Linking individual-level foraging interactions of piscivores to food-web dynamics in pelagic systems

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Abstract

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Aquatic ecosystems are structured by environmental gradients, including temperature, depth, and water clarity. These gradients can mediate the strength of trophic interactions by influencing the distribution, physiology, and behavior of predators and prey. My dissertation addressed the following questions: 1) What factors determine the foraging success of pelagic piscivores during encounters with prey? and 2) How do temperature and depth mediate direct and indirect trophic interactions in lakes? First, I conducted feeding experiments to quantify the effects of turbidity and prey shoaling behavior on the foraging efficiency of Chinook salmon during encounters with Pacific herring. Chinook salmon successfully consumed herring during only 1-4% of encounters, limited by the rates of attacks per encounter and capture success (prey consumed per attack). Capture success declined with increasing turbidity and prey shoaling. These results indicate post-encounter processes can strongly limit feeding rates of pelagic piscivores and they provide the necessary parameters to incorporate these processes into foraging models. Second, I conducted field sampling in Lake Chelan, Washington to quantify how the strengths of trophic interactions between zooplankton, mysid shrimp, kokanee, and lake trout changed along environmental gradients. Bioenergetics and population models revealed strong predation impacts of lake trout on kokanee, which were initially masked from detection by ecological time lags. Mysids influenced kokanee through two negative indirect interactions, which differed in strength between contrasting lake basins. Mysids competed for zooplankton prey more strongly in a deeper, cooler basin due to their low thermal optimum. However, mysids provided greater energetic support to lake trout diet in a shallower basin, where lake trout were greater in density and inflicted greater predation risk on kokanee. A diel vertical migration model predicted mysids were more vulnerable to lake trout predation at shallower sites within the lake, and this prediction was supported by stable isotope analysis of lake trout diets. These findings revealed a mechanism by which mysids could cause greater food-web impacts in shallower systems where they are more vulnerable to predation. In conclusion, my results show strong associations between the physical environment, the behaviors of individual predators and prey, and the dynamics of populations and food webs.

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DEDICATION

To my wife Jenny and my daughter Maya. Thank you for all your love and support.

Chapter 1. From interactions between individual predators and prey to community dynamics

INTRODUCTION

A focal question in ecology is why some trophic interactions are strong while others are weak (Paine 1980, Polis and Strong 1996, Terborgh and Estes 2010). That is, under what conditions do predators more strongly limit the population dynamics of their prey, and under what conditions do prey enhance their growth rates and densities of their predators? Like many problems in ecology, these questions are productively addressed by complementary investigations at different levels of organization (Levin 1992). Trophic ecology has advanced by combining insights from foraging ecology focused at the scale of individuals with food-web patterns and dynamics at the scales of populations and communities (Werner and Anholt 1993, Mittelbach and Osenberg 1994). Aquatic ecologists have pioneered the development of many central ideas in food web ecology, including trophic cascades, spatial subsidies, and the non-consumptive effects of predators (e.g., Werner et al. 1983, Carpenter et al. 2001, Nakano and Murakami 2001). However, adapting these concepts from small, simple streams, ponds, and intertidal zones to large, complex rivers, lakes, and oceans has often proven challenging. My dissertation used investigations at multiple scales to examine how the strengths of aquatic food-web interactions are mediated by the physical environment, the sensory and behavioral constraints of individual predators and prey, and community structure. My research focused on piscivorous fishes in pelagic habitats. Here, I review some established concepts and approaches relevant to the trophic ecology of pelagic piscivores, and I identify the knowledge gaps that I investigated in the following chapters.

Aquatic ecosystems are structured by environmental gradients, including temperature, depth, and water clarity. These gradients can mediate the strength of trophic interactions by influencing the distribution, physiology, and behavior of predators and prey. For example, changes in temperature can alter trophic dynamics through asymmetric shifts in the production and consumption rates of ectothermic species (Taniguchi et al. 1998, Rahel and Olden 2008, Fey and Herren 2014). Depth also structures aquatic food webs: smaller, shallower lakes and fjords tend to exhibit stronger top-down control than larger, deeper systems (Jeppesen et al. 1997, Tessier and Woodruff 2002, Aksnes et al. 2004). Stronger predation in shallower waters can be explained by a lack of refuge for pelagic prey (Tessier and Woodruff 2002, Aksnes et al. 2004) or greater benthic resource subsidies that enhance the densities of apex predators (Schindler et al. 1996, Vander Zanden et al. 2005). Further, most pelagic fishes feed visually (Loew and McFarland 1990), and optical conditions strongly influence their distribution, foraging rates, and predation risk (Beauchamp et al. 1999, Aksnes et al. 2004).

The distributions of aquatic organisms are structured by these environmental gradients at large scales and self-organizational behavior at small scales (Rose and Leggett 1990). Mobile fish and invertebrates can reduce their vulnerability to predators by seeking refuge in dark or turbid waters, or forming schools. For example, many species migrate vertically, often taking advantage of “antipredation windows” at dawn and dusk when intermediate light levels permit them to forage effectively but limit their visibility to predators (Eggers 1978, Clark and Levy 1988, Scheuerell and Schindler 2003, Jensen et al. 2006, Gjelland et al. 2009, Hansen and Beauchamp 2015). High-turbidity environments such as river plumes can provide similar refuge benefits to planktivorous fish (De Robertis et al. 2003), and high densities of larval and juvenile fishes are often observed in these habitats (Grimes and Kingsford 1996, Schabetsberger et al. 2003).

