Chapter 5

Aquatic Ecology: the Role of Organic Matter and Invertebrates

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Introduction

Closure of Glen Canyon Dam and the beginning of flow regulation of the Colorado River through Grand Canyon in 1963 changed the river through the canyon considerably. The river changed from having highly variable discharge rates and temperatures and high suspended-sediment loads to having a relatively constant flow regime (Topping and others, 2003), cold and constant water temperatures, and suspended-sediment loads that are dramatically reduced relative to predam levels (see chapter 1, this report). These changes in the physical environment, coupled with changes in the quantity and types of organic matter present in the Colorado River and intentional introductions of aquatic invertebrates that occurred shortly after Glen Canyon Dam was closed (Blinn and Cole, 1991), have led to substantial changes in the kinds of aquatic invertebrates present in the Grand Canyon ecosystem. Since the closure of the dam, considerable effort has been directed toward understanding the aquatic ecology of this altered ecosystem (Blinn and Cole, 1991).

This chapter describes the results of the research and monitoring activities that have investigated the kinds of organic matter and invertebrate communities in the Colorado River below Glen Canyon Dam. Collectively, organic matter and the aquatic invertebrates that consume it largely constitute the food base for fish in the Colorado River ecosystem. This chapter focuses on patterns, trends, and important controls on the amount and sources of organic matter and invertebrates that are primary food resources for humpback chub (*Gila cypha*) and rainbow trout (*Oncorhynchus mykiss*) in an effort to understand the role that food plays in determining the distribution, population density, and growth of these fish in this ecosystem. Furthermore, most of the research and monitoring that have been conducted on organic matter and invertebrates in this ecosystem have centered on the food items that are important for these two species. This chapter also addresses how organic matter and invertebrates are affected by the timing and magnitude of water releases from Glen Canyon Dam, including the modified low fluctuating flow (MLFF) alternative, which was implemented in 1996 and continues as the operating regime for Glen Canyon Dam today. Finally, this chapter concludes with a brief discussion of recommended research directions and management actions.

Background

Virtually all food webs, including those in rivers, are fueled by energy that comes from autotrophs (also known as primary producers), which are organisms that can convert sunlight into chemical energy. Examples of autotrophs include vascular plants and algae. Without autotrophs there would be no food energy available to other organisms that lack the capability to fix light energy. In rivers, this autotrophic material can come from two places: the terrestrial environment, such as leaves falling into a river from trees lining the river's banks, or the aquatic environment, such as algae growing on river rocks. Terrestrially derived material is an extremely abundant source of energy in many streams and rivers (Bayley, 1989; Meyer and Edwards, 1990). Although algae often represent just a small fraction of the available energy in river ecosystems, they are frequently an important energy source that contributes to secondary production (Bilby and Bisson, 1992; Lewis and others, 2001; Thorp and Delong, 2002) because they are far more nutritious than terrestrial material (Anderson and Sedell, 1979). Aquatic or terrestrial autotrophic material is also called "organic matter" and provides the energy that supports consumers at higher trophic levels. Trophic levels are groups of organisms that occupy the same position in a food web (fig. 1).

The importance of understanding patterns, trends, and controls of organic matter and invertebrates is reflected in the goals of the Glen Canyon Dam Adaptive Management Program. For example, the program's first goal is to "protect or improve the aquatic foodbase so that it will support viable populations of desired species at higher trophic levels" (Glen Canyon Dam Adaptive Management Program, 2001, p. 11). Two additional goals are to maintain populations of rainbow trout in the Lees Ferry reach and maintain, and ultimately increase, populations of native fish, particularly endangered humpback chub, in sections of the river downstream of the Lees Ferry reach. Recent trends for important fish in the Grand Canyon ecosystem may be partly due to changes in food resources or to an increase in the severity of competition between humpback chub and other fish and highlight the need for continued research on organic matter and invertebrates. The number of rainbow trout in the Lees Ferry reach has generally been high since intensive population measurements began in 1991, but the condition of fish as determined by weight relative to length declined during the late 1990s (McKinney and others, 2001). Also, the average condition (Meretsky and others, 2000) and size of humpback chub populations have declined considerably since intensive measurements began in 1986 (see chapter 2, this report).

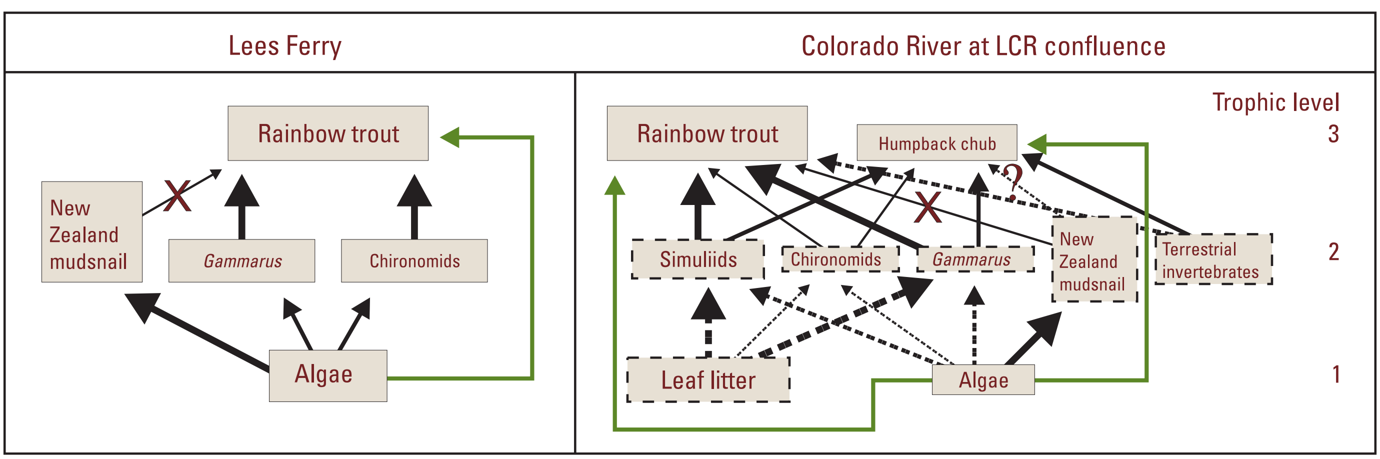

Figure 1. Idealized and simplified food-web diagrams for two different sections of the Colorado River ecosystem, the Lees Ferry reach and the Colorado River at the Little Colorado River (LCR) confluence. The sizes of the boxes reflect qualitative differences in the standing mass within trophic levels, and the size of the arrows reflects qualitative differences in the amount of food energy moving between trophic levels. Green arrows linking algae to fish are used to highlight the fact that fish consume algae but do not actually derive significant nutrients or energy from them. Rainbow trout also consume New Zealand mudsnails, but the snails often survive passage through the gut alive and intact, which is noted with the **X**. Humpback chub may be capable of actually digesting mudsnails because they are capable of crushing their shells; however, it is unclear whether humpback chub ingest snails. Areas of greatest uncertainty are noted with dashed lines.

