Bonneville Power Administration
Fish and Wildlife Program FY99 Proposal

Section 1. General administrative information

Evaluate Effects Of Food Web Changes On Native Fish Restoration Strategies

Bonneville project number, if an ongoing project 9111

Business name of agency, institution or organization requesting funding
Flathead Lake Biological Station (FLBS), The University of Montana

Business acronym (if appropriate)

Proposal contact person or principal investigator:

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Subcontractors.

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NPPC Program Measure Number(s) which this project addresses.
2.2A, 2.2C, 5.7, 5.9, 7.1, 10.1A, 10.1B, 10.1C, 10.3, 13.1F

NMFS Biological Opinion Number(s) which this project addresses.

Other planning document references.

Section III.B.3 of Willams et al. 1997. Review of the Columbia River Basin Fish and Wildlife Program as directed by the 1996 amendment to the Power Act. Report of the Independent Scientific Review Panel for the Northwest Power Planning Council. ISRP Report 97-1.

Conclusions of Willians et al. 1997b. Return to the River: Restoration of salmonid fishes in the Columbia River ecosystem. Development of an alternative conceptual foundation and review and synthesis of science underlying the Fish and Wildlife Program of the Northwest Power Planning Council . Report of the Independent Scientific Group.

Subbasin.
Flathead Basin, MT

Short description.
Research critical structuring/limiting foodweb interactions where hydroelectric operations and exotic species introductions are causing declines in native fishes in spite of traditional mitigation efforts.

Section 2. Key words

Mark	Programmatic Categories	Mark	Activities	Mark	Project Types
	Anadromous fish		Construction		Watershed
X	Resident fish		O & M		Biodiversity/genetics
	Wildlife		Production		Population dynamics
	Oceans/estuaries	X	Research	X	Ecosystems
	Climate		Monitoring/eval.		Flow/survival
	Other		Resource mgmt		Fish disease
			Planning/admin.		Supplementation
			Enforcement		Wildlife habitat enhancement/restoration
			Acquisitions		

Other keywords.

food web, exotic species, ecological interactions

Section 3. Relationships to other Bonneville projects

Project #		Nature of relationship
9101903		Coordination, sample collection,

		equipment sharing
9101901	Hungry Horse Mitigation	Coordination, sample collection, equipment sharing
9101904	Hungry Horse Mitigation - Supplementation	Monitoring

Section 4. Objectives, tasks and schedules

Objectives and tasks

Obj 1,2,3	**Objective**	**Task a,b,c**	**Task**
1	1. Describe a biophysical template for Flathead Lake based on spatial and temporal habitat heterogeneity.	a	Determine joint sampling sites for the study. The lake will be divided into cells (ca. 40) as a way of logically nesting primary habitat descriptors (e.g. substrate, seasonal current patterns, depth, thermal regime, turbidity) which vary spatially.
2	2. Conduct time-series (2 years) sampling of the food web with sampling regime based on the variability in type of data collected.	a	Quantify spatial (sites according to the template in objective 1) and temporal (sampling at least 15 times per year) abundance and size structure of dominant food web components (fishes, M. relicta, zooplankton, phytoplankton (chl a)).
3	Correlate foodweb response variables (objective 2) with the biophysical template (objective 1) to develop inferences about foodweb controls in time and space.	a	Conduct multivariate and geostatistical analyses of data collected under objectives 1 and 2.
4	Demonstrate foodweb interactions using spatio-temporal distributions (objectives 1-3) and testing for pairwise coexistence of species by diel cycle, habitat, and season, and through gut analyses.	a	Analyze the distribution and consumption patterns of higher trophic linkages: large zooplankton and fish.
5	Perform sensitivity analyses on	a	Model food web interactions,

	modeled foodweb interactions to identify transfers of energy that are critical in foodweb structuring		using two models: a) energetics-based foodweb simulator (i.e., top down effects, Beauchamp et al., Utah State University) and b) nutrient-based ecosystem simulation (i.e., bottom-up effects, Levitan and Hall, FLBS)
		b	Perform sensitivity analyses on both models.
6	Identify and quantify roles of hypothesized strong interacting species in foodweb regulation.	a	Use the foodweb and the ecosystem models to explore how M. relicta is affecting foodweb; compare to time series trends observed in the lake.
7	Determine probable response of foodweb to lake trout suppression.	a	Use the foodweb and the ecosystem models to demonstrate potential ramifications of suppression of foodweb interactors such as lake trout, lake whitefish and/or Mysis relicta
8	Determine the inherent tertiary production capacity of Flathead Lake under different foodweb configurations, given current nutrient loading.	a	Use spatial and temporal responses of the phytoplankton community to nutrient loading (i.e., the long term water quality data base collected continuously by FLBS since 1977) in the ecosystem model to elucidate the likelihood of top down controls.
9	Conduct a retrospective analysis of the structure and function of the historical lake foodweb: prior to fish introductions (<1900) and after non-native fish introductions, but pre-Mysis (1930-1980).	a	Collate and examine all historic abundance, distribution, and life history data of native and non-native lake biota in context of the foodweb problem at hand.
10	Put study results into regional context by comparing our understanding of Flathead Lake foodweb with what is known about other lentic food webs in the Columbia Basin.	a	Literature review of existing data for lentic systems in Columbia basin, including British Columbia similar to Flathead Lake.
		b	Synthesize and compare understanding of food web dynamics in Flathead Lake to regional lentic food web problems.

