed and release small amounts of material downstream.

As the number of steps increases, the channel profile changes from simple to complex (Figure 6). As steps convert high-gradient reaches into complex channels, the presence of step pools allows exploitation of headwater streams with average reach gradients greater than 10% by Dolly Varden and cutthroat trout for spawning and rearing. Step pools formed by large wood in headwater reaches create a heterogeneous gradient with a series of low-gradient sections and short and irregular falls, which are often easily ascended by fish. The small, shallow pools formed in the small patches of high-gradient reaches push habitat available to fish, other vertebrates, and invertebrates further upstream. In most instances, these small pools do not support larger salmonids that may be predators on newly emerged fry of cutthroat trout and Dolly Varden, and may be important refuge habitats during their early life history, as was observed by Harvey and Stewart (1991) for warm water species. Step pools formed by large wood composed nearly the entire useable habitat for fish in these reaches.

Catastrophic channel-clearing events, such as landslides, are more common in headwater stream reaches than in lower-gradient reaches. These events remove most structures (coarse and large wood) in headwater stream channels. By analogy, these now become straight pipes for the movement of sediment and organic matter downstream. Within a watershed under a natural disturbance regime, some reaches would be in the early recovery stage from a step-removing disturbance (i.e., landslide), most would be at some intermediate stage, and a few a "dynamic steady state" where LWD recruitment = LWD loss. Headwater streams bordered by an uneven-age forest stand are more likely to be in a "dynamic steady state" than one surrounded by a young (less than 75 years) even-age forest stand. Furthermore, shorter recovery times are more likely in streams with an uneven-age riparian forest, where large trees may be recruited within a 5- to 20-year time span. Where riparian trees have been harvested, such as those in the Maybeso Creek watershed, recovery periods greater than 50 years may be expected following a landslide (Figure 4).

An increasing number of studies of headwater streams, including the studies in the Maybeso Creek watershed, illustrate the complexity and importance of headwater streams to the productivity of forested watersheds. Headwater streams are conduits that link upslope terrestrial processes to aquatic systems (Figure 8). They support a complex array of physical and biological processes, including sediment transport and invertebrate and vertebrate production, including fish. These, in turn, are linked to larger downstream reaches at various spatial scales. Because they are closely linked to terrestrial and riparian conditions, headwater streams can be greatly influenced by land management activities. Activities that adversely affect a single stream may result in relatively small effects across the watershed, but when many small headwater streams are affected, the effects on downstream reaches may become large and last for centuries.

Considerable progress has been made toward understanding many of the processes that operate in headwater streams and adjacent hillslopes. At least for forested watersheds of southeast Alaska, four topographic units appear in headwater stream catchments and have identifiable processes. Physical processes that affect channel morphology are reasonably well known and parts of the biological processes have also been described. The diagram presented in Figure 3 provides a conceptual model of processes and linkage through a headwater stream and their connections

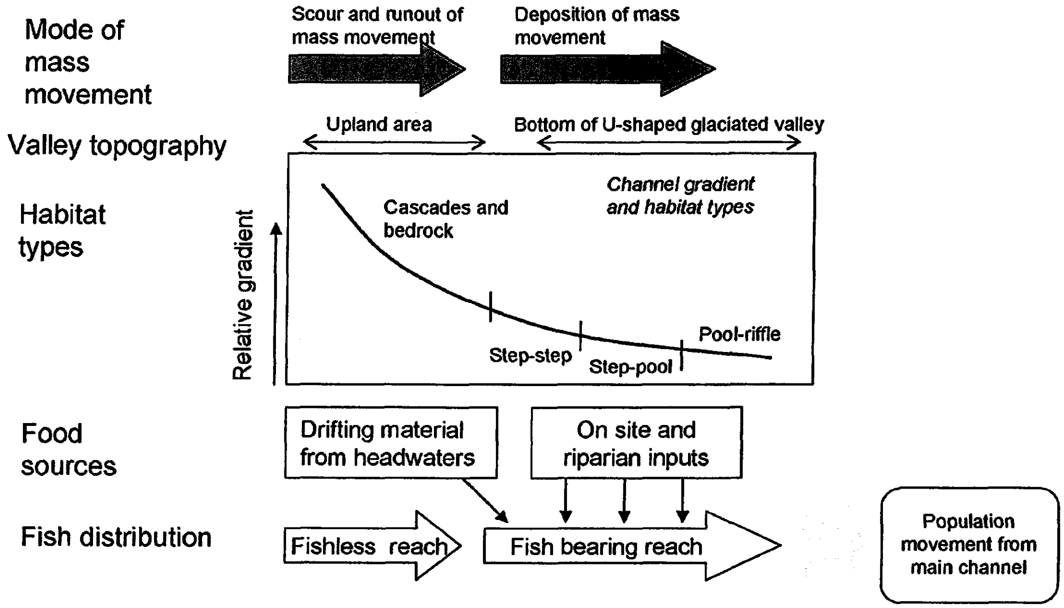

Figure 8. Linkages between physical and biological processes and their influence on salmonid distribution in headwater streams. Mass movement and valley topography is based on Johnson et al. (2000) and Gomi et al. (2004). Distribution of channel habitat types is based on Montgomery and Buffington (1997) and Gomi et al. (2003). Fish distribution is based on Bryant et al. (2004). Food sources are based on Piccolo and Wipfli (2002) and Allan et al. (2003).

with downstream habitats. At the landscape scale, the spatial and temporal linkages of physical and biological processes are affected by management effects that create a legacy of mass movement and a range of recovery states, as well as naturally occurring disturbance events. A more quantitative understanding is needed that can be used to determine the influence of these processes and links on multiple trophic levels, including fish.

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