Several of the hypothesized causes of humpback chub decline are, in part, based on the assumption that there is a limited amount of food available in the river to support populations of humpback chub and other fish. For example, Gloss and Coggins (see chapter 2, this report) list competition with nonnative and native fish as one of several possible reasons for the decline of the endangered humpback chub populations. Thus, documenting the food resources that humpback chub and rainbow trout are dependent on and whether these resources vary over space and time will help determine the validity of the food-limitation hypothesis. This information will also clarify the role that food availability plays in determining the population density and condition of both native and nonnative fishes and may prove useful as an indicator of ecosystem health.

Figure 2. A preserved *Gammarus lacustris* (also known as a scud or side-swimmer), which is consumed by humpback chub and rainbow trout. Live animals are more translucent (photograph by Michael Booth).

Status and Trends

Identifying the Food Items of Fish

A great deal is known about the types of food items consumed by humpback chub and rainbow trout. In general, both fish appear to consume mostly the introduced invertebrate *Gammarus lacustris* (small crustaceans, also called scuds or side-swimmers, hereafter *Gammarus*) (fig. 2), larval chironomids (midges, also called bloodworms), larval simuliids (black flies), terrestrial invertebrates, and the filamentous algae *Cladophora glomerata* (hereafter *Cladophora*) (fig. 3). The small aquatic invertebrates mentioned range from about 0.25 to 1 inch (6 to 25 mm) in length, and individual *Cladophora* filaments can attain nearly 20 ft (about 6 m) in length.

Gut pumping was used to nondestructively investigate the food items consumed by humpback chub collected from two known chub aggregations, the Little Colorado River confluence aggregation (at about RM 61) and the Middle Granite Gorge aggregation (at about RM 127) (Valdez and Ryel, 1995). *Cladophora* represented 24% of gut contents by volume for chub at the Little Colorado River confluence site, with invertebrates representing the remaining 76%. In contrast, humpback chub at the Middle Granite Gorge site consumed exclusively invertebrates. Of the invertebrates, simuliids, *Gammarus*, and terrestrial invertebrates were the most common items consumed. Valdez and Ryel (1995) also quantified the density of algae and specific invertebrates in the drift (fig. 4) and then compared chub diets with the availability of food items in the drift to determine whether chub were "selectively" feeding. These analyses indicated that chub selectively avoided consuming *Cladophora*, even though it represented 88%–93% of potential food in the drift, and chub generally consumed simuliids, chironomids, and *Gammarus* in "approximate proportion to their availability in the drift" (Valdez and Ryel, 1995, p. 9–13).

The feeding habitats of rainbow trout in the Lees Ferry reach were determined by McKinney and Speas (2001). They analyzed the stomach contents of 658 rainbow trout caught in the Lees Ferry tailwater from 1991–97 and found that *Cladophora, Gammarus*, and chironomids accounted for more than 90% of the stomach contents by volume. Of the invertebrates consumed by these fish, *Gammarus* and chironomids together accounted for more than 90% of the total by volume.

For a complete understanding of the energy sources that are driving a food web, it is important to know not only what the fish are consuming but also what the invertebrates themselves are consuming. To this end, the diets of some aquatic invertebrates that are commonly consumed by fish have also been investigated by using gut-content analysis and habitat-choice experiments. Pinney (1991) found that diatoms, a class (Bacillariophyceae) of microscopic algae common in aquatic environments, made up more than 93% by volume of gut contents for *Gammarus* in the Lees Ferry reach. Shannon and others (1994) used field and lab-based habitat-choice

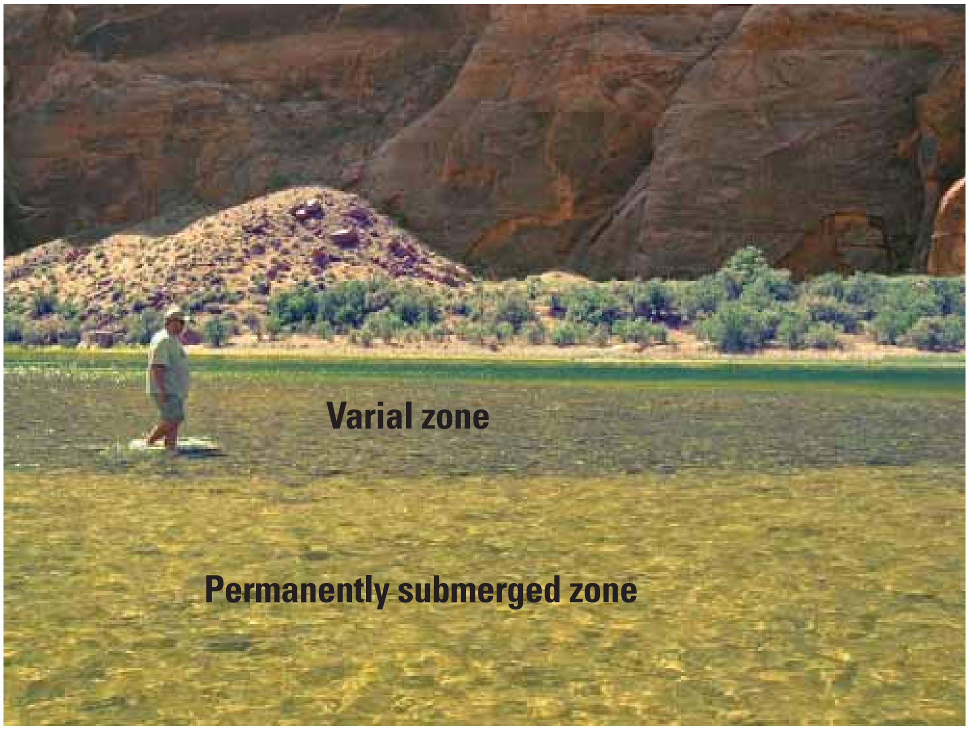

Figure 3. Cobble bar in Glen Canyon showing the varial zone (shoreline habitat that is both inundated and exposed to air for long periods each day) and the presence of the filamentous algae *Cladophora* in the permanently submerged zone. *Cladophora* is unable to grow in the varial zone because dam operations result in discharge rates that regularly expose the varial zone to air (photograph by Theodore Kennedy, U.S. Geological Survey).

