GCDAMP Knowledge Assessment: Drivers & Constraints

Resource Topic:	Aquatic food base
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Resource Characteristic	Driver or Constraint	Strength	Direction	Confidence	Rationale: Strength & Direction	Rationale: Confidence	Recommendations	Key References
Secondary production	Flow fluctuation	Strong	Unknown	Low	Resource characteristic refers to drift concentration or emergence production. Hydropeaking can negatively impact drift through two mechanisms--limiting insect diversity owing to egg mortality, and reducing benthic densities over the long term owing to export (drift) that exceeds replacement rate. In constrast, hydropeaking causes large within day increasese drift concentrations of invertebrates as was documented by Miller and Judson (2014) in Flaming Gorge and by Kennedy et al (2014) in Glen Canyon. The relative balance between these negative and positive effects is unclear (i.e., are effects of hydropeaking on drift a net positive, or a net negative?).	Only low confidence, because this a complex relationship, and drift rates can likely be increased over the short term by peaking.	Management: 1) Consider testing bug flows to see if reduced egg mortality during weekends leads to higher drift concentrations during weekday hydropeaking. Research: 1) Consider additional studies of interrelationships between discharge flucatuations and drift.	
Secondary production	Spring flood disturbance (HFEs)	Strong	Positive Effect	Low	Resource characteristic refers to drift concentration or emergence production. The 2008 spring HFE shifted assemblage towards insects, and insects drift at much higher rates than non-insects. Thus, spring-timed HFEs should increase drift concentrations.	Only rated Low confidence owing to a single Spring flood being well studied.	Management: 1) To maximize invertebrate drift and food for fishes, consider testing spring HFEs in concert with macroinvertebrate production flows. Additional spring HFEs, as experiments, would improve confidence in status and trends of results. Research: 1) Opportunities for learning about spring HFEs are limited without additional testing of spring HFEs.	1) Cross, Wyatt F., et al. (2011) Ecological Applications 21, no. 6: 2016-2033. 2) Kennedy, Theodore A., et al. (2014) Freshwater Biology 59, no. 3: 557-572.
Secondary production	Fall flood disturbance (HFEs)	Moderate	Negative Effect	Low	Resource characteristic refers to drift concentration or emergence production. Recent fall HFEs appear to favor NZ mudsnails and disfavor aquatic insects. Insects drift at high rates whereas mudsnails are a trophic dead end and cannot be digested by most fishes. Thus, we conclude that fall HFEs have a moderate negative effect on food base diversity.	Only rated Low confidence because HFE implementation strategy (fall HFEs in 4 of 5 years, without a comparable period of no HFEs or spring HFEs) does not allow strong inferences to be drawn from current drift observations.	Management: 1) To maximize invertebrate drift, consider testing spring HFEs in concert with macroinvertebrate production flows. Additional spring HFEs, as experiments, would improve confidence in status and trends of results. Research: 1) Opportunities for learning about fall HFEs are limited without additional testing of spring HFEs or a cessation of fall HFEs. 2) Complete analysis of long-term drift monitoring data.	
Secondary production	High sustained discharges (e.g., equalization)	Strong	Unknown	Low	Resource characteristic refers to drift concentration or emergence production. High flows increase habitat area, while steady flows should provide favorable egg laying conditions for aquatic insects. Thus, high and steady flows typical of equalization years should increase drift and secondary production via both of these mechanisms. Uncertainty concerning short (wiltout peaking drift might be low?) vs. long term effects (steady and high discharge should lead to high benthic biomass?) are reason for unknown direction.	Very limited monitoring was in place in 2011 during the last equalization. Not much to go on here.	Research: 1) Ensure robust monitoring is in place during next equalization flow. Only rudimentary food base monitoring was in place during the last equalization flow in 2011.	

Secondary production	Cool water temperatures	Moderate	Negative Effect	Low	Resource characteristic refers to drift concentration or emergence production. Warmer water should increase growth rates and drift of invertebrates	Growth response of rainbow trout and humpback chub to warmer water has been highly variable, indicating the prey base is not always keeping pace with increases in fish metabolic demands. New evidence suggests nutrients and water temperatures released from Lake Powell co-vary, and in years when nutrients are low but water temperature is high, drift concentration does not increase sufficiently to compensate for increased metabolic demands of fishes.	Research: 1) Conduct stress tests of invertebrate assemblages (growth experiments over extreme range of water temperatures) to identify how the nearctic assemblages present downstream of Glen Canyon Dam will respond to the very warm water temperatures that may occur in the future.	