11	Based on the empirical and modeled results, develop a limnological and fisheries monitoring protocol that encompasses all relevant trophic levels so that future manipulations of the foodweb in Flathead Lake (e.g. lake trout suppression; native salmonid	a	Synthesize data and analyses of this study in a monitoring context for foodweb management.
		b	Conduct consultations with all water quality and fisheries management entities with Flathead Lake mandates.
		c	Conduct sensitivity analyses of selected monitoring variables using both models.

Objective schedules and costs

Objective #	Start Date mm/yyyy	End Date mm/yyyy	Cost %
1	10/1998	4/1999	5
2	4/1999	4/2001	30
3	6/1999	6/2001	5
4	6/1999	6/2001	5
5	5/1999	6/2001	10
6	5/1999	6/2001	5
7	5/1999	6/2001	20
8	10/1998	8/1999	5
9	5/2000	10/2001	10
10	5/2000	10/2001	5
			TOTAL 10000.00%

Schedule constraints.

Completion date.
2001

Section 5. Budget

FY99 budget by line item

Item	Note	FY99
Personnel		$270,021
Fringe benefits		$78,660
Supplies, materials, non-expendable property		$52,000
Operations & maintenance		$10,000
Capital acquisitions or improvements (e.g. land, buildings, major equip.)		$169,600
PIT tags	# of tags:	$0
Travel		$36,310
Indirect costs		$117,999
Subcontracts		$269,736
Other		$19,411
TOTAL		$1,023,737

Outyear costs

Outyear costs	FY2000	FY01	FY02	FY03
Total budget	$771,768	$692,780		
O&M as % of total	3.00%	4.00%		

Section 6. Abstract

Research critical structuring/limiting foodweb interactions where hydroelectric operations and exotic species introductions are causing declines in native fishes in spite of traditional mitigation efforts. Using Flathead Lake, MT as a study system, develop a lake biophysical template based on spatial and temporal habitat heterogeneity to be used in formulating a whole foodweb sampling regime. After sampling the food web for 2 year, correlate foodweb response variables with the biophysical template to develop inferences about foodweb controls in time and space. Demonstrate foodweb interactions using spatio-temporal distributions and gut analyses. Perform sensitivity analyses on modeled foodweb interactions to identify transfers of energy that are critical in foodweb structuring. Identify roles of hypothesized strong interacting species (*Mysis relicta*, lake trout, lake whitefish). Determine probable response of the foodweb to lake trout suppression. Conduct a retrospective analysis of the structure and function of the historical lake foodweb: prior to fish introductions (<1900) and after non-native fish introductions, but pre-*M. relicta* (1930-1980) to test the hypothesis that the lake foodweb

was largely unaffected by introductions until *M. relicta* induced strong novel species interactions. Place study results into a regional context by comparing our understanding of Flathead Lake foodweb with what is known about other lentic food webs in the Columbia Basin and disseminate information to downstream regional managers with a regional workshop.

Section 7. Project description

a. Technical and/or scientific background.

Many populations of resident native fish in the Columbia Basin are undergoing numerical declines. In order to address the highest priority of the resident fish goals of the Columbia River Fish and Wildlife Plan, to rebuild to sustainable levels weak, but recoverable, populations of native fish injured by the hydropower system, Bonneville Power Administration (BPA) has reconstructed physical habitat, engaged in artificial propogation, and developed hydropower operational guidelines. However, populations of native fish continue to decline. An adequate understanding the dominant interactions structuring food webs in the Columbia River system has been a major impediment to implementation of ecosystem level restoration strategies (Williams *et al*. 1997)

We present a framework that will address management and research needs that are critical to the recovery/in place mitigation, of native species throughout the Columbia River system. Using an collaborative approach involving co-operating state, tribal and academic institutions, we provide a robust research agenda that will materially improve the understanding of how key salmonids interact in with exotic invaders in complex food webs, while directly addressing critical uncertainties that hinder effective fisheries management. We choose to perform this research in Flathead Lake, MT, because a long-term data base exists for many crucial food web components, institutional co-operative agreements and working relationships have been developed, the biological uncertainties hampering native fish restoration in Flathead Lake are almost universal in the Columbia River system, and resident bull trout are declining and likely will be ESA listed. Flathead Lake is small enough to enable meaningful detailed research yet is large enough that in many respects it functions in a similar manner to the lower Columbia oceanic-riverine system. Using our approach, the scientific knowledge gained, and associated management initiatives developed from studying Flathead Lake adfluvial native fishes will be directly applicable to both other Columbia basin water bodies (e.g. Pend Oreille, Roosevelt, Banks, Priest, John Day). For example, Flathead lake will be used as a model system to ascertain attainable food web states for lentic systems with similar species complements.

Flathead Lake is a large (495.5 km^2) oligotrophic lake, renowned for its high water quality, in northwest Montana. The lake is co-managed by the State of Montana Fish Wildlife and Parks (MFWP) and the Confederated Salish and Kootenai Tribes (CSKT). Seven major tributaries drain the Flathead catchment (18,379 km^2), but the Swan River and the 3 forks of the Flathead River produce most of the water that enters Flathead Lake annually (≈95%)(Stanford *et al.* 1997). Over 75% of nutrients (nitrogen (N) and phosphorus (P)) and suspended solids enter the lake via the Flathead River, the majority of which enters in a sediment plume during spring runoff (Stanford *et al.* 1997).