experiments to determine that *Gammarus* preferred *Cladophora* as habitat over all other choices, including *Oscillatoria* spp. (another species of filamentous algae), gravel, and detritus. These same researchers determined that *Gammarus* were only relying on *Cladophora* as habitat and were actually eating diatoms that were attached to *Cladophora*. Stevens and others (1997) determined the diet composition of chironomids by using gut-content analysis and found that the relative importance of algae in chironomid diets declined with distance downstream from the dam: algae represented 61.4% of chironomid diets at Lees Ferry, 30.7% at RM 32, and only 7.5% at RM 224. This trend is consistent with observed downstream declines in algae biomass (discussed below) and indicates that algae may not be the most common form of organic matter consumed by invertebrates at downstream locations.

Identifying the food items consumed by fish and invertebrates by using gut-content analysis provides an indication of the food resources that are most important to fish; however, relying solely on this approach also has weaknesses. First, gut contents only reflect the items consumed by fish or invertebrates within about an hour of their capture, providing only a “snapshot” of the food items consumed. Even in this short timeframe, however, labile food items may be more readily digested than others, leaving behind the more resistant items and the appearance that these items are the most important food sources. Furthermore, if, for example, rainbow trout consume other fish very infrequently, the snapshot taken through gut-content analysis is unlikely to detect this relatively rare event. Yet these infrequent events of predation may be a significant source of calories and nutrients for the fish and may represent an important type of food that might be overlooked when using only gut-content analysis. Second, just because an item is consumed by a fish does not mean that it is actually an important source of energy or nutrients. For example, both humpback chub and rainbow trout regularly consume the filamentous algae *Cladophora*, but energetic and stable-isotope analyses (discussed below) indicate that this material is not actually assimilated because it is difficult to digest and is low in essential nutrients such as fatty acids, nitrogen, and phosphorus (Angradi, 1994; McKinney and Speas, 2001). It has been suggested that the humpback chub and rainbow trout that consume *Cladophora* may actually be after the more nutritious invertebrates that are imbedded in *Cladophora* (Valdez and Ryel, 1995). Finally, the relative contribution of terrestrial and aquatic organic matter to invertebrate growth

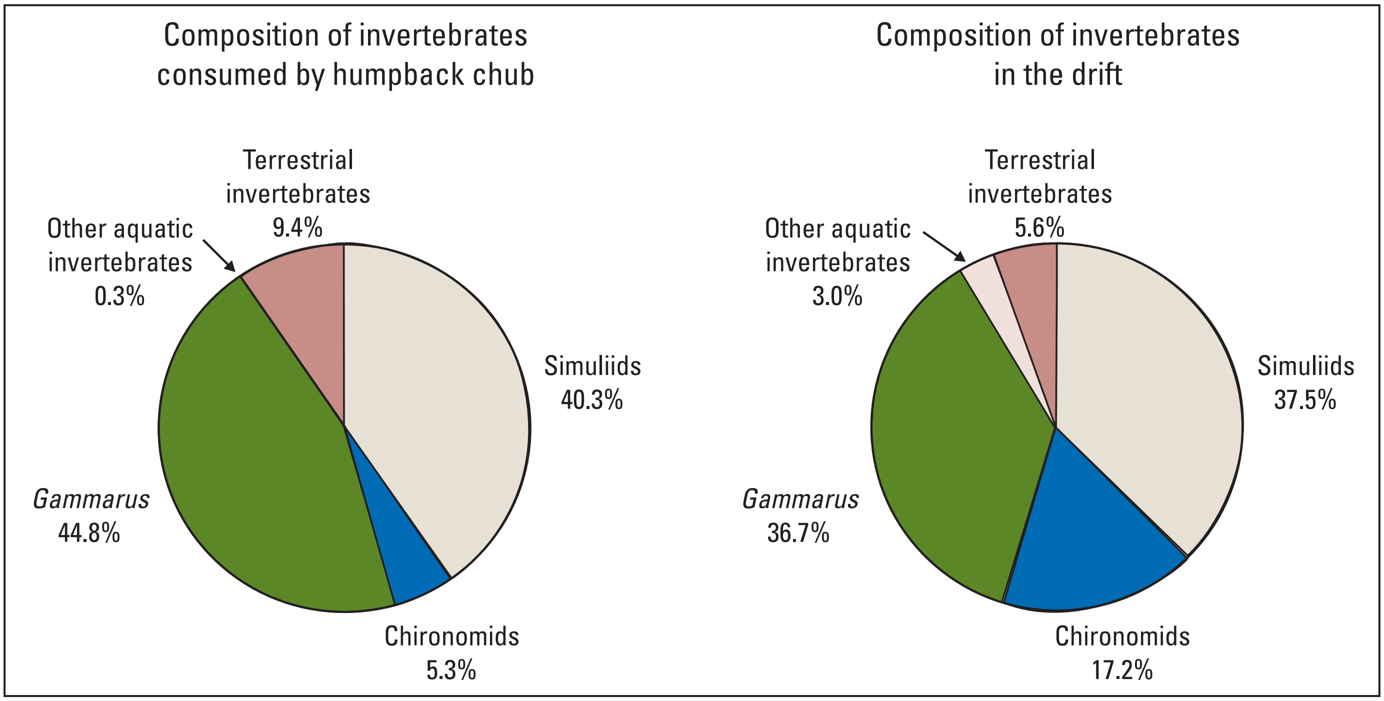

Figure 4. Volume of specific invertebrates in humpback chub stomachs from the Little Colorado River confluence aggregation (about RM 61) and composition of these same items in the drift. Data were collected during 1992–93 and exclude algae (*Cladophora*) that were consumed by chub. Modified from Valdez and Ryel (1995).

and production, and hence fish growth and production, is often unclear when only gut-content analysis is used.