Secondary production	Nutrients	Strong	Positive Effect	Medium	Resource characteristic refers to drift concentration or emergence production. Nutrients stimulate production of invertebrates as evidenced by recent analyses of Phosphorus v. primary production, drift, and fish condition presented at ARM. This relationship applies to both algae and detritus dominated streams. Nutrient levels in the Colorado River are perpetually low, because Lake Powell is a sink for nutrients. Nutrients in releases are elevated in years of high inflows to Lake Powell that resuspend nutrients that have previously settled in in-flow deltas.		Management: 1) Evaluate feasibility of nutrient supplementation program. Research: 1) Consider mesocosm/tank experiments where nutrients are manipulated and growth response of invertebrates is quantified. 2) Consider short duration nutrient addition as a research experiment to better resolve strength of nutrient-invertebrate drift relationship.	1) Minshall, G. W., et al. (2014). Freshwater Science, 33(4), 1009-1023 2) Cross, W. F., et al. (2006). Ecology, 87(6), 1556-1565.
Secondary production	Low dissolved oxygen (<5mg/L) in water column and/or substrate	Strong	Negative Effect	Low	Resource characteristic refers to drift concentration or emergence production. Over the range of observed conditions dissolved oxygen is unlikely a significant constraint on drift concentrations. Note that low DO values are a moderate concern in the Lees Ferry reach only, because Grand Canyon rapids ensure DO is high and never a concern in downstream reaches.	Higher DO values are beneficial to aquatic life. However, only medium confidence, because low DO (<5 mg/L at the dam) has only occurred once in the past 15 years, and no studies of invertebrate response to low DO have occurred downstream of GCD.	Management: 1) If generation was added to jet tubes, then mitigating low DO as a management tool could be accomplished through operation of jet tubes (additional evaluations would be required). Research: 1) Continued montoring of invertebrate drift combined with dissolved oxygen montoring will help resolve effects of DO on drift.	
Secondary production	Turbidity and suspended sediment	Moderate	Negative Effect	Low	Resource characteristic refers to drift concentration or emergence production. More turbid rivers with high suspended sediment (or mobile bed sediment) loads generally have lower diversity than clear-water rivers; however, this is also confounded by substrate quality (see above), and is scale-specific. Diverse assemblages of aquatic insects that include high EPT diversity are present in other tailwaters in the Basin where turbidity and sediment is low. However, diverse assemblages of aquatic insects are also present in Cataract Canyon that has high turbidity and highly mobile sediment, and is probably the closest reference condition we have to the pre-dam GCD tailwater.	Simple chain of logic based on conditions elsewhere in the Basin, combined with basic stream ecology theory from textbooks.	Research: 1) Continued drift and light trap monitoring in Glen, Marble, and Grand Canyon will help clarify role of turbidity in constraining secondary production (drift and emergence production).	

Secondary production	Substrate quality	Strong	Positive Effect	Medium	Resource characteristic refers to drift concentration or emergence production. Higher-quality substrate for aquatic invertebrates has more cobble bars overall, less armoring, less embeddedness, and less bed sand. High quality substrates with lots of inter-stitial spaces and well oxygenated water increase the habitat available to invertebrates. Cross et al. 2013 and Stevens et al. 1997 documented much higher abundance and diversity of invertebrates in cobble habitats throughout Glen, Marble, and Grand Canyon compared to cliff faces and sandy habitat.	Only medium confidence, because effects of among habitat variation (e.g., sand vs. cliff vs. cobble) on invertebrates have been assessed, but variation in quality within cobble/gravel habitats per se have not been assessed.	Management: 1) Consider testing spring timed HFEs, because the timing of HFEs may influence substrate quality. Recent fall HFEs appear to be promoting colonization by aquatic macrophytes, which provide habitat for invasive New Zealand mudsnails. Spring HFEs likely knock back macrophytes to a greater degree than fall HFEs, similar to how pruning trees in spring can cause mortality whereas pruning trees in fall does not. Research: 1) Ongoing research by Larry Stevens may clarify role of habitat quality in constraining food base diversity in Glen Canyon. 2) Consider studies that compare habitat quality of cobble/gravel in Glen vs. Grand Canyon and that include direct manipulations of substrates (power washing cobbles, scraping cobbles) 3) In the absence of a switch in HFE timing, consider studies that disturb macrophytes in spring and/or fall (e.g., by raking or dredging) to understand how HFE timing affects macrophyte response.	