The patterns of water flux and availability of historic range to adfluvial fish species in Flathead Lake are controlled in part by upstream hydroelectric dams. Collectively Swan (1902), and Hungry Horse Dam (1952) on the South fork of the Flathead regulate 42% of the annual influx of water, and runoff and adfluvial habitat availability of 41% of the catchment area. Kerr Dam (1938), has changed the timing and duration of both full and minimum pool levels of Flathead Lake (Stanford *et al.* 1997). Hydroelectric mediated management of river discharge and associated nutrient and thermal effects, coupled with disruption of habitat connectivity interact synergistically with introduced species to stress native fish species in the Flathead basin and throughout the Columbia River system. Management initiatives in the lower Columbia River system to enhance salmon survivorship can affect Flathead and other upstream systems by dictating flow regimes over dams.

The biological history of Flathead Lake is complex. Historically, the Flathead Lake zooplankton community was dominated by cladocerans (*Daphnia thorata, D. longiremis, Bosmina longirostris, Leptodora kindtii*), copepods (*Epishura nevadensis*, *Diaptomus ashlandi*, *Diacyclops bicuspidatus*) and many rotifer species. The native fish community was dominated by native salmonids (westslope cutthroat trout, bull trout, mountain and pygmy whitefish), catostomids (longnose and largescale suckers), and cyprinids (peamouth, squawfish and redside shiner). Although little is know about fish production levels, the Flathead Lake fishery was traditionally an integral part of local native American lifestyle prior to European settlement.

The components of the Flathead Lake food web have been greatly altered. Lake whitefish, lake trout, kokanee salmon and perch had all been introduced into the lake system by the 1930's. By 1963 the sport fish catch was dominated by kokanee salmon (76-95%), with over 100,000 fish harvested annually (Beattie *et al.* 1988, Robbins 1966). Kokanee were used heavily by native wildlife including grizzly bears and bald eagles (Spencer *et al.* 1991). During this time, lake trout, feeding heavily on kokanee, provided a trophy fishery with fish over 18 kg not uncommon.

In 1981 *Mysis relicta*, a freshwater shrimp that appears to play a dominant role in food web (re)structuring processes, was documented in Flathead Lake. Within seven years two of the four principal cladocerans (*D. longiremis and L. kindtii*) disappeared from lake samples and the two others (*D. thorata and B. longirostris*) persisted but at greatly reduced densities (Figure 1)(Spencer *et al.* 1991). Similar trends occurred in copepod populations. Although kokanee salmon numbers had previously been affected by hydroelectric dam induced redd dewatering in both Flathead Lake and the Southfork of the Flathead River (Fraley *et al.* 1989, Decker-Hess and Graham 1982), the kokanee population collapsed after *M. relicta* colonization (Spencer *et al.* 1991, Beattie and Clancy 1989). In spite of recent massive restocking efforts funded by BPA, kokanee are virtually absent from Flathead Lake. Lake trout and lake whitefish populations have greatly increased whereas native salmonids continue to decline (see Donald and Alger 1993)(Figure 2). Since 1981-83 bull trout have decreased from an average 2.1 fish per survey gillnet to an average of 0.2 in 1992-96. Westslope cutthroat have decreased from 2.7 to 0.7 fish per net, lake trout have increased from 0.1 to 1.7 and lake whitefish have increased from 2.7 to 9.7 fish per net. Concurrently bull trout redd counts at State monitoring sites have decreased from a high of 600 in 1982 to 114 in 1997 (State of Montana Fish Wildlife and Parks, unpublished data). It is important to note that the exotic fishes of concern were well established by the 1930's yet native species of concern did not decline to dangerously low levels until the recent introduction of *M. relicta*, increased nutrient loading into Flathead lake, and concurrent increases in lake trout and lake whitefish populations.

Since 1977 the Flathead Lake Biological Station has monitored N and P concentrations, primary production, algal biomass (chl *a*), water clarity, oxygen concentrations, and phytoplankton and zooplankton communities as indicators of lake nutrient loading. Although it is recognized that other interactive limnological processes also can influence these response variables, a number of important relations regarding the influence of external nutrient supply on water quality and basal food web components are apparent in the long-term record. Annual primary productivity, a strong indicator of nutrient level is increasing gradually (Figure 3), and blooms of the bluegreen algae *Anabaena* sp., also indicative of increased nutrient loading, are now being recorded for the first time in observations spanning over 90 years (Stanford *et al.* 1997, unpublished data). Evidence is also accumulating to suggest that higher trophic levels influence both basal food web components and nutrient fluxes in lakes (Schindler *et al*. 1997). However, the inter-relationships and mechanisms of how increased nutrient loading is influencing higher trophic levels and associated native fishes, and how in Flathead Lake changes in fish communities may be affecting lower trophic levels and nutrient fluxes is largely unknown (*sensu* Carpenter *et al.* 1985).

In November 1997, an expert, independent scientific panel convened to examine the potential effects of non-native lake trout on bull trout and other native species in the Flathead basin. The panel concluded that lake trout have caused the decline in native species and kokanee in Flathead Lake. Further, the panel stated that two mutually exclusive management scenarios were biologically possible for the lake: 1) It could be managed for restoration of native species and a kokanee fishery, or 2) It could be managed for the recently developing lake trout-lake whitefish fishery. The panel believed it was possible (70-90% chance) to control lake trout enough to restore bull trout to near 1980's levels; however, such a control program would need to continue indefinitely. Before any major manipulations to the system are implemented the feasibility and biological ramifications of this management option should be thoroughly evaluated. Moreover, more information is needed to design a monitoring plan that can assess the success, and complete food web effects of any such management program and provide insight about how to refine it over time. Successful attempts to reduce lake trout abundance will require guidance on technical feasibility and cost-effectiveness. For example, it is not known what other species might be vulnerable to lake trout removal efforts. How many lake trout could be removed? How will other species, especially *M. relicta* and lake whitefish, respond to significant lake trout reductions? What are the implications of lake trout suppression for the structure, function, and long-term stability of the entire food web?