To determine what is being consumed and actually assimilated by fish and small invertebrates and to quantify the relative importance of terrestrial and aquatic organic matter in fueling fish growth require a combination of gut-content analysis and a specialized technique known as stable-isotope analysis. Terrestrial and aquatic organic matter often has distinct stable-isotope signatures (Fry and Sherr, 1984) that are largely conserved up the food chain, and these signatures provide information about the source of energy at the base of the food web (Peterson and Fry, 1987). For example, if *Gammarus* consume exclusively algae, then they will have a carbon stable isotope signature identical to that of algae, as will a fish that consumes exclusively *Gammarus*. In contrast, nitrogen stable isotope values change predictably with each link in a food chain, increasing at a rate of 3.4 parts per thousand (‰) with each link, and therefore provide an indication of trophic position (Minagawa and Wada, 1984). Thus, herbivores typically have nitrogen stable isotope signatures that are 3.4‰ higher than plants, and primary carnivores in turn have nitrogen stable isotope signatures that are 3.4‰ higher than herbivores and 6.8‰ higher than plants. Also, stable-isotope analyses provide time-integrated measures of diet. That is, the carbon and nitrogen stable isotope signatures for a large fish will usually reflect the food it has consumed and assimilated over the past several months, which provides a contrast to the snapshot picture of diets obtained with gut-content analysis.

A combination of gut-content analysis of rainbow trout and stable-isotope analysis of the entire food web provided a clear picture of the aquatic food web in the Lees Ferry reach of the Colorado River (Angradi, 1994). Rainbow trout gut-content data collected by Angradi (1994) were remarkably similar to those reported by McKinney and Speas (2001): both studies showed *Gammarus*, chironomids, and *Cladophora* to be the dominant food items. Analysis of stable-isotope ratios showed that rainbow trout were assimilating nutrients from only the *Gammarus* and chironomids and not from the *Cladophora* they consumed (Angradi, 1994). Furthermore, *Gammarus* and chironomids were feeding almost exclusively on benthic algae, which are algae attached to the bottom of the riverbed. Thus, the entire food web of the Colorado River in the Lees Ferry reach, from aquatic invertebrates to fish, was based on algae.

Our understanding of the aquatic food web at sites downstream of Lees Ferry is much more limited.

Although gut-content analysis for humpback chub and rainbow trout collected at downstream locations indicated that both species consume mostly aquatic invertebrates and algae, the relative importance of terrestrial and aquatic energy sources remains unclear. Using stable-isotope analysis, Haden and others (1999) investigated the diet of humpback chub and other fish in the Little Colorado River, the largest tributary of the Colorado River in Grand Canyon and the single most important breeding habitat for humpback chub. They found a complex food web in the Little Colorado River with small chub, less than 6 inches (<150 mm) in length, relying heavily on invertebrates, especially chironomids, mayflies (Ephemeroptera), and caddisflies (Trichoptera), while large chub, greater than 6 inches (>150 mm) in length, were found to be relying on invertebrates and small fish. They also found evidence that terrestrial and aquatic organic matter was fueling the food web, although they were unable to determine the proportional contribution of each energy source. Angradi (1994) investigated food-web structure in tributary streams of the Colorado River and found that the food web in some tributaries was supported by leaf litter from streamside vegetation while others were supported by leaf litter from upland plants. Shannon and others (2001a) collected samples of algae, aquatic invertebrates, and eight species of fish (rainbow trout and humpback chub were collected, but the identity of the other six species was not specified) from seven sites that span the entire Grand Canyon ecosystem and found that carbon isotope values for algae increased consistently with downstream distance. Further, they found that invertebrate and fish isotope values roughly tracked the downstream shift in algae isotope values, providing evidence that algae is contributing to invertebrate and fish growth along the entire length of the Grand Canyon ecosystem.

Spatial and Temporal Patterns in Organic Matter and Invertebrates

There are very few data on the relative abundance of terrestrial or aquatic organic matter, or the density or kinds of invertebrates present, in the Grand Canyon ecosystem before the construction of Glen Canyon Dam (Blinn and Cole, 1991). In general, aquatic invertebrate diversity (the number of different species) has declined following closure of Glen Canyon Dam, while invertebrate density and biomass have probably, perhaps even dramatically, increased (Blinn and Cole, 1991, and references therein). Comparison of invertebrate diversity in tributaries relative to the mainstem provides an indication of changes in the invertebrate fauna that have occurred following closure of Glen Canyon Dam; Hofknecht (1981) found 52 insect families in tributaries of the Grand Canyon ecosystem, compared to just 5 insect families for the mainstem Colorado River. Haden and others (2003) studied relatively pristine and free-flowing sections of the lower Green River and the Colorado River in Canyonlands National Park in Utah to determine what the food web in the predam Colorado River in Grand Canyon might have looked like. They found that terrestrial organic matter was the primary energy source for aquatic invertebrates in this free-flowing reach because high levels of suspended sediment prohibited algae growth. They also found an invertebrate community that was markedly different from that in the Grand Canyon ecosystem; the invertebrate community in the free-flowing reach was dominated by filter feeders (simuliids and caddisflies) and collectors (mayflies and chironomids), reflecting the importance of terrestrial organic matter to this system. Prior to the closure of Glen Canyon Dam, the Colorado River contained large quantities of coarse woody debris (i.e., whole trees and branches) and other terrestrial plant material that were transported from upstream sources (Valdez and Carothers, 1998). This material accumulated along river banks and in eddies and supported a high diversity and abundance of terrestrial invertebrates. When this material was entrained by the river during spring floods, the terrestrial invertebrates probably served as an important food resource for fish in the Colorado River (Valdez and Carothers, 1998).