Secondary production	Algae and aquatic macrophyte quantity and quality	Strong	Positive Effect	Low	Resource characteristic refers to drift concentration or emergence production. Some algae and aquatic macrophytes are high quality food resources, while others are inedible or can even make water conditions toxic. In general, however, streams/river with greater quality and quantity of primary production have higher secondary production of invertebrates.	This is a complex relationship, and can be location and conditions-specific.	Research: 1) Consider new research studies of macrophyte-invertebrate interactions in Lees Ferry. 2) Continued monitoring of primary production, combined with drift and light trap monitoring of the food base will help clarify role of primary production in controlling invertebrate secondary production.	
Secondary production	Leaf litter and similar inputs (allochthonous input)	Moderate	Positive Effect	High	Resource characteristic refers to drift concentration or emergence production. Leaf litter and similar resources generally provide food for invertebrates, and increased resource availability generally fosters invertebrate secondary production.	See stream ecology textbooks.	Research: 1) Consider regular stable isotope analysis of aquatic insects captured in light traps and drift nets to clarify trophic-basis of insect production (i.e., leaf litter vs. algae) in Lees Ferry and Grand Canyon.	
Food base diversity	Flow fluctuation	Strong	Negative Effect	Medium	The majority (~80%) of aquatic insects have river-edge egg laying behaviors that are incompatible with the artificial intertidal zone created by hydropeaking. Desiccation trials indicate insect eggs experience acute mortality when subject to brief drying. Hydropeaking waves propogate all the way downstream to lake mead, creating an intertidal zone of ~2ft in height. Collectively, these insights demonstrate that daily flow fluctuations exerting a strong and negative influence on food base diversity.	The hypothesis and logic chain presented in Kennedy et al. 2016 BioScience paper is simple and robust, and no flaws in the logic have been identified. The model and data used to test the hypothesis include the largest dataset of insect emergence ever assembled and comparison of insect diversity across 16 dammed rivers in the west. However, only rated medium confidence, because of robust populations of 1-2 species of caddisflies and the occassional mayfly at Davis and Parker Dam tailwaters.	Management 1) Food base diversity might be increased through macroinvertebrate production flows that stabilize flows every weekend during periods of peak aquatic insect activity. 2) Consider repatriation of native Colorado River invertebrates such as caddisflies from Davis and Parker to "jump start" colonization. Research 1) Consider new research at Hoover, Davis and Parker Dams to better understand life history of the caddisflies that are abundant in Davis and Parker segments, which have substantially greater hydropeaking than in Glen.	1) Poff, et al., 2007, Proceedings of the National Academy of Sciences, v. 104, no. 14, p. 5732-5737. 2) Statzner and Bêche, 2010, Freshwater Biology, v. 55, p. 80-119. 3) Kennedy, et al. (2016). BioScience 66 (7): 561-575. 4) Poff and Schmidt, 2016, Science, v. 353, no. 6304, p. 1099-1100.

Food base diversity	Spring flood disturbance (HFEs)	Moderate	Positive Effect	Low	Spring HFEs may foster diversity by providing conditions favorable to recolonizing insect species, similar to what was observed in 2008, but this effect is likely to be small relative to EPT taxa. In terms of relative abundance of existing taxa, the 2008 spring HFE was documented by Rosi Marshall et al. (2010) and Cross et al. (2011) as positively impacting insects, and knocking back NZMS for >18 months. Spring HFEs in the March-June timeframe are within the realm of natural flood timing for this river, as evidenced by spring high flow releases being conducted annually on many upper basin dams (e.g., Fontenelle, Flaming Gorge, Navajo). Thus, effects of spring flood disturbances on food base diversity are likely to be more positive than negative.	Role of disturbance in maintenance of diversity is well established in the general ecology literature, including in the stream ecology literature specifically.	Management 1) Consider testing spring timing for HFEs, because the 2008 HFE favored aquatic insects thereby increasing food base diversity. Research 1) Consider assessing shorter-term effects of HFEs, rather than year-averaged trends.	1) Fisher, et al., 1982, Ecological Monographs, v. 52, no. 1, p. 93–110. 2) Resh, et al., 1988, Journal of the North American Benthological Society, v. 7, no. 4, 433–455. 3) Poff, et al., 1997, BioScience, v. 47, no. 11, p. 769-784. 4) Rosi-Marshall, et al., 2010, U.S. Geological Survey Open-File Report 2010-1031, 28 p. 5) Cross, et al., 2011, Ecological Applications, v. 21, no. 6, p. 2016–2033.