Food web components may interact in very discrete locations over limited periods. For example, since the mid-1980's the ubiquitous distribution of *M. relicta* along the deeper lake bottom may provide a forage base in habitats that was previously lacking that also provided refuge from cannibalism. Also, physical and environmental factors, mediated by various river flow and lake current regimes may contribute to the interannual variability in the magnitude of species interactions. For example, temperature and turbidity affects the physiological consumption capacity and foraging efficiency (visual encounter rates with prey) of predators. Thus direct predation losses of a specific species could be significantly reduced in years with high runoff because of lower temperatures with higher and prolonged turbidity in the northern region of the lake.

We propose a research approach that addresses both the potential for both “top-down” (i.e. predation) and “bottom-up” (i.e. nutrient loading) food web regulation, and the potential interaction of these two driving forces, in a manner that incorporates environmental heterogeneity and is temporally and spatially explicit. We will use both empirical based methodologies, and a series of existing simulation models to formalize and investigate food web dynamics.

Products that will result from this project include: scientific publications and presentations at societal meetings, technical transfers of information for local environmental management in the form of workshops involving CSKT, MFWP, Montana Department of Environmental Quality, academic institutions and NGO’s, a regional technical workshop that will disseminate management data and conclusion to Lower Columbia fisheries managers, a person formally trained in hydroacoustics/food web interactions to aid State and Tribal fisheries managers, working bioenergetic models applicable to other Columbia Basin systems, a whole-food web monitoring framework. Improved understanding of the ecology of Flathead Lake attained in the course of this proposal may contribute to the ongoing management decision process.

b. Proposal objectives.

1. Describe a biophysical template for Flathead Lake based on spatial and temporal habitat heterogeneity.
2. Conduct time-series (2 years) sampling of the food web with sampling regime based on endpoint variability and concern for bycatch
Ho: Food web components are uniformly distributed in time and space.
Ha: Food web components exhibit spatial structure.
Ha: Food web components vary in distribution over time (e.g. show season or diel periodicity)
3. Correlate food web response variables (objective 2) with the biophysical template (objective 1) to develop inferences about food web controls in time and space.
Ho: Species abundances are not correlated with limnological variables (e.g. nutrients, temperature, turbidity).
Ha: Species abundances are correlated with limnological variables and species distributions are predictable insofar as cycles and patterns in limnological variables can be identified.
4. Demonstrate food web interactions using spatio-temporal distributions (objectives 1-3) and testing for pairwise coexistence of species by diel cycle, habitat, and season, and through gut analyses.
Ho: Food web components do not coexist in time or space so direct predation is not possible.
Ha: Direct predation is possible because species coexist in time and space.
5. Perform sensitivity analyses on modeled food web interactions to identify transfers of energy that are critical in food web structuring.
Ho: All species are equally important in determine the food web of Flathead Lake.
Ha: All species are not equally important in determine the food web of Flathead Lake.
6. Identify roles of hypothesized strong interacting species in food web regulation.
Ho: Observed changes in fish communities are caused by *M. relicta* induced changes in food resources (excluding fish preying on other fish).
Ha: Observed changes in fish communities are caused by interactions among fish species.
7. Determine probable response of food web to lake trout suppression.
Ho: Lake trout suppression will increase survivorship of native species by decreasing direct predation mortality by lake trout and no other food web components will be affected by direct or indirect feedback mechanisms.
Ha: There will be biological ramifications of lake trout suppression other than increased survivorship of native species through decreases in direct lake trout predation.
8. Determine the inherent tertiary production capacity of Flathead Lake under different food web configurations, given current nutrient loading.
Ho: Food web configuration has no controlling effect on phytoplankton (primary productivity is controlled by external nutrient supply);

Ha: Food web configuration interacts with nutrient supply to determine phytoplankton productivity.
9. Conduct a retrospective analysis of the structure and function of the historical lake food web: prior to fish introductions (<1900) and after non-native fish introductions, but pre-Mysis (1930-1980).
Ho: The lake food web was largely unaffected by introductions until Mysis relicta induced strong interactions
Ha: Fish introductions and other environmental changes initiated strong interactions from the outset
10. Put study results into regional context by comparing our understanding of Flathead Lake food web with what is known about other lentic food webs in the Columbia Basin.
Ho: Flathead Lake food web responses have general applicability to understanding food webs in lake and reservoir systems throughout the Columbia River and in context of salmonid restoration problems basin wide.
Ha: The food web legacy of Flathead Lake is unique.
11. Based on the empirical and modeled results, develop a limnological and fisheries monitoring protocol that encompasses all relevant trophic levels so that future manipulations of the food web in Flathead Lake (e.g. lake trout suppression; native salmonid supplementation) can be quantitatively evaluated.

c. Rationale and significance to Regional Programs.