Because Glen Canyon Dam has created clear water conditions that allow sunlight to reach the river bottom, algal standing mass is extremely high in the Lees Ferry reach of the Grand Canyon ecosystem. Much of the terrestrial organic matter that formerly moved through the Colorado River system is now trapped behind Glen Canyon Dam. Stevens and others (1997) quantified river-bottom algae and invertebrate standing mass at 11 stations between Lees Ferry and Diamond Creek on a bimonthly basis during 1991. They found that *Cladophora* was the dominant algae throughout the Lees Ferry reach, exhibiting an average of 0.5 oz carbon (C)/yd² (15.5 g C/m²). Downstream of the Paria River confluence, *Cladophora* standing mass abruptly decreased to 0.01 oz C/yd² (0.5 g C/m²), and it remained low at the remaining downstream sampling stations (fig. 5). *Oscillatoria* spp., mat-forming algae, tended to dominate aquatic habitats at sites downstream of Lees Ferry with average biomass of 0.02 oz C/yd² (0.6 g C/m²) at the site immediately downstream of the Paria River.

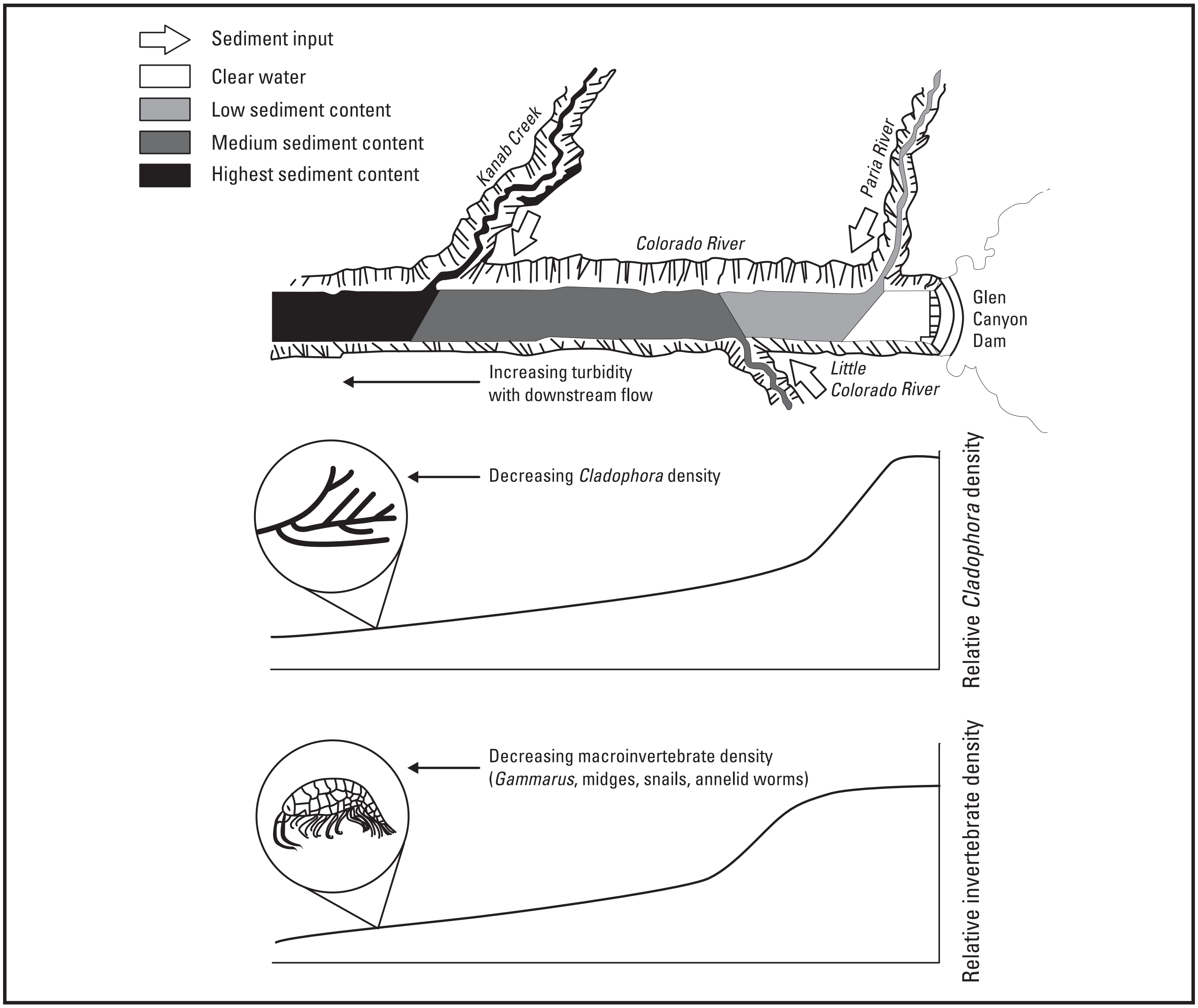

Figure 5. Downstream patterns of sediment concentration and biomass of *Cladophora* and macroinvertebrates along the Colorado River ecosystem. Modified from *The Colorado River Through Grand Canyon* by Steven W. Carothers and Bryan T. Brown. © 1991 The Arizona Board of Regents. Reprint by permission of the University of Arizona Press.

The species composition and biomass of aquatic invertebrates also vary with distance downstream. Stevens and others (1997) reported that *Gammarus* and chironomids were the dominant aquatic invertebrates in the Lees Ferry reach, while simuliids were the dominant invertebrates at sites downstream from the Paria River. Sublette and others (1998) identified 38 species of chironomids in the Grand Canyon ecosystem, and Stevens and others (1998) studied the factors that influence chironomid distribution in the Grand Canyon ecosystem. Stevens and others (1998) found that turbidity strongly influenced chironomid diversity, with 11 species present in the clear water of the Lees Ferry reach, 18 species present in what they termed the "variably turbid" segment of the Colorado River (Lees Ferry to Little Colorado River confluence), and 24 species in the "usually turbid" segment (Little Colorado River confluence to Diamond Creek). In contrast, the biomass of invertebrates declined downstream (Stevens and others, 1997), with mean biomass of 0.09 oz C/yd^2 (2.9 g C/m^2) in the Lees Ferry reach and much lower values, less than 0.003 oz C/yd^2 (<0.1 g C/m^2), at downstream locations.