Food base diversity	Fall flood disturbance (HFEs)	Moderate	Negative Effect	Low	Recent fall HFEs appear to favor NZ mudsnails and disfavor aquatic insects. However, mudsnails were abundant, and insects scarce, prior to the start of fall HFEs in 2012. Thus, we conclude that fall HFEs have a moderate negative effect on food base diversity.	Low confidence because effects of unusually or uniquely timed disturbances on diversity is not well established in the stream ecology literature. Note that the current experimental design of HFE implementation will not allow confidence to be increased. That is, fall HFEs have been tested in 4 of last 5 years, but no comparable duration period without HFEs or alternative HFE timing is possible under current HFE implementation strategy.	Management 1) Consider testing alternative timing for HFEs, because recent fall HFEs appear to have favored New Zealand Mudsnails. Note that reducing uncertainty concerning effects of fall HFEs on food base (i.e., are effects neutral OR negative) requires either a cessation of fall HFEs or a change in timing of HFEs. Research 1) Consider assessing shorter-term effects of HFEs, rather than year-averaged trends.	1) Poff, et al., 1997, BioScience, v. 47, no. 11, p. 769-784.
Food base diversity	High sustained discharges (e.g., equalization)	Moderate	Unknown	Low	Stable flows (i.e., less daily peaking, but still with seasonal-scale changes), whether low or high, is equivalent to a long duration 'bug flow'. Based on the multiple lines of evidence presented in our BioScience paper this should facilitate greater diversity and EPT. However, these type of equalization flows will only occur infrequently (e.g., we've only had one equalization in the ~10 years since the interim guidelines were finalized). Thus, equalization is likely to only have a weak effect on diversity.	Very limited monitoring was in place in 2011 during the last equalization. Not much to go on here.	Research: 1) Ensure robust monitoring is in place next time equalization flows occur.	

Food base diversity	Cool water temperatures	Strong	Negative Effect	Medium	Cool water temperatures are undoubtedly filtering out many taxa resident in tributaries and limiting colonization by taxa that might otherwise be able to survive in this river segment.	This is well established in the literature, but Tapeats Creek and the mainstem have nearly identical temperature regimes, so rated confidence Medium.	Research 1) Consider investigating temperature tolerances of Tapeats invertebrates. 2) Consider "stress testing" temperature change effects on current "Big 4" taxa.	1) Lehmkuhl, 1972, Journal of the Fisheries Research Board of Canada, v. 29, no. 9, p. 1329-1332. 2) Elliott, J.M., 1978, Freshwater Biology, v. 8, no. 1, p. 51–58. 3) Allan, J.D., and Castillo, M.M., 2007, Stream ecology: structure and function of running waters (2nd ed.): Dordrecht, The Netherlands, Springer, 436 p.
Food base diversity	Nutrients	Moderate	Positive Effect	Medium	Nutrient fertilization of the regulated Kootenai led to small increases in insect diversity per sample. No new taxa colonized this river segment following fertilization, but the number of taxa found in individual samples increased. Gammarus abundance was high in 2011 when nutrients were high.	Medium confidence owing to a single published study in a large river.	Management 1) Evaluate feasibility of nutrient supplementation program. Research 1) Restart Lake Powell monitoring. 2) Begin monitoring nutrients downstream.	1) Minshall, et al., 2014, Freshwater Science, v. 33, no. 4, p. 1009-1023.
Food base diversity	Low dissolved oxygen (<5mg/L) in water column and/or substrate	Strong	Negative Effect	Low	Over the range of observed conditions dissolved oxygen is unlikely a significant constraint on EPT diversity. Note that low DO values are a moderate concern in the Lees Ferry reach only, because Grand Canyon rapids ensure DO is high and never a concern in downstream reaches.	Higher DO values are beneficial to aquatic life. However, only medium confidence, because low DO (<5 mg/L at the dam) has only occurred once in the past 15 years, and no studies of invertebrate response to low DO have occurred downstream of GCD.	Management 1) If generation was added to jet tubes, then mitigating for low DO might be accomplished through their operation (additional evaluations would be required). Research 1) LF hyporheic anoxia study by Larry Stevens may shed light on DO effects. 2) Consider additional, direct studies on DO effects on invertebrates.	1) Allan, J.D., and Castillo, M.M., 2007, Stream ecology: structure and function of running waters (2nd ed.): Dordrecht, The Netherlands, Springer, 436 p.