This proposal is directly responsive to recommendation III.B.3 of the Review of the Columbia River Basin Fish and Wildlife Program as directed by the 1996 amendment to the Power Act. However, Williams *et al*. (1997), in their review of fisheries ecology in the Columbia basin specifically recommended quantification of food web dynamics and their associated effects on juvenile salmonid ecology. The highest priorities of the resident fish goals of the Columbia Basin Fish and Wildlife plan include the rebuilding to sustainable levels, weak but recoverable, native populations injured by the hydropower system, to fund resident fish projects that also benefit wildlife and that support important fisheries (native or introduced). The Council recognizes that these goals will often require basin-wide coordination of all agencies involved in management (Sectons 2.2A, 2.2C, 10.1A-C). This proposal , using the Flathead lake-river system as a model, will enhance recovery/mitigation efforts of weak populations of native fish that were important fisheries, both historically for native Americans and more recently for sport anglers, have been quantitatively documented to benefit wildlife (e.g. Spencer *et al.* 1991) and have been deemed recoverable by a panel of internationally renowned experts (e.g. Jack MacIntyre 1998, *in prep*). This proposal involves all agencies and political jurisdictions that have a stake in this management issue.   By providing insight into efficacy and ramifications of potential predator control measures (removal of lake trout) this proposal addresses section 5.7; by documenting, researching and monitoring the combined effects of hydromanipulation and exotics on native food webs and desired introduced fish species (kokanee) this proposal addresses sections 5.9, 7.1 and 10.3; by introducing new methodologies and techniques aimed at fisheries mitigation this proposal addresses section 13.1F of the Fish and Wildlife Plan.

d. Project history

e. Methods.

This study is a collaboration with the ongoing management activities of the Confederated Salish Kootenai Tribes (Barry Hanson) and Montana Fish Wildlife and Parks (Mark Deleray), both of which will perform fish sampling (except larvae) for this project. All management concerns for Flathead Lake rest with these two agencies. Academic collaborators are FLBS (limnology, ecosystem modeling, and technology transfer), Utah State University (Dave Beauchamp, energetics modeling), and The University of Washington (Don Gunderson, hydroacoustics).

Our approach will combine direct sampling and modeling techniques into an integrative and interactive framework. We will use existing models that have been coupled to link upland process that dictate nutrient flux into Flathead Lake (Regional Hydroecological Simulation System – RHESSys, Nemani *et al.* 1993), with a whole-lake production model that had been developed at the Flathead Lake Biological Station (Flathead Lake Model – FLM, Nass 1990, Levitan *et al.* unpublished) . These models predict nutrient levels entering Flathead Lake and then, using a spatially explicit cellular approach, describes and predicts the mass flux of matter and energy between compartments. To date the model has been developed to incorporate only primary and secondary production, not tertiary (Figures 3 and 4). Our sampling regime will use a compatible cellular approach with all pertinent food web variables (nutrients, basic limnological data, phytoplankton biomass (chl a), phytoplankton and zooplankton community structure, *M relicta* and fish abundance, size, fecundity etc. as needed to address each listed objective). Each objective will be jointly performed by all participating agencies.

Objective 1

We will synthesize existing data (e.g. Deleray *et al.* 1998 draft, Stanford *et al.* 1991) describing habitat (e.g. substrate, lake zonations, seasonal current patterns, depth, thermal regime, turbidity, light penetration, biological characteristics etc.) and define habitat types that are ecologically relevant to the processes being studied. Data will be augmented by fieldwork where needed. An assumption of this work is that the Flathead food web is coherent at the sampling scale chosen. Knowledge of key physiological limitations (e.g. McLaren 1963), habitat preferences (e.g. Neill 1990), and statistical analyses (e.g. principal components analyses (Johnson and Wichern 1992)) will be used to prioritize and reduce the dimensionality of the habitat data to enable the definition of habitat cells. Habitat cells will likely number between 20 and 40. Using current theory (e.g. Dixon and Chiswell 1996, Whitfield 1996) we will develop a food web sampling regime that will allow the formalization of the food web and quantification of food web change in time (diel, seasonal, interannual) and space (among habitat cells).

Objective 2

Different species and life stages are vulnerable to different sampling methods. We will expand the Flathead Lake Biological Stations' existing monitoring program to physical lake data, phytoplankton, *M. relicta* and zooplankton samples approximately 15 times per year (Stanford *et al*. 1997). Egg ratio analysis will be included for cladocerans (Paloheimo 1974, Gabriel *et al*. 1987), so that seasonal planktivore consumption demand can be compared to production as well as standing stock biomass. Using this methodology we will discriminate between predation losses and food/thermal effects on zooplankton dynamics by coupling egg ratio analyses with zooplanktivore consumption. Some age 2+ fisheries data will be supplied by the ongoing gillnetting monitoring program of the Confederated Salish Kootenai Tribes (CSKT) and the State of Montana Fish, Wildlife and Parks (MTFWP). Fish gut contents will be provided by CSKT and MTFWP to be analyzed by Utah State University. We will augment these data as necessary with hydroacoustic performed by Dr. Donald Gunderson, University of Washington, School of Fisheies and expert in hydroacoustical fisheries investigations (see also Beauchamp *et al.* 1997, Brandt 1996, Parkinson *et al.* 1994, Dawson 1972). For some species or life stages, passive netting and hydroacoutics are not effective or cannot capture the required information at the appropriate temporal or spatial resolution (e.g. finding spawning areas, assessing time budgets between nearshore and offshore zones or among depth strata). In these situations we will employ underwater video (Bergestedt and Anderson 1990), SCUBA surveys, light trapping, and ichthyoplankton netting, and sonic tagging in a complementary, stratified sampling design. By tracking a subset of sonically-tagged individuals, diel and seasonal data on depth, location and time budgeting among habitats can be acquired and integrated with the more static snapshots of distribution patters provided by conventional netting (Winter 1996, Warren and Quinn 1995, Dolloff *et al*. 1996)). Larval fish identifications will be performed by the Larval Fish Laboratory of Colorado State University. Assurance has been given from MTFWP and CSKT that all required permits will be issued. Age 0 fishes will be identified by Colorado State Larval Fish Laboratory. Age 0 fish have not been targeted for sampling in Flathead Lake to date. Methodologies will be developed and refined based on performance.