Even though the Lees Ferry reach accounted for only 6.9% of the aquatic habitat in the 242 mi (390 km) of river studied by Stevens and others (1997), it supported 63.5% of the primary producer biomass and

87% of the invertebrate biomass in the entire study area. Stevens and others (1997) attributed the downstream decline in *Cladophora* biomass, and hence the invertebrates which are dependent on *Cladophora* and its attached diatoms (i.e., especially *Gammarus* and chironomids), to episodic inputs of suspended sediments from tributaries such as the Paria and the Little Colorado Rivers that reduce water clarity and light penetration enough to limit algal production (fig. 5).

In contrast to the patterns described above, river-bottom detritus (nonliving organic matter), which can be derived from both terrestrial and aquatic sources, peaked at approximately RM 124. This peak could have occurred here because detritus is transported from upstream locations and accumulates in this region of the river. Detritus is an important component of the aquatic food web because fish at downstream locations regularly consume simuliids that feed on detritus via filter feeding. In general, the overall quantity of drifting organic matter increases and the composition changes from predominantly aquatic to terrestrial material with distance downstream (Shannon and others, 1996; Benenati and others, 2001). Shannon and others (1996) noted that tributary inputs of organic matter constituted less than 0.1% of the total organic drift of the Colorado River. We suspect, however, that 0.1% is a gross underestimate of tributary organic inputs because it does not appear that sampling of tributary organic inputs was carried out during periods of flooding. Determining whether tributary inputs of organic matter and energy are important to the food web within the Colorado River will be a major focus of future aquatic ecology efforts, as outlined in the Discussion and Future Research Needs section of this chapter.

The density of many important components of the aquatic food web appears to vary with season. The densities of *Cladophora*, the dominant algae in the Lees Ferry reach, and *Oscillatoria*, the dominant algae at downstream locations, vary over time with peak density occurring during summer (Stevens and others, 1997). The highest density of aquatic invertebrates also occurred during the summer (Stevens and others, 1997). In contrast, the concentration of river-bottom detritus was greatest during autumn (Stevens and others, 1997), perhaps because this is when trees adjacent to the river were dropping their leaves or because lower river flows during this time of year allowed the material to settle out of the water column and accumulate on the river bottom.

It should be noted that because of logistical challenges, samples from only about 10 locations along the entire 241 mi (386 km) of the Grand Canyon ecosystem have been used to characterize spatial and temporal variability of organic matter and invertebrates. Further, much of the sampling (e.g., Shannon and others, 1994, 2001b; Blinn and others, 1995, 1998; Stevens and others, 1997; Benenati and others, 1998; McKinney and others, 1999) focused heavily on quantifying organic matter and invertebrate dynamics at cobble bar habitats; yet, cobble bars make up less than 10% of the aquatic habitat downstream from Glen Canyon Dam (Mietz, 2003). Thus, these results may not accurately characterize spatial and temporal variability of organic matter and invertebrates within the Grand Canyon ecosystem.

Mathematical modeling is a powerful tool that can be used to predict or estimate variables of interest (e.g., algae productivity) across large areas, such as the Grand Canyon ecosystem, where logistics prevent intensive field sampling. Yard and others (2005) measured and modeled the influence of canyon orientation and topographic complexity on solar inputs to the Grand Canyon ecosystem. Light is the resource that most often limits the growth of algae and plants in aquatic environments (Wetzel, 2001), so these results provide an indication of potential algae growth across the entire Grand Canyon ecosystem. One of the most striking results of these modeling efforts is that river reaches that are oriented east-west receive far less solar radiation during the winter months relative to north-south reaches because the sun is lower on the horizon at this time of year. That is, the river has a clear view of the sun as it traces a path across the horizon during the winter months along north-south reaches, but the sun never gets high enough on the horizon to shine on the river along east-west reaches. Thus, Yard and others (2005) forecast that algae production should vary predictably with canyon orientation and season because of differences in solar radiation and because of the general downstream decline in algae production that is associated with tributary sediment inputs that reduce water clarity and light penetration.

The Influence of Dam Releases on Organic Matter and Invertebrates

Understanding how Glen Canyon Dam discharge regimes influence *Cladophora* and associated invertebrates has been a major focus of recent research efforts (Angradi, 1994; Shannon and others, 1994, 1996, 2001b; Valdez and Ryel, 1995; McKinney and Speas, 2001). With discharge from Glen Canyon Dam fluctuating as much as 8,000 cubic feet per second (cfs) daily, there exists a large varial zone of shoreline habitat that is both inundated and exposed to air for long periods each day (fig. 3). Several studies have determined that the varial zone supports a relatively low density of algae, which is often dominated by *Oscillatoria* spp. because *Cladophora* and associated invertebrates cannot thrive in the varial zone (Blinn and others, 1995; Shaver and others, 1997; Benenati and others, 1998). Specifically, Blinn and others (1995) found fourfold higher invertebrate mass in permanently submerged zones compared to the varial zone. Using a series of in situ experiments, they determined that snails readily recolonized cobbles that were resubmerged after initially being subjected to long-term desiccation; however, the density of *Cladophora*, *Gammarus*, and chironomids on resubmerged cobbles was still less than 30% of control sites after 4 mo.

Fluctuations in river flows also have an impact on drifting organic matter because periodic desiccation can weaken algae and invertebrates, making them more susceptible to fragmentation and entrainment by the river. Moreover, higher river flows lead to more turbulent and faster water that is more likely to entrain organic matter and invertebrates. Shannon and others (1996) found that the quantity of drifting organic matter increased with discharge.

Historical data are insufficient to quantitatively determine what impact the MLFF alternative has had on organic matter and invertebrates; however, it is possible to qualitatively describe the likely impacts of this flow regime based on the research described above. By restricting daily fluctuations in discharge to less than 8,000 cfs and limiting minimum discharge to 5,000 cfs, MLFF flows have reduced the size of the varial zone and increased the amount of river bottom that is permanently submerged. Both of these changes probably increased the productivity and standing mass of important components of the aquatic food web, including *Cladophora* and *Gammarus*; however, abrupt changes in monthly release volumes that are permitted under the Record of Decision and MLFF may be detrimental to algae and aquatic invertebrates. For example, when monthly release volumes are decreased, the amount of river-bottom habitat that is permanently submerged also decreases. It seems likely that there is a subsequent, abrupt decrease in the quantity of food available for fish in the Grand Canyon ecosystem. Further, when monthly release volumes are abruptly increased, algae and invertebrates that were in shallow, nearshore habitats may find themselves under several yards of water. While this increase in monthly volume may eventually lead to an increase in the quantity of food available (by increasing available habitat), it seems likely that there is a short-term decrease in food as algae and invertebrates adjust to the new conditions.