Food base diversity	Turbidity and suspended sediment	Moderate	Negative Effect	Low	More turbid rivers with high suspended sediment (or mobile bed sediment) loads generally have lower diversity than clear-water rivers; however, this is also confounded by substrate quality (see above), and is scale-specific. Diverse assemblages of aquatic insects that include high EPT diversity are present in other tailwaters in the Basin where turbidity and sediment is low. However, diverse assemblages of aquatic insects are also present in Cataract Canyon that has high turbidity and highly mobile sediment, and is probably the closest reference condition we have to the pre-dam GCD tailwater.	Simple chain of logic based on conditions elsewhere in the Basin, combined with basic stream ecology theory from textbooks.	Research: 1) Continued light trap monitoring of the food base will help clarify role of turbidity in constraining EPT diversity in Grand Canyon.	1) Allan, J.D., and Castillo, M.M., 2007, Stream ecology: structure and function of running waters (2nd ed.): Dordrecht, The Netherlands, Springer, 436 p.

Food base diversity	Substrate quality	Strong	Positive Effect	Medium	Higher-quality substrate for aquatic invertebrates has more cobble bars overall, less armoring, less embeddedness, and less bed sand. Substrate quality strongly affects diversity and abundance of invertebrate assemblages. For example, Cross et al. 2013 and Stevens et al. 1997 documented higher abundance and diversity of invertebrates in cobble habitats throughout Glen, Marble, and Grand Canyon.	Only medium confidence, because effects of among habitat variation (e.g., sand vs. cliff vs. cobble) on invertebrates have been assessed, but variation in quality within cobble/gravel habitats per se have not been assessed.	Management: 1) Consider testing spring timed HFEs, because the timing of HFEs may influence substrate quality. Recent fall HFEs appear to be promoting colonization by aquatic macrophytes, which provide habitat for invasive New Zealand mudsnails. Spring HFEs likely knock back macrophytes to a greater degree than fall HFEs, similar to how pruning trees in spring can cause mortality whereas pruning trees in fall does not. Research: 1) Ongoing research by Larry Stevens may clarify role of habitat quality in constraining food base diversity in Glen Canyon. 2) Consider studies that compare habitat quality of cobble/gravel in Glen vs. Grand Canyon and that include direct manipulations of substrates (power washing cobbles, scraping cobbles) 3) In the absence of a switch in HFE timing, consider studies that disturb macrophytes in spring and/or fall (e.g., by raking or dredging) to understand how HFE timing affects macrophyte response.	1) Allan, J.D., and Castillo, M.M., 2007, Stream ecology: structure and function of running waters (2nd ed.): Dordrecht, The Netherlands, Springer, 436 p.
Food base diversity	Algae and aquatic macrophyte quantity and quality	Strong	Positive Effect	Low	Some algae and aquatic macrophytes are high quality food resources, while others are inedible or can even make water conditions toxic. In general, however, streams/river with greater quality and quantity of primary production have higher food base diversity.	This is a complex relationship, and can be location and conditions-specific.	Research: 1) Consider new research studies of macrophyte-invertebrate interactions in Lees Ferry. 2) Continued monitoring of primary production, combined with light trap monitoring of the food base will help clarify role of primary production in constraining EPT diversity in Grand Canyon.	1) Allan, J.D., and Castillo, M.M., 2007, Stream ecology: structure and function of running waters (2nd ed.): Dordrecht, The Netherlands, Springer, 436 p.
Food base diversity	Leaf litter and similar inputs (allochthonous input)	Moderate	Positive Effect	High	Leaf litter and similar resources generally provide food for invertebrates, and increased resource availability generally fosters diversity (although the response is likely stronger for invertebrate abundance and density).	See stream ecology textbooks.	Research: 1) Consider regular stable isotope analysis of aquatic insects captured in light traps and drift nets to clarify trophic-basis of insect production (i.e., leaf litter vs. algae) in Lees Ferry and Grand Canyon.	1) Allan, J.D., and Castillo, M.M., 2007, Stream ecology: structure and function of running waters (2nd ed.): Dordrecht, The Netherlands, Springer, 436 p.