Objective 3

Correlate food web response variables with the biophysical template using uni-, and multivariate correlative techniques (e.g. Pearson and Kendall correlations, Mantels test (Johnson and Wichern 1992)) as well as geostatistics (Rossi *et al.* 1991).

Objective 4
Using the same statistical techniques as in Objective 3, test for pairwise coexistence of species by diel cycle, habitat and season, and through gut analyses. Using descriptive statistics and rank-transformed ANOVA we will analyze the effects of different temporal, spatial, and ontogenetic/size-related factors on the proportion of each major prey category in the diet by weight. Evidence of potential interactions based on physical association, coupled with gut analyses will provide linkage strength data.

Objectives 5-7
Bioenergetic simulations will identify which sizes of predators/competitors impose the greatest control on other components of the food web. By coupling bioenergetics modeling with population dynamics and life history data, daily through annual consumption rates can be calculated for the major fish species (by age class) and mysids (Brandt and Hartman 1993; Hansen *et al.* 1993). The Wisconsin Bioenergetics Model estimates consumption by balancing consumption with the energy required to satisfy estimated incremental growth (including reproduction), plus metabolism and waste, given the size and thermal experience of the consumer over specified time intervals. When spatial-temporal consumption demand is compared to the spatial-temporal availability of prey populations, we can evaluate whether predation, competition, or environmental factors control the population dynamics of species (e.g., Brandt *et al*. 1992; Luecke *et al*. 1992; Beauchamp *et al.* 1995; Beauchamp 1996; Cartwright *et al.* 1998). Species- and stage-specific physiological parameters are available for most species (or closely-related species) in the Flathead Lake assemblage: lake (and bull) trout (Stewart *et al.* 1983), kokanee (Beauchamp *et al.* 1989), cutthroat trout (Beauchamp *et al*. 1995), coregonids (Rudstam 1994), yellow perch (Kitchell *et al.* 1977; Post 1990), northern squawfish (Petersen and Ward, in review), and mysids (Rudstam 1989).

Estimated seasonal growth, size-specific and seasonal diet composition, thermal experience, abundance (or relative abundance) and survival rates of fish and mysids from Objectives 1-2 will be used as inputs to the bioenergetics model. Daily or seasonal prey consumption by fish populations can be compared to the instantaneous standing stock and production rate of the prey community. Different scenarios can be simulated to help managers predict the likely outcome of changes in abundance, mortality, or growth of consumers, changes in thermal regime or prey availability. This modeling framework can then be used to plan potential management options, evaluate observed versus predicted system responses, then recommend the next logical actions in an adaptive management context. are most likely to achieve a balanced community structure.

Objective 8
Estimating production capacity for different trophic level for different food web configurations will involve limnological sampling linked to ecosystem models like Ecopath/Ecosym and Dowing and Plante. Objectives 5,6, and 7 estimate trophic transfer and carrying capacity from the top down, this approach examines the question from the bottom up. Inclusion of both complementary approaches will reveal considerable insight into limitations to fish production. Data requirements include monitoring of nutrient chemistry and physical data.

Objective 9
In order to most effectively use the knowledge about the Flathead Lake food web gained in this study in a management context, current biological conditions should be compared with historic conditions. The Confederated Salish and Kootenai tribes and early settlers have a rich oral history of the flathead Lake ecosystem. Tribal knowledge and local newspapers accounts about historic spatio-temporal distributions, relative abundances and harvest rates of native species will be compiled, synthesized and used to interpret data collected in this study. The value of historic information will be critically analyzed from an ecological, biogeographical perspective. Values will be input into developed models to reconstruct historic food webs and model output compared with existing conditions.

Objective 10
To aid in study interpretation and to ensure maximum utilization of study results we will conduct a literature review and synthesize existing knowledge about food webs linkages and structuring forces in Columbia basin lentic systems similar to Flathead. This comparative lake study will be used as the basis for an interjurisdictional, multi-agency workshop to be held at a yet undetermined site.

Objective 11
Using current theory (e.g. Dixon and Chiswell 1996, Whitfield 1996) and sensitivity analyses of our two models, we will develop a food web monitoring regime that will allow the quantification of food web change in time (diel, seasonal, interannual) and space (among habitat cells).

Factors that may limit the success of this project are methodological. Some fisheries techniques, especially those involving early life-history stages, have not been attempted before in the Flathead system and will require development.

f. Facilities and equipment.