Experimental high flows, or controlled floods, have been used principally as a tool to restore sandbars in the Grand Canyon ecosystem, but these floods also impact organic matter and invertebrates. Blinn and others (1999) found that the 1996 beach/habitat-building flow scoured more than 90% of the primary producer biomass (i.e., algae and submerged aquatic plants) and about 50% of the river-bottom invertebrates from a site at Lees Ferry; primary producers (1 mo) and invertebrates (2 mo) quickly recovered to preflood levels. In contrast, McKinney and others (1999) found that the 1996 beach/habitat-building flow caused short-term reductions in the standing mass of primary producers and invertebrates only in depositional habitats (i.e., areas of sand/silt) and not in more resistant habitats like cobble bars (fig. 6). Brock and others (1999) found that the 1996 beach/habitat-building flow actually led to significant increases in algae production rates (the rate at which photosynthesis is occurring within the algae); they hypothesized that algae production increased because the flood removed senescent, or old, material and detritus from the algae. Marzolf and others (1999) measured oxygen production, a byproduct of photosynthesis, along several river segments within the Lees Ferry reach and found that those segments produced less oxygen after the flood relative to preflood values. These data suggest that the 1996 beach/habitat-building flow did in fact scour large quantities of algae and aquatic macrophytes from the Lees Ferry reach, resulting in a systemwide reduction in primary production. Even though the flood may have reduced the standing mass of invertebrates from some areas in the Lees Ferry reach, the quantity of food items in rainbow trout stomachs was actually greater immediately after the flood relative to before the flood (McKinney and others, 1999). Blinn and others (1999) used stable-isotope analyses to determine that riparian vegetation and upland vegetation were the dominant types of drifting organic matter during the flood, while river-bottom algae were the dominant drifting organic matter during normal dam operations. Thus, experimental high flows can scour benthic algae and invertebrates and capture large quantities of terrestrial organic matter, which may temporarily increase the amount of food available for fish.

Recent Findings

New Zealand Mudsnail Invasion

Biological invasions represent a significant threat to the persistence of resident species because invaders are capable of altering food-web structure, rates of disease

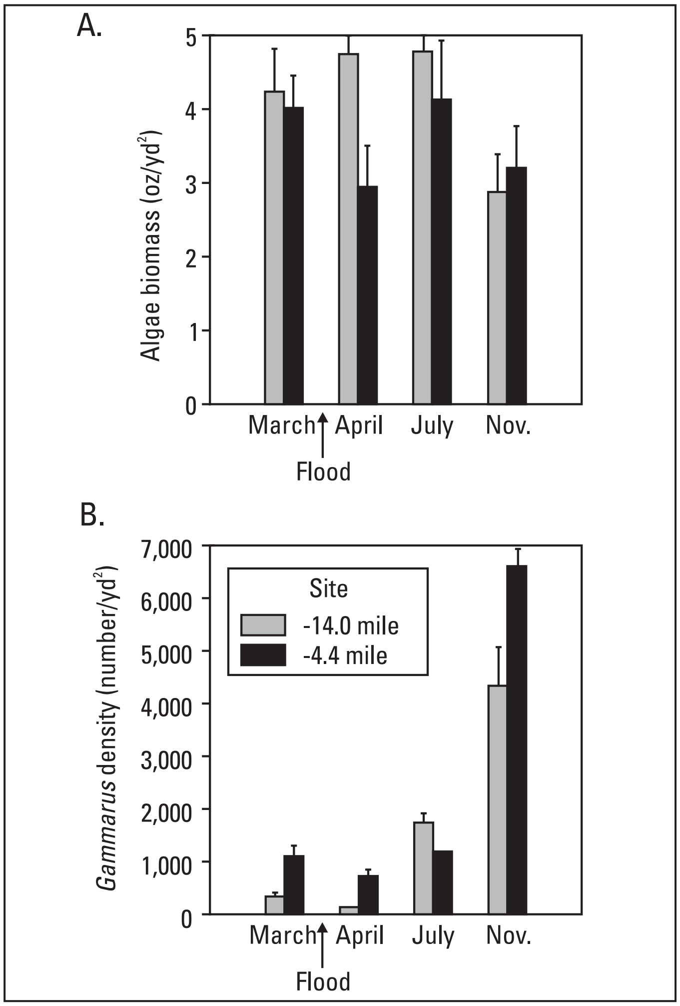

Figure 6. Algae (A) and invertebrate (B) response to the 1996 beach/habitat-building flow. The flood occurred between the March and April sampling dates. Bars represent average standing mass (algae) or density (*Gammarus*) at cobble bars in the Lees Ferry reach, while the thin lines on top of each bar represent 1 standard error (an indication of the uncertainty associated with each estimate). Data from McKinney and others (1999), table 1, p. 251.

or parasitism, and the amount or type of energy at the base of a food web (Vitousek, 1990; Wilcove and others, 1998; Kennedy and Hobbie, 2004). Although the food web in the Colorado River below Glen Canyon Dam has already been dramatically changed because of the installation of the dam and intentional introductions of nonnative sport fish, it is still susceptible to the impacts of biological invasions.

The New Zealand mudsnail (*Potamopyrgus antipodarum*), a species that is rapidly spreading throughout North American rivers and lakes (Hall and others, 2003, and references therein), has recently invaded the Grand Canyon ecosystem. The presence of the mudsnail in Grand Canyon was first identified from samples collected in March 2002; however, the analysis of archived collections revealed that mudsnails were actually present as early as May 1995 (Benenati and others, 2002). Presently, this small snail (fig. 7), which measures approximately 0.2 inch (about 5 mm), occurs in high densities throughout the Grand Canyon ecosystem, particularly in the Lees Ferry reach where densities of more than 32,800/yd² (40,000 snails/m²) have been found (Benenati and others, 2002). Before the New Zealand mudsnail invasion, snails represented a minor component of total invertebrate mass in the Lees Ferry reach (less than 6% of the total in 1992). Snails are now the dominant category of invertebrate in the Lees Ferry reach, representing more than 66% of invertebrate mass in 2001 (Benenati and others, 2002).