Pelagic piscivores must find and capture prey in these dynamic, three-dimensional landscapes. Visual foraging models provide an approach for integrating environmental variables and species distributions to predict which conditions represent greater feeding opportunities for piscivores or predation risk for their prey (Breck 1993, Beauchamp et al. 1999). This approach helps to explain observed patterns of habitat selection, diel vertical migration, feeding, and growth of pelagic fishes (Hardiman et al. 2004, Jensen et al. 2006, Mazur and Beauchamp 2006, Mazur et al. 2007, Hansen et al. 2013). A shared prediction of several visual foraging model applications is that piscivorous fishes encounter far more prey than they consume (Beauchamp et al. 1999, Jensen et al. 2006, Turesson and Bronmark 2007). Yet, a review of bioenergetic evidence indicates their predation rates are generally limited by feeding rate, rather than digestive capacity (Armstrong and Schindler 2011). Together, these results suggest that behavioral constraints prevent piscivores from consuming most of the prey they encounter. Indeed, for piscivorous fish and other predators of mobile prey, such as mammalian carnivores and predatory arthropods, the post-encounter stage can include multiple steps of stalking, attacking, subduing, and ingesting prey, each with some chance of failure (Elliott et al. 1977, Beauchamp et al. 2007). Recent work across a variety of taxa suggests these constraints can limit predation rates substantially and should receive greater empirical attention (Jeschke et al. 2002, Brechbühl et al. 2011, Casas and Steinmann 2014). However, little is known about post-encounter constraints on pelagic piscivorous fish, or how they are influenced by environmental conditions or prey behavior.

At the community level, the strengths of trophic interactions are most convincingly measured through direct experimentation (Paine 1980, Schindler 1998). By manipulating rocky intertidal communities, Paine (1966, 1974) identified a strong interaction between the seastar *Pisaster* and its preferred prey, a dominant blue mussel which outcompeted other sessile filter feeders in the absence of predation. Whole-system experiments also revealed the strong interactions that drive trophic cascades in small lakes (Carpenter et al. 1987, Carpenter et al. 2001). However, manipulative experiments are not feasible in many large, unique, or sensitive systems. When experimentation is impractical, interaction strength can be evaluated indirectly by comparing the rate of consumption by predators to the production of prey (Stewart et al. 1981, Ney 1990, Beauchamp et al. 2007), by comparing population trends of interacting species over time (Stenseth et al. 1997, Springer et al. 2003, Worm and Myers 2003), or by making biogeographical comparisons (Donald and Alger 1993, Wellborn et al. 1996, Jackson et al. 2001). These approaches are complementary.

Energetic approaches to quantifying consumption and production rates can provide a detailed, mechanistic view of food-web interactions, but require intensive sampling and are generally practical only for relatively short periods. Further, interaction strengths cannot be inferred directly from patterns of energy flow (Paine 1988, 1992, Polis and Strong 1996), and many energetics applications fail to consider indirect and non-consumptive effects among the species of interest. However, much can be learned about trophic dynamics from energetic patterns (expressed as predation rates) in combination with knowledge of the ecology of predators and prey (Ney 1990, Beauchamp et al. 2007). For example, even in the case of strong energetic linkages, predation interactions are weakened when prey have access to a refuge, are donor controlled (e.g., terrestrial insects falling into a stream), or when predator densities are limited by some factor other than food (Walters and Martell 2004).

Time series and biogeography can give valuable insight into the relevance of interactions on larger temporal and spatial scales, but are not sufficient to identify causal relationships or mechanisms of interaction (Werner and Peacor 2003, White et al. 2006). Interpreting abundance trends also requires information on the processes that introduce time lags between changes in predator and prey populations (e.g. generation time or ontogenetic dietary shifts). A combination of energetic and time-series approaches may be especially informative for long lived predators (Stewart et al. 1981), especially when they are recently introduced or highly manipulated (e.g., Ruzycki et al. 2003), and as such are not expected to conform to a stable age distribution or equilibrium population dynamics.

An important goal for community ecologists is translating the theory of indirect trophic interactions into practical guidelines for resource managers. Indirect interactions are believed to be widespread, but determining which ones are strong enough to influence community dynamics is challenging (Werner and Peacor 2003, Knight et al. 2005, Wootton and Emmerson 2005). Community ecologists recently have begun to explicitly consider indirect interactions in applications such as ecosystem-based fisheries management (Mangel and Levin 2005), biological control of agricultural pests (van Veen et al. 2006), and management of mosquito populations (Blaustein and Chase 2007). However, in many cases, a lack of empirical data and predictable patterns prevents widespread applications.

In particular, little information is available to allow managers to distinguish among the multiple possible indirect interactions between species within the same trophic level. These interactions include resource competition or boosting shared natural enemies (called "apparent competition" by Holt 1977, and "hyperpredation" by Smith and Quin 1996). Disentangling these effects can lead to more effective conservation and management by allowing practitioners to focus on the most limiting interaction (Noonburg and Byers 2005, White et al. 2006). However, relatively few case studies have evaluated the support for both resource competition and apparent competition in the same system (e.g., Petren and Case 1996, Hanley et al. 1998, Juliano 1998, Ellis et al. 2011), and little is known about how the strengths of these interactions vary under different environmental conditions, such as temperature or depth gradients. The role of predators in mediating interactions between prey species is an important consideration in lakes, where apex predator densities have been widely enhanced through species introductions and stocking (Eby et al. 2006).

Determining the relative strengths of resource competition and apparent competition also has high applied value in invasion ecology. The “enemy release” hypothesis predicts nonnative species have greater ecological impacts when they are less vulnerable to natural enemies, including predators, parasites, and pathogens (Pimm 1991, Ghazoul 2002, Keane and Crawley 2002, Fey and Herren 2014). Conversely, an alternative “enemy of my enemy” hypothesis predicts that in some cases nonnative species will have greater impacts when they are more vulnerable to predators, due to stronger apparent competition (Colautti et al. 2004, Noonburg and Byers 2005). The empirical evidence for both of these hypotheses remains equivocal (Colautti et al. 2004, Urban et al. 2007, Ricciardi et al. 2013).

The overarching goal of my dissertation research was identifying and quantifying ecological factors that strengthen or weaken trophic interactions in aquatic ecosystems. I examined this topic at multiple levels of organization from individual-level behavioral interactions to population and community dynamics, using a combination of field sampling, laboratory experimentation, and modeling approaches, including bioenergetics and population dynamics models. My dissertation chapters addressed the following general questions: 1) What determines the foraging success of pelagic piscivores during encounters with prey? and 2) How do temperature and depth gradients mediate direct and indirect trophic interactions in lakes? Within these overall themes, each chapter focused on specific research objectives with implications for applied aquatic ecology and fisheries management.

REFERENCES

Aksnes, D. L., J. Nejstgaard, E. Soedberg, and T. Sornes. 2004. Optical control of fish and zooplankton populations. Limnology and Oceanography **49**:233-238.

Armstrong, J. B. and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature **476**:84-87.

Beauchamp, D. A., C. M. Baldwin, J. L. Vogel, and C. P. Gubala. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences **56 Suppl. 1**:128-139.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Blaustein, L. and J. M. Chase. 2007. Interactions between mosquito larvae and species that share the same trophic level. Annual Review of Entomology **52**:489-507.

Brechbühl, R., J. Casas, and S. Bacher. 2011. Diet choice of a predator in the wild: overabundance of prey and missed opportunities along the prey capture sequence. Ecosphere **2**:Article 133.

Breck, J. E. 1993. Foraging theory and piscivorous fish: Are forage fish just big zooplankton? Transactions of the American Fisheries Society **122**:902-911.

Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecological Monographs **71**:163-186.

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. Vonende. 1987. Regulation of lake primary productivity by food web structure. Ecology **68**:1863-1876.

Casas, J. and T. Steinmann. 2014. Predator-induced flow disturbances alert prey, from the onset of an attack.

Clark, C. W. and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist **131**:271-290.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters **7**:721-733.

De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences **60**:1517-1526.

Donald, D. B. and D. J. Alger. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology **71**:238-247.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends In Ecology & Evolution **21**:576-584.

Eggers, D. M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnology and Oceanography **23**:1114-1125.

Elliott, J. P., I. M. Cowan, and C. Holling. 1977. Prey capture by the African lion. Canadian Journal of Zoology **55**:1811-1828.

Ellis, B., J. Stanford, D. Goodman, C. Stafford, D. Gustafson, D. Beauchamp, D. Chess, J. Craft, M. Deleray, and B. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences **108**:1070-1075.

Fey, S. B. and C. M. Herren. 2014. Temperature-mediated biotic interactions influence enemy release of nonnative species in warming environments. Ecology **95**:2246-2256.

Ghazoul, J. 2002. Seed predators and the enemy release hypothesis. Trends in Ecology & Evolution **17**:308.

Gjelland, K. O., T. Bohn, J. K. Horne, I. Jensvoll, F. R. Knudsen, and P. A. Amundsen. 2009. Planktivore vertical migration and shoaling under a subarctic light regime. Canadian Journal of Fisheries and Aquatic Sciences **66**:525-539.

Grimes, C. B. and M. J. Kingsford. 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? Marine and Freshwater Research **47**:191-208.

Hanley, K. A., K. Petren, and T. J. Case. 1998. An experimental investigation of the competitive displacement of a native gecko by an invading gecko: no role for parasites. Oecologia **115**:196-205.

Hansen, A. G. and D. A. Beauchamp. 2015. Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. Journal of Animal Ecology **84**:532-544.

Hansen, A. G., D. A. Beauchamp, and C. M. Baldwin. 2013. Environmental constraints on piscivory: Insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout. Transactions of the American Fisheries Society **142**:300-316.

Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society **133**:1366-1378.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology **12**:197-229.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences **58**:157-170.

Jensen, O. P., T. R. Hrabik, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community II. Modeling trade-offs at an intermediate trophic level. Canadian Journal of Fisheries and Aquatic Sciences **63**:2296-2307.

Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. Hydrobiologia **342**:151-164.

Jeschke, J. M., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs **72**:95-112.

Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: Interspecific resource competition or apparent competition? Ecology **79**:255-268.

Keane, R. M. and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution **17**:164-170.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature **437**:880-883.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1967.

Loew, E. R. and W. N. McFarland. 1990. The underwater visual environment.*in* R. H. Douglas and M. B. A. Djamgoz, editors. The visual system of fish. Chapman and Hall, London.

Mangel, M. and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. Philosophical Transactions Of The Royal Society B-Biological Sciences **360**:95-105.

Mazur, M. M. and D. A. Beauchamp. 2006. Linking piscivory to spatial-temporal distributions of pelagic prey fishes with a visual foraging model. Journal of Fish Biology **69**:151-175.

Mazur, M. M., M. T. Wilson, A. B. Dougherty, A. Buchheister, and D. A. Beauchamp. 2007. Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. Journal of Fish Biology **70**:816-836.

Mittelbach, G. G. and C. W. Osenberg. 1994. Using foraging theory to study trophic interactions. Pages 45–59 *in* D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, SC.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings Of The National Academy Of Sciences Of The United States Of America **98**:166-170.

Ney, J. J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. Reviews In Aquatic Sciences **2**:55-81.

Noonburg, E. G. and J. E. Byers. 2005. More harm than good: When invader vulnerability to predators enhances impact on native species. Ecology **86**:2555-2560.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65-&.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia **15**:93-120.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure - the 3rd Tansley lecture. Journal of Animal Ecology **49**:667-685.

Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development. Ecology **69**:1648-1654.

Paine, R. T. 1992. Food-web analysis through field measurement of per-capita interaction strength. Nature **355**:73-75.

Petren, K. and T. J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology **77**:118-132.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois.

Polis, G. A. and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813-846.

Rahel, F. J. and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology **22**:521-533.

Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs **83**:263-282.

Rose, G. A. and W. C. Leggett. 1990. The importance of scale to predator prey spatial correlations - An example of Atlantic fishes. Ecology **71**:33-43.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications **13**:23-37.

Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fisheries Oceanography **12**:523-540.

Scheuerell, M. D. and D. E. Schindler. 2003. Diel vertical migration by juvenile sockeye salmon: Empirical evidence for the antipredation window. Ecology **84**:1713-1720.

Schindler, D. E., S. R. Carpenter, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, and P. A. Soranno. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. Pages 96–105 *in* G. A. Polis and K. O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, New York.

Schindler, D. W. 1998. Replication versus realism: The need for ecosystem-scale experiments. Ecosystems **1**:323-334.

Smith, A. P. and D. G. Quin. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. Biological Conservation **77**:243-267.

Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences of the United States of America **100**:12223-12228.

Stenseth, N., W. Falck, O. Bjørnstad, and C. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. Proceedings of the National Academy of Sciences of the United States of America **94**:5147.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society **110**:751-763.

Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences **55**:1894-1901.

Terborgh, J. and J. A. Estes, editors. 2010. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, DC.

Tessier, A. J. and P. Woodruff. 2002. Cryptic trophic cascade along a gradient of lake size. Ecology **83**:1263-1270.

Turesson, H. and C. Bronmark. 2007. Predator-prey encounter rates in freshwater piscivores: effects of prey density and water transparency. Oecologia **153**:281-290.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2007. The cane toad's (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proceedings of the Royal Society B: Biological Sciences **274**:1413-1419.

van Veen, F. J., R. J. Morris, and H. C. J. Godfray. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. Annual Review of Entomology **51**:187-208.

Vander Zanden, M. J., T. E. Essington, and Y. Vadeboncoeur. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? Canadian Journal of Fisheries and Aquatic Sciences **62**:1422-1431.

Walters, C. and S. Martell. 2004. Fisheries Ecology and Management. Princeton University Press, Princeton, New Jersey.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics **27**:337-363.

Werner, E. E. and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist **142**:242-272.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540-1548.

Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology **84**:1083-1100.

White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. Diversity and Distributions **12**:443-455.

Wootton, J. T. and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology, Evolution, and Systematics **36**:419-444.

Worm, B. and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology **84**:162-173.

Chapter 2. Effects of turbidity and shoaling on capture success of Chinook salmon feeding on Pacific herring

ABSTRACT

Piscivorous fishes are generally food-limited, yet foraging models predict they encounter far more prey than they consume. These patterns suggest significant environmental or behavioral constraints on capturing highly mobile prey, but these post-encounter dynamics are poorly understood. Reduced water clarity and patchy prey may limit the foraging efficiency of visual predators, and these factors are highly variable in the coastal habitats of juvenile salmon. We quantified post-encounter constraints on yearling Chinook salmon *Oncorhynchus tshawytscha* foraging on Pacific herring *Clupea harengus* in tank experiments, including their attack rates (attacks / encounter), capture success (CS; prey consumed per attack), and time allocation during encounters. We tested the competing hypotheses that increasing turbidity *a)* enhances CS or *b)* reduces CS. We also hypothesized that CS would decrease with increasing prey density and shoal size due to predator confusion. Salmon exhibited an overall mean attack rate of 18% and CS ranging from 5-22%; thus, they consumed a herring during only 1-4% of encounters. CS declined by two-thirds across turbidity levels ranging from 0-2.3 beam attenuation / m (0-5.5 nephelometric turbidity units). CS was unchanged across prey density levels ranging from 0.24-20 prey fish / m^3, at both low and high turbidity levels (0 and 1.6 beam attenuation / m). In clear-water trials, for which we could determine the outcomes of individual attacks, salmon achieved nearly three times greater CS when attacking solitary prey than when attacking shoals. The data provided a similar level of support for a continuous effect of decreasing CS with increasing shoal size. During prey encounters, predators spent most (83%)

of their time stalking prey, magnifying the time cost of unsuccessful encounters to predation rates. Post-encounter constraints including low rates of attacks / encounter, low CS, and high stalking time may substantially limit predation rates in nature. Based on our results, these limitations are exacerbated by prey shoaling and reduced visibility due to, for example, phytoplankton booms or river plumes. Piscivore foraging models would benefit by including post-encounter constraints that can be readily related to ambient environment conditions and prey densities.

INTRODUCTION

A primary goal of foraging ecology is to determine how environmental conditions, prey availability, and the behaviors of consumers and prey interact to determine predation rates (Stephens et al. 2007). Towards this goal, ecologists have developed encounter rate models describing how consumers search for food under a wide range of sensory and environmental constraints (Charnov 1976, Hughes and Dill 1990, Shipley et al. 1996, Beauchamp et al. 1999, McGill and Mittelbach 2006, Humphries et al. 2012). However, for predators like piscivorous fish, mammalian carnivores, and predatory arthropods, finding prey is only the first stage of the process. The post-encounter stage can also include multiple steps of stalking, attacking, subduing, and ingesting highly mobile prey, each with some chance of failure (Elliott et al. 1977, Beauchamp et al. 2007). Recent work suggests these constraints can limit predation rates substantially and should receive greater empirical attention (Jeschke et al. 2002, Brechbühl et al. 2011, Casas and Steinmann 2014).

Piscivorous fishes are generally food-limited (Armstrong and Schindler 2011), yet encounter rate models predict they encounter far more prey than they consume (Beauchamp et al.

1999, Jensen et al. 2006, Turesson and Bronmark 2007, Hansen et al. 2013a), suggesting important post-encounter constraints on predation. Accordingly, experimental and field studies indicate the rates of attack (attacks / encounter) and capture success (prey consumed / attack; hereafter CS) of piscivores can be quite low, such as < 25% (Howick and O'Brien 1983, Parrish 1993, Scharf et al. 2003). Further, if piscivores stalk prey for some time before attacking or rejecting them, then low attack or CS rates increase the fraction of the predator's time that is wasted on unsuccessful encounters, further reducing predation rates (Christensen 1996, Jeschke et al. 2002). To incorporate post-encounter constraints into models of piscivore foraging, key questions are: 1) how limiting and how variable are these processes, and 2) do they vary predictably with respect to environmental factors? Both the attack rate and CS of piscivores are strongly limited by prey size and morphology (Werner and Gilliam 1984, Juanes 1994, Scharf et al. 2003), but the effects of other factors such as visibility and prey density are less clear. Here, we examined post-encounter visual and behavioral constraints on piscivorous fish, to better understand why some encounters succeed and others fail.

Reduced visibility appears to enhance CS in some cases, but reduce it in others. Piscivores often achieve greater feeding rates under low-light conditions (Beauchamp 1990, Petersen and Gadomski 1994, Mazur and Beauchamp 2003, Hansen et al. 2013a), potentially due to inhibited shoaling and evasion by prey fish (Howick and O'Brien 1983, Gjelland et al. 2009). Elevated turbidity also inhibits the evasive responses of prey fish to simulated predators (Meager et al. 2006, Kimbell and Morrell 2015), suggesting real predators would achieve greater CS in turbid conditions. However, small fish generally have smaller turning radii and greater rates of acceleration than larger fish (Domenici 2001), suggesting that prey fish would benefit when predators and prey can only detect each other within a reduced visual range. Correspondingly, CS of sablefish (*Anoplopoma fimbria*) feeding on juvenile chum salmon (*Oncorhynchus keta*) declined from 20% in clear water to approximately 1% at higher turbidity in a tank experiment (De Robertis et al. 2003).

Predator confusion can inhibit piscivores and other raptorial predators from fully utilizing large groups of prey. For example, largemouth bass (*Micropterus salmoides*) readily attacked and captured solitary silvery minnows (*Hybognathus nuchalis*), but their CS was reduced considerably and their stalking time increased for larger shoals of ≥ 8 minnows (Landeau and Terborgh 1986). Similarly, coordinated evasion behaviors by Norwegian herring (*Clupea harengus*) schools appeared to confuse killer whales (*Orcinus orca*), making it difficult to isolate single prey, and whales attacked larger schools less frequently (Nottestad and Axelsen 1999). However, predator confusion is not evident in many predator-prey systems, and these effects appear to be taxa-specific (reviewed by Jeschke and Tollrian 2007).

Visibility and fine-scale prey density might also affect CS. Some anti-predator benefits of prey aggregations, including collective vigilance and coordinated evasive behaviors, may be less effective in low-visibility conditions, diminishing the effects of predator confusion (Flynn and Ritz 1999, Kimbell and Morrell 2015). If so, this would have important implications for piscivores in estuarine and coastal habitats where larval and forage fishes often aggregate in turbid habitats such as upwelling zones and river plumes (Grimes and Kingsford 1996, Schabetsberger et al. 2003).

In this study, we examined post-encounter factors limiting the foraging success of a pelagic piscivorous fish, Chinook salmon (*Oncorhynchus tshawytscha*). Recent declines and marked fluctuations in Chinook salmon returns highlight the need for a better understanding of the factors that limit these populations (Kruse 1998, Krueger et al. 2009). The size and growth rates of Chinook salmon during early marine residence are considered a critical influence on their overall ocean survival (Beamish and Mahnken 2001, Duffy and Beauchamp 2011, Tomaro et al. 2012, Woodson et al. 2013). Juvenile Chinook salmon generally spend their early marine period in estuarine or coastal habitats, which range widely in water clarity due to phytoplankton blooms and suspended sediment (Dean et al. 1989, Stabeno et al. 1999, Hillgruber and Zimmerman 2009). Many important prey of juvenile Chinook salmon form dense schools or swarms, including Pacific herring (*Clupea pallasii*), other forage fish species, and euphausiids (Brodeur et al. 2007). Thus, if turbidity or fine-scale prey density limit Chinook salmon feeding rates, this could have important implications for their growth and survival during critical early marine periods.

Our goals in this study were to identify post-encounter processes that potentially limit feeding rates of Chinook salmon, to test for effects of turbidity and prey density on CS, and finally to quantify these patterns with functional relationships that could be coupled with existing visual encounter rate models. We conducted tank experiments with Chinook salmon predators foraging on Pacific herring, and we quantified the overall rates of attacks per encounter, CS, and the time allocation patterns of salmon. In addition, we tested three hypotheses about factors influencing CS: 1) Increasing turbidity *a*) enhances CS or *b*) reduces CS; 2) CS declines with increasing prey density or shoal size; and 3) CS declines more strongly with increasing prey density in clear water than in turbid water.

METHODS

We video-recorded interactions of hatchery-origin yearling Chinook salmon feeding on age-0 Pacific herring across a range of ecologically relevant turbidity and prey density levels.

We recorded the rates that salmon encountered, attacked, captured, and consumed prey, as well as the time intervals spent stalking, attacking, and handling prey. We quantified overall rates of attack rate for low-turbidity conditions in which all encounters could be enumerated. We first compared CS across a turbidity gradient and then across a range of prey densities at low and high turbidity levels. We conducted the experiments during summer 2011 in a saltwater tank at Marrowstone Marine Field Station (MMFS) operated by U. S. Geological Survey in Nordland, Washington.

Collection and maintenance of experimental fish

Yearling Chinook salmon smolts were obtained on April 27, 2011 from Hoodsport Hatchery in Hoodsport, Washington (Washington Dept. Fish and Wildlife). Age-0 Pacific herring were captured in June-August 2011 from Port Townsend Bay and Admiralty Inlet, Washington by dip netting surface aggregations. We located these "bait balls" of herring by searching for aggregations of feeding seabirds, and we often observed piscine and mammalian predators in the vicinity. We considered the herring we collected to be behaviorally competent because although they had been located by predators, they had avoided predation up to the time of capture. All fish were transported to indoor flow-through holding tanks supplied with 9-12˚C filtered seawater at MMFS. The holding tanks were illuminated by natural daylight filtered through skylights, supplemented with fluorescent ceiling lights during the day. Holding tanks were shrouded from external visual stimuli with black plastic sheeting. Chinook salmon were held in captivity at the experimental facility for 84 days before experiments began, and their fork lengths (FL) ranged 202-259 mm during the experiments. Herring (FL = 61 mm mean ± 5 mm SD) were captured in multiple batches and held in captivity for 2-18 days before use in experiments. The ratio of mean prey FL to mean predator FL ranged from 0.23-0.30 across all experiments. Juvenile Chinook salmon shift to heavily piscivorous feeding over 70-200 mm FL, are capable of consuming prey fish 40-50% of their own body length, and routinely eat herring in this size range in estuarine and coastal marine habitats (Duffy et al. 2010).

All experimental fish were fed a ration of pelleted feed allowing for moderate growth. To condition the Chinook salmon to capture live fish, we also routinely fed them live herring, Pacific sand lance (*Ammodytes hexapterus*), and chum salmon (*O. keta*) during the pre-experimental holding period, and the Chinook salmon consistently displayed a strong predatory response. All Chinook salmon were also conditioned with live prey fish in the experimental arena during the pre-trial holding period. Preliminary satiation experiments showed that individual Chinook salmon were capable of consuming up to six herring within 30 minutes. This equaled the greatest number of prey consumed by any pair of salmon during the experimental trials, so we assumed that satiation did not substantially limit feeding behaviors during the experiments.

Experimental arena

All experiments were conducted in an indoor, circular flow-through tank (4.6 m diameter, 1.5 m depth). The tank was lined with a flexible gray PVC material to provide a neutral visual background, following previous experiments (Vogel and Beauchamp 1999, Mazur and Beauchamp 2003, Moss and Beauchamp 2007, Hansen et al. 2013b). A reference grid of black dots spaced 20 cm apart marked the arena bottom to calibrate overhead cameras. The tank was illuminated from above with natural light filtered through a skylight and supplemented with two overhead fluorescent light fixtures (two T8, 32-W lamps per fixture; color temperature = 6,500 kelvins). We selected the spectra of these lamps to match the spectral sensitivity of salmonids and to mimic the light environment of typical epipelagic salmon habitat (see Hansen et al.

2013b). Sheets of white nylon fabric suspended above the arena diffused the overhead light. Experimental light levels ranged 64-214 lx at the water surface, consistently higher than the saturation intensity threshold of Chinook salmon (25 lx; Hansen et al. 2013b), above which additional light has no effect on the reaction distance to prey. The arena was shrouded with a layer of black plastic sheeting to block any external visual stimuli (Figure 2.1). We recorded each trial on video using four fixed-focus, black-and-white security cameras (Speco Technologies model CVC-321WP) mounted 2.5 m above the tank bottom. We saved video files on the hard drive of a desktop computer using a video capture card (Bluecherry model PV-183-8) and Blue Iris LE version 2.0 software (Perspective Software).

General experimental protocol

Before each trial, we filled the tank to a depth of 0.5 m with a suspension of pulverized kaolin clay in seawater to achieve a target turbidity level. We randomly removed a designated number of prey fish from their holding tank, counted them in duplicate using a hand clicker, introduced them to the arena, and allowed them to acclimate for 30 minutes. We measured light levels and collected a water sample for turbidity measurements before and after each trial. We collected an integrated 1 L water sample from four locations within the water column of the arena. We measured light levels at the surface of the water from four locations around the perimeter of the arena using a handheld photometric sensor (Sper Scientific model 840006), and calculated the mean of the pre- and post-trial measurements to determine the nominal light level for the trial.

To begin each trial, we began recording video and introduced two predators to the arena. We used two predators in each trial because pilot trials and previous studies indicated predators were more active in pairs than alone (Savitz and Bardygula-Nonn 1997, De Robertis et al. 2003, Mazur and Beauchamp 2003). The trial duration was 60 min for experiment 1 and 30 min for experiment 2 (described in detail below). To end each trial, we collected a second water sample; this disruption caused the predators to stop foraging and sink to the bottom of the arena. Video review confirmed that no further attacks occurred after this point. Predators were confined to a small portion of the arena with a hand seine, removed with a dip net, and measured for FL. After partially draining the arena, we removed and counted the surviving prey in duplicate to confirm how many were consumed during the trial. A fine-mesh screen affixed to the outlet drain ensured that no prey fish escaped the arena. We fully drained, rinsed, and refilled the arena before conducting each subsequent trial to remove residual kaolin and any chemical alarm cues that could potentially influence fish behavior (McIntyre et al. 2012). We rotated Chinook salmon ($N = 40$) between trials to maintain equal experience levels. Surviving prey fish were not re-used in later trials.

We measured the turbidity of each water sample as beam attenuation, the sum of light absorption and scattering, which is the most common measure of turbidity in oceanographic studies (Kirk 2010). We measured the percent of light transmitted through a 10 mm cuvette using a Spectronic 21 DV spectrophotometer (Milton Roy) set to a wavelength of 660 nm. Beam attenuation was calculated using the formula $T = e^{-cr}$, where T is the proportion of light transmitted through a path length r (m) at an attenuation rate c (m^{-1}) (Kirk 2010). The turbidity level of each trial was reported as the mean of five pre-trial and five post-trial water samples. Beam attenuation did not change during pilot and experimental trials, indicating that clay remained in full suspension through the duration of the trials (paired t-test, $N = 80$, $t = 0.592$, $p > 0.5$). We also analyzed a subset of water samples using a LaMotte 2020e turbidity meter. This instrument quantified the amount of light scattered at a 90° angle to the beam in nephelometric turbidity units (NTU). We developed conversions from the beam attenuation rate c to NTU to allow our results to be compared with those of freshwater studies, which generally report turbidity in NTU. Due to a supply disruption, we used different types of kaolin for the first and second experiments. The relationships were

$$\mathrm{NTU} = 2.49c - 0.14 \tag{2.1}$$

($N = 24$, $r^2 = 0.98$, $p < 0.001$), for experiment 1 and

$$\mathrm{NTU} = 3.13c + 0.17 \tag{2.2}$$

($N = 25$, $r^2 = 0.99$, $p < 0.001$) for experiment 2.

To maximize the visibility of the predators and prey to the video cameras, we limited the water depth in the tank to 0.5 m during the main experiments. We conducted a pilot experiment to test whether reducing the water level from the full 1.0 m working depth of the tank influenced the results. We conducted five trials at each water depth with clear water (no kaolin added), using 33 herring per trial, and compared the attack rate, CS, and predation rate between the 0.5 and 1.0 m water depth treatments using t-tests. None of these metrics differed between treatments ($N = 10$, $p > 0.7$ for all comparisons). Based on our direct observations, salmon generally attacked along the same horizontal plane as their prey even in the deeper-water trials.

Behavioral analysis

Chinook salmon displayed generalized and repeated sequences of foraging behaviors, which we recorded following the predation sequence terminology of Wahl and Stein (1988) and Beauchamp et al. (2007). We synchronized and viewed the video files from the four cameras and recorded behaviors using VidSync scientific video analysis software (www.vidsync.org; Figure 2.1). Predators initially searched for prey by swimming slowly around the tank. When a predator encountered an individual or group of prey, it would generally *orient* its body to face the prey and pause briefly. This stereotypic "reaction" behavior has been quantified in many prior laboratory studies of reaction distance (e.g., Howick and O'Brien 1983, Hansen et al. 2013b). For each orient behavior, we recorded whether the predator oriented to a *shoal*, *individual,* or *unknown prey*.

During an encounter, a predator might approach or follow moving prey at a normal swimming speed. At any point, the predator might *attack* the prey, swimming at burst speed. Attacks generally caused ripples on the water's surface, and we could quantify them at relatively high turbidity levels (up to 3 beam attenuation / m). We recorded the target of each attack as a *shoal*, *individual,* or *unknown prey*. A prey fish was considered an individual if no other prey fish was within 20 cm (one grid unit; approximately 3-4 body lengths) at the start of the attack. We recorded the start and end times of each attack and whether it resulted in a *capture, miss,* or *unknown outcome.* Each capture was followed by a *handling* sequence. We recorded the start and end times of each handling sequence, as well as its outcome: *prey consumed, prey escaped,* or *unknown outcome*. After a missed attack, predators sometimes executed a single turn and approached the same prey again. We considered this a continuation of the same encounter. At any point during an encounter, if a predator exhibited more than one distinct movement away from the prey or turned away for more than 5 s, we recorded a *reject* behavior, marking the end of the encounter and a return to search. When the prey could not be reliably seen in the video (generally at turbidity ≥ 2 beam attenuation / m), we could not identify orient or reject behaviors, so we simply recorded attacks without grouping them into encounters.

We reviewed each trial in its entirety to record all attacks and handling sequences and grouped these behaviors into discrete encounters by recording the first reject behavior or prey consumption after each attack. To determine the proportion of encounters that did not result in an attack, we also reviewed randomly selected 5-min subsets of footage from nine randomly selected trials in greater detail, recording each orient, pursuit, and reject behavior. We calculated attack rate as the overall rate of attacks / encounter. We determined the total number of prey consumed from the count of surviving prey at the end the 30- or 60-min trial, and calculated CS as the number of prey consumed divided by the number of attacks. From the time stamps of the recorded behaviors, we calculated the time salmon spent stalking, attacking, and manipulating prey.

Finally, for each orient and attack behavior, we defined the variable "shoal size" to represent the approximate number of prey fish involved in the interaction. For interactions with individual prey, we assigned a value of shoal size = 1, and for interactions with shoals, we set shoal size equal to the total number of prey in the trial. Although we could not count the exact numbers of fish in shoals from the video footage, we observed that nearly all prey formed a single shoal during the experiments. Smaller secondary shoals rarely formed, and they usually rejoined the main shoal rapidly. This approach slightly overestimated actual shoal size at times, due to temporary separation of individuals from the shoal or attrition from predation, but these measurement errors were infrequent and small compared to the overall range of shoal sizes in the experiments (1-164 fish).

Effects of turbidity on capture success

We conducted 21, 60-minute feeding trials across a range of turbidity levels (0-2.3 beam attenuation / m; NTU = 0-5.5), at a prey density of 4 fish / m^3 (33 herring per trial). These trials encompassed a wide range of turbidity levels experienced by juvenile Chinook salmon in coastal habitats including clear oceanic waters, dense phytoplankton blooms (Lovvorn et al. 2001), river plumes (Emmett et al. 2006), and coastal habitats with bottom sediments resuspended by tides, storms, or bottom trawl fisheries (Churchill et al. 1994, Pilskaln et al. 1998). This range also encompassed the turbidity levels of most (> 95%) oligotrophic and mesotrophic lakes (Hansen and Beauchamp 2015).

We tested for an effect of turbidity on CS using logistic regression models, weighted by the number of attacks per trial. To account for potentially confounding effects of prey size and time-varying effects such as predator experience, we also tested for effects of the ratio of mean prey FL to mean predator FL (hereafter "size ratio") and date. We fit a hierarchical set of eight models including a global model with effects of turbidity, size ratio, and date, and all possible reduced models including an intercept-only model.

Effects of prey density on capture success at low and high turbidity levels

We conducted 24, 30-minute feeding trials using the same procedure described above to examine variability in CS in response to a factorial combination of four prey density treatments: 0.24, 1.0, 4.0, and 20 prey / m^3 (2, 8, 33, and 164 prey per trial) and two turbidity treatments (0 and 1.6 beam attenuation / m). These treatments represent a natural range of fine-scale pelagic prey fish densities observed in the wild (Misund 1993, Pitcher and Parrish 1993, Beauchamp et al. 1999, Domenici et al. 2000). We selected 1.6 beam attenuation / m as the upper turbidity level because it was high enough to induce a meaningful decline in CS based on the first experiment, yet low enough to confidently enumerate all attacks during the video analysis. These low and high turbidity levels simulated a contrast between clear oceanic waters and a dense phytoplankton bloom or a moderately turbid river plume.

We tested for effects of prey density and an interaction between prey density and turbidity on CS. We modeled CS as a binomial process, weighted by the number of attacks. We fit a hierarchical set of 20 models including a global model with effects of prey density ($\log_e$

transformed), turbidity level, a prey density X turbidity interaction, size ratio, and date, and all possible reduced models including an intercept-only model.

Effects of shoaling on capture success at low turbidity

We analyzed a subset of the data from both experiments to test whether the potential effects of prey density or shoaling on CS were best explained by 1) prey density, 2) shoaling (a categorical predictor for solitary prey or shoals of multiple prey), or 3) shoal size (number of prey attacked, where shoal size = 1 for attacks on solitary prey). We tested these hypotheses by analyzing individual attacks within trials. This behavioral-level analysis accounted for the numbers of prey involved in each attack, rather than simply the overall density of prey in the tank; however, this was only possible for clear water trials, for which we could determine the outcomes of most (> 90%) attacks directly from the video footage. For this analysis, we used the 30 clear-water (i.e., turbidity < 0.3 beam attenuation / m) trials from both experiments described above. To make the 60- and 30-min trials comparable, we restricted the analysis to attacks within the first 30 min of all trials ($N = 288$).

We modeled CS with logistic mixed effects models in which each attack resulted in a success or failure, and we accounted for lack of independence of attacks within trials by specifying trial as a random effect in all models. We tested four models including each of the following fixed explanatory variables: prey density ($\log_e$ transformed), shoaling, and shoal size ($\log_e$ transformed), as well as an intercept-only model. We log transformed prey density and shoal size because the prey density treatment levels were roughly evenly spaced on a log scale. To account for potentially confounding effects, we also tested eight models including each of the fixed effects above plus 1) size ratio, 2) date, and 3) size ratio + date. Thus, we tested 12 total models representing the three variables of interest and two potential confounding variables.

Statistical analysis

We fit models in the R version 3.1.3 software package (R Core Team 2015) using the base glm function for generalized linear models and the glmer function from the package lme4 for generalized linear mixed models (Bates et al. 2014). For all models, we rescaled continuous predictors by subtracting the mean of each variable and dividing by its standard deviation; this allowed us to compare the strengths of model coefficients. We selected the most parsimonious models using AIC_c (Burnham and Anderson 2002). We evaluated how well the best models explained the data using pseudo-r^2 for generalized linear models (Nagelkerke 1991) and $r^2_{\mathrm{GLMM(m)}}$ for generalized linear mixed models (Nakagawa and Schielzeth 2013). These metrics indicated the proportion of the deviance explained by the fixed effects of the model, ranging from 0-1, with 0 representing the deviance explained by a null model with only an intercept term and any random effects.

RESULTS

Overall attack rate, capture success, and time allocation of foraging Chinook salmon

Across both experiments, Chinook salmon consumed a herring during 1-4% of encounters on average, with predation rates limited both by attack rate given an encounter and capture success given an attack. We enumerated 953 salmon encounters with herring and 2198 salmon behaviors associated with these encounters. An additional 737 behaviors were enumerated under high-turbidity conditions for which we could not group behaviors into discrete encounters. Salmon exhibited an overall mean attack rate of 17.7% ($n = 9$; SE = 6.0%). Most (86%) encounters ended without an attack, a smaller fraction (11%) included a single attack, and very few (< 3%) included more than one attack (Figure 2.2). The maximum number of attacks recorded within a single encounter was 10. CS was highly variable across the range of experimental conditions and among trials, with negative effects of increased turbidity and shoaling (see below). Captured prey were successfully consumed 85.4% of the time. During encounters, salmon spent most (83%) of their time stalking their prey (mean = 11 s per encounter, range 0-49 s). In comparison, salmon spent only an average of 1.0 s (range 0-12 s) per encounter attacking their prey at burst speed, and an average of 1.3 s manipulating captured prey (range 0-92 s).

Experiment 1: Effect of turbidity on capture success

Salmon successfully consumed herring in 4.5% of attacks (range within individual trials: 0-11.4%). Increasing turbidity from 0 to 2.3 beam attenuation / m reduced the CS and predation rate of salmon by two-thirds (Figure 2.3; Table 2.1). CS declined with increasing turbidity (Figure 2.3; $\Delta AIC_c = 0$; pseudo-$r^2 = 0.27$). Based on this relationship, CS declined from an expected mean ± SE of 7.4% ± 1.4% in clear water (0 beam attenuation / m) to 2.5% ± 0.9% at 2.3 beam attenuation / m, the highest turbidity level at which we could reliably quantify all attacks. No alternative models were supported by the data (all $\Delta AIC_c > 2$).

Experiment 2: Effect of prey density on capture success at low and high turbidity levels

Salmon successfully consumed herring in 22.3% of attacks (range: 4.8-100%). Prey density did not measurably influence CS at either low or high turbidity levels (Table 2.2). Salmon achieved slightly greater CS on average at lower prey densities, but the strength of this effect was minimal and it received a similar level of support from the data ($\Delta AIC_c = 1.2$; pseudo-

$r^2 = 0.05$) than the simpler intercept-only model ($\Delta AIC_c = 0$). The data also did not support an interaction between prey density and turbidity ($\Delta AIC_c = 6.2$).

Effects of shoaling and shoal size on capture success at low turbidity

Based on the analysis of individual attacks within trials, salmon achieved 2.8-times greater CS when attacking solitary herring than shoals (Table 2.3). The most parsimonious model predicted that CS was greater for attacks on solitary herring than on shoals of multiple herring ($\Delta AIC_c = 0$). A model predicting CS as a continuous, negative function of shoal size (log-transformed) received similar support from the data (Figure 2.4, $\Delta AIC_c = 1.3$). According to the categorical model, CS declined from 20.0% for attacks on solitary herring to 7.1% for attacks on shoals of 2-164 herring. Based on the continuous model, expected CS declined by 73% as shoal size increased, from 19.2% success for attacks on solitary herring (shoal size = 1 fish) to 5.2% success for attacks on the largest shoals (shoal size = 164 fish). Models including size ratio or date received somewhat less support, indicating the effects of shoaling were relatively consistent across the size ranges of fish we tested and over time (Table 2.3).

DISCUSSION

Yearling Chinook salmon faced substantial post-encounter limitations when foraging on Pacific herring. Salmon attacked herring in less than 20% of encounters and successfully consumed prey in only 5-22% of attacks on average during the two experiments. Thus, salmon successfully consumed a herring during only 1-4% of encounters. Further, the data supported the hypotheses that increasing turbidity and increasing shoal size reduce CS. Salmon exhibited overall CS rates on the low end of the range previously reported for other pelagic piscivores:

4.5% in experiment 1 and 22% in experiment 2; we attributed the increased CS to the generally lower turbidity and prey-density treatment levels in experiment 2. In previous experimental studies with pelagic piscivores, sablefish (*Anoplopoma fimbria*) achieved similarly low CS rates when feeding on juvenile chum salmon (De Robertis et al. 2003), but bluefish (*