Office space exists for all personnel at all institutions. The combined field equipment of the co-operating agencies include: a fully equipped Freshwater Research Laboratory that includes an EPA certified elemental and nutrient analysis lab, optics room and microscopes, zoobenthos and plankton identification lab and museum, sample prep facility, electronics repair shop, photographic lab, image analyses system (for gut analyses and zooplankton counting), complete equipment array to embed and analyze fish otoliths for fish aging, a scintillation counter (for primary productivity determination), field fluorometer, spectrophotometers, multisensor (CTD) systems (for limnological variables), integrating light meters, Hydrolabs, an ion chromatograph with integrating calculators , an elemental analyzer, CHN analyzer, technicon autoanalyzer, ATP photometer and chromatograph, limited sonic fish tracking equipment. Equipment also includes a radar equipped 30' all-weather, all-season twin-diesel powered research vessel equipped with hydrolic starboard davit and stern gypsy winch to deploy both light and very heavy sampling gear, additional large all-weather, all-season research outboards and inboards, 4x4 vehicles.

Some equipment purchases are needed to complete this proposal. Simrad hydroacoustical and field validation sampling equipment (trawls, nets), ultrasonic fish tracking equipment (depth-sensing sonic tags, sonobuoys, mobile ultrasonic receiver), and underwater remote video cameras are needed to enable non-lethal abundance/distribution estimates of native fish species. Computers and a personnel printer are required for technical personnel. A global positioning system (GPS) base station and D-GPS units are needed to ensure spatial accuracy of sampling. A large format color printer is needed for presentation of spatially explicit food web data. All new equipment will be housed at FLBS.

g. References.

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Section 8. Relationships to other projects

We do not think that the FWP goals for Flathead Lake can be realized without the product of this research. Large expenditures of time and financial resources have been lost by attempting mitigation without this information. This project will be coordinated with three other ongoing projects, the sum total of which will have the power to answer the critical uncertainties of the system. Ongoing projects (No.'s 9101901 and 9010903) have been collecting fisheries data which will be continued, but augmented by this proposal to generate the resolution necessary for complete bioenergetic modeling. This proposal will be especially useful in supporting the currently unfunded collection needs for describing the lower trophic levels.

In the larager context of salmonid restoration basin-wide, this proposal is the first synthetic food web analyses of lentic systems. This work will be directly transferable to other systems. Therefore the results apply to all aspects of projects concerned with trophic interactions and effects on salmonid survival.

Section 9. Key personnel

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EDUCATION:

B.S.	Fisheries Science	Colorado State University	1969
M.S.	Limnology	Colorado State University (E. B. Reed, Advisor)	1971
Ph.D.	Limnology	University of Utah (A. R. Gaufin, Advisor)	1975

PROFESSIONAL EXPERIENCE:

Jessie M. Bierman Professor of Ecology, The University of Montana (1985-present). Ongoing research includes ecosystem-level consequences of river regulation, dynamics of lotic and hyporheic zoobenthos, especially Plecoptera, advective circulation of nutrients as controls on microbial production and other food web interactions in Flathead and other lakes of glacial origin and influences biophysical gradients on life history energy balance of biota.

Director, Flathead Lake Biological Station (1980-present). Administrative responsibility for all Biological Station activities, including the academic program and limnological research in the Freshwater Research Laboratory.

SELECTED PUBLICATIONS (from 101 total in peer-reviewed books and journals):

Spencer, C. N., B. R. McClelland and J. A. **Stanford**. 1991. Shrimp stocking, salmon collapse and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. BioScience 41(1):14-21.

Hall, C. A. S., J. A. **Stanford** and F. R. Hauer. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos 65:377-390.

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CURRICULUM VITA

David Anthony Beauchamp, Utah Cooperative Fisheries and Wildlife Research Unit, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5255.

EDUCATION: B.S. Fisheries 1980, M.S. Fisheries 1982, Ph.D. Fisheries 1987, University of Washington, Seattle, Washington.

Assistant Professor (September 1994 to present). Assistant Leader-Fisheries, Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, Utah. Research Associate, Tahoe Research Group, Division of Environmental Studies, UC Davis.

Research Assistant Professor (March 1993 to September 1994). Department Fish and Wildlife, Utah State University, Logan, Utah. Research Associate, Tahoe Research Group, Division of Environmental Studies, UC Davis.

Post-doctoral Research Associate (June 1990 to February 1993). Utah State University.

Senior Fish Biologist/Consultant (halftime: 1987-1990) University of Washington.

Fisheries Consultant (1986-1996). D.A. Beauchamp, Fisheries Scientist.

TEACHING: Population Assessment (4 credits), Hydroacoustics (3 credits), Bioenergetics Modeling (3 credits), Fisheries Management (3 credits), Limnology (5 credits), Aquatic Ecology Lab (3 credits), Ecology and Management of Lakes and Reservoirs short course).

RESEARCH ACTIVITIES AND FUNDING: PI or co-PI $1.4 million in contracts and grants 1991-1997 from state and federal sources. Funding for quantifying aquatic food web interactions and population dynamics of fish and invertebrates in large lakes.

SELECTED PUBLICATIONS:

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Transactions of the American Fisheries Society. 118:597-607.

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Beauchamp, D. A. Modeling lake trout predation on kokanee in Flathead Lake, Montana. (To be submitted to North American Journal of Fisheries Management).

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M.S. in Fisheries Science, Oregon State University, 1986
B.A. with High Honors in Zoology, University of Montana, 1982

Theses: M.S.: A hierarchical stream habitat classification system: development and
Ph.D.: Cumulative effects of land use on salmon habitat in southwest Oregon

Research Positions:

- Research Assistant Professor, The University of Montana, Flathead Lake Biological Station, 1993-present
- Research Assistant Professor, Department of Fisheries and Wildlife, Oregon State University, 1994-95
- Postdoctoral Research Associate (Faculty appointment), Department of Fisheries and Wildlife, Oregon State University, 1992-1994
- Research Assistant (Faculty appointment), Oak Creek Laboratory of Biology, Department of Fisheries and Wildlife, Oregon State University, 1985-1992

Fields of Interest:

Cumulative impacts of human activities and natural events on stream habitat and stream biota; Ecology, biogeography, and conservation biology of fishes and aquatic communities in relation to environmental change; Design of aquatic conservation reserves; Classification and geomorphology of montane watersheds and aquatic habitat; Natural resources planning and policy

Five Relevant Publications:

•Baxter, C.V., C.A. Frissell, and F.R. Hauer. In press. Geomorphology, logging roads and the distribution of bull trout *(Salvelinus confluentus)* spawning in a forested river basin: Implications for management and conservation. *Transactions of the American Fisheries Society.*
•Frissell, C.A., and D.G. Lonzarich. 1996. Habitat use and competition among stream fishes. Chapter 23 in F.R. Hauer and G.A. Lamberti (eds.) *Methods in Stream Ecology*. Academic Press, San Diego.
•Frissell, C.A., and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. *Water Resources Bulletin* 32:229-240.
•Stanford, J.A., J.V. Ward, W.J. Liss, C.A. Frissell, R.N. Williams, J.A. Lichatowich, and C.C. Coutant. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management* 12:391-413.

•Frissell, C.A. 1993. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California, USA. *Conservation Biology* 7:342-354

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Education

1998	**Doctor of Philosophy** (Aquatic Ecology) expected completion August 1998, University of Montana
1994	**Master of Science** (Aquatic Ecology), University of Calgary, Alberta
1990	**Honors Bachelor of Science** (Biology), University of Guelph, Ontario

Current Employer

University of Montana; Using a replicated whole-lake study I am researching the effects of fish on aquatic foodwebs in montane lakes.

Pertinent Previous Employment

Instructor in Lake Ecology (1997) Flathead Lake Biological Station
Was the major instructor for a senior undergraduate course in lake ecology.

Overview of Expertise

Mr. Wicklum has a broad range of experience and formal training in aquatic ecology and uni-, bi- and multivariate statistics. He has expertise in taxonomy of all aquatic organisms, experimental design, data presentation and interpretation.

One of Dan's major strengths is his ability to tailor studies to address specific questions while maintaining the scientific rigour and integrity of the investigation. His combination of formal ecological and statistical training, and practical field experience make him uniquely suited for foodweb research issues. He has served as a peer reviewer for Journal of the American Water Resources Association, Regulated Rivers, Journal of Environmental Management

Five Selected Publications

Wicklum, D. and R.W. Davies. 1997. Mortality, preference, avoidance, and activity of a predatory leech exposed to cadmium. Archives of Environmental Contamination and Toxicology 32:178-183.

Wicklum, D. and R.W. Davies. 1996. The effects of chronic cadmium stress on energy acquisition and allocation in a freshwater benthic invertebrate predator. Aquatic Toxicology. 35:237-252.

Scrimgeour, G.J. and **D. Wicklum**. 1996. Aquatic ecosystem health and integrity: problems and potential solutions. Journal of the North American Benthological Society 15:254-261.

Davies, R.W., R.N. Singhal and **D. Wicklum**. 1995. Changes in reproductive potential of the leech *Nephelopsis obscura* (*Erpobdellidae*) as biomarkers for cadmium stress. Canadian Journal of Zoology 73:2192-2196.

Wicklum, D. and R.W. Davies. 1994. Ecosystem health and integrity? Canadian Journal of Botany 73:997 - 1000.

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Education
B. A. Colgate University 1965
M.S. Penn State University 1966
Ph.D. University of North Carolina 1970

Current Positions
Professor, SUNY Syracuse
Faculty Affiliate, Flathead Lake Biological Station

Professional Interests: The application of integrative tools of science, especially simulation modeling to understand management of complex systems of nature and of people and nature.

Selected Publications (from 95)

Hall, C. A. S. 1988. An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. Ecol. Model 43:5-31.

Hall, C. A. S., J. H. Jourdonnais and J. A. Stanford. 1989. Assessing the impacts of stream regulation in the Flathead River Basin, Montana, U.S.A. I. Simulation modelling of system water balance. Regulated Rivers 3:61-77.

Hall, C. A. S. 1990. What constitutes a good model and by whose criteria? Ecol. Model. 43:125-127.

Hall, C. A. S., M. R. Taylor and E. Everham. 1992. A geographically-based ecosystem model and its application to the carbon balance of the Luquillo Forest, Puerto Rico. Water, Air, and Soil Pollution 64:385-404.

Hall, C. A. S. and M. H. P. Hall. 1993. The efficiency of land and energy use in tropical economies and agriculture. Agriculture, Ecosystems and Environment 46:1-30.

Section 10. Information/technology transfer

To ensure effective implementation and information transfer we will have a position that will coordinate effort and organize workhops. We will publish findings in scientific peer-reviewed journals and present findings that are important from either a scientific or management perspective at recognized societal meetings.

To ensure maximum utilization and integration of this research we will compare what is known about other lentic food webs in the Columbia River basin with what is learned in this study. To disseminate study results to downstream managers we will hold a interjurisdictional, multiagency workshop.