The potential impacts of the New Zealand mudsnail invasion on the aquatic food web of the Grand Canyon ecosystem are significant because nonnative rainbow trout apparently cannot easily digest the snails (fig. 1); snails eaten by trout often survive intact after passage through the gut (Mike Yard, oral commun., 2004), perhaps because of the snails' protective operculum. Humpback chub have pharyngeal gills that are capable of crushing snail shells and therefore might be able to more completely digest them; however, the only detailed diet analysis for chub was conducted before the mudsnail invasion of the Colorado River ecosystem. Because

Figure 7. New Zealand mudsnails on a concrete anchor in Glen Canyon. The density of snails shown here is typical for the Glen Canyon ecosystem (photograph by Michael Booth).

rainbow trout cannot easily digest the mudsnail, the mudsnail may have a competitive advantage over other herbivores such as *Gammarus*, potentially allowing it to displace these other organisms as it continues to spread. If the density of *Gammarus* and other invertebrates that are regularly consumed by fish declines because of competition with the New Zealand mudsnail, it seems likely that these changes will affect fish density and condition. Even if mudsnails do not compete with or displace herbivores such as *Gammarus*, which seems unlikely given their extremely high density, they dramatically alter important ecosystem functions, including rates of nutrient cycling and primary production (Hall and others, 2003). Unfortunately, historical data are inadequate to determine whether the density or biomass of *Gammarus* and other invertebrates that are important food items for fish in the Colorado River ecosystem has been affected by the New Zealand mudsnail invasion.

Discussion and Future Research Needs

With recent declines in the size of native fish populations and the condition of rainbow trout (see chapter 2, this report), understanding what food resources drive fish growth and production, as well as what sources of energy drive production of these food resources, becomes increasingly important. Previous research on the aquatic food web has produced a relatively clear picture of the food habits of fish in the Grand Canyon ecosystem. Aquatic invertebrates—particularly *Gammarus*, simuliids, and chironomids—appear to be the most important food items for both rainbow trout and humpback chub. In the upper reaches of the Colorado River near Lees Ferry, it appears that invertebrates, and therefore the fish that consume them, are fueled almost exclusively by algae, particularly diatoms attached to *Cladophora*. Although there is evidence that the invertebrates consumed by fish at downstream locations are relying on both aquatic and terrestrial organic matter, the relative importance and sources of this material remain unclear. This uncertainty prevents a complete understanding of the role that food availability plays in determining the condition and population size of native and nonnative fish.

Food-web analysis provides a framework for quantifying the movement of terrestrial and aquatic material into higher trophic levels, the trophic positions of consumers, and the importance of interactions such as competition and predation. Applied research efforts have repeatedly benefited from studying an ecosystem from a food-web perspective (Winemiller and Polis, 1996). Fisheries management, in particular, can benefit from a food-web perspective because it is critical for accurately predicting the responses of both predators and prey to management actions (Parsons, 1992). Although many food-web studies of terrestrial and aquatic systems have focused on trophic pathways based exclusively on aquatic production, it is increasingly recognized that leaf litter and other types of terrestrial organic matter play a major role in determining ecosystem structure and function (Winemiller and Polis, 1996).

In the case of the Grand Canyon ecosystem, previous research efforts on the aquatic food web have focused almost exclusively on trophic pathways associated with aquatic organic matter, namely the filamentous algae *Cladophora*, the diatoms attached to this algae, and the invertebrate consumers of these attached diatoms (Usher and Blinn, 1990; Hardwick and others, 1992; Shannon and others, 1994). Focusing on these aquatic sources of organic matter seems appropriate for the tailwater section of the Colorado River, that is, from the dam to Lees Ferry. Yet, the tailwater is not representative of downstream portions of the river and accounts for less than 7% of the total wetted area of the Grand Canyon ecosystem. A thorough analysis of the trophic significance of terrestrially derived material has never been conducted, although there are some correlative data that support the contention that the downstream decline in algae production limits secondary production at downstream sites (Shaver and others, 1997; Stevens and others, 1997). Importantly, the one detailed food-web analysis that has been conducted in the Grand Canyon ecosystem indicates that terrestrially derived carbon is contributing to invertebrate and fish production at downstream tributaries (Angradi, 1994).

Given these considerations, it seems clear that future research and monitoring efforts should take a broader view of the food web and attempt to document the relative importance of aquatic and terrestrial organic matter to invertebrate and fish production. For example, if invertebrates, and by extension humpback chub and rainbow trout, are dependent on algae throughout the ecosystem, a systemwide reduction in algae production would likely have strong negative consequences for fish, especially because algae biomass is already very limited at downstream sites. Alternatively, if terrestrial organic matter is fueling production of invertebrates at downstream sites, then findings from the proposed food-web research would provide managers with some of the information necessary to assess the effects of proposed management actions, including sediment augmentation and thermal modifications, on fish production.

Food-web analysis should continue to focus on the two most ecologically and economically important fish species, humpback chub and rainbow trout, and use a combination of gut-content and stable-isotope analysis. To determine whether the resource base of the food web shifts downstream and is affected by tributary inputs of organic matter, a food-web analysis should encompass the entire study area including the major tributaries of the Colorado River, including the Paria and Little Colorado Rivers. Shannon and others (2001a) found downstream shifts in the isotopic composition of algae, invertebrates, and fish. This downstream shift may complicate interpretation of stable-isotope data, but another technique for determining trophic linkages, known as quantitative fatty acid analysis (Iverson and others, 2004), may allow investigators to resolve any uncertainties associated with stable-isotope analysis. Manipulative experiments involving New Zealand mudsnails also represent an important research direction because these experiments could help scientists determine whether or not this invasive species is having a negative impact on important food items for fish and identify the factors that control New Zealand mudsnail density. Collectively, these activities will determine the short- and long-term feeding habits of humpback chub and rainbow trout, the energy resources at the base of the food web, whether humpback chub are consuming and digesting New Zealand mudsnails, and the impact of the mudsnail invasion on the aquatic food web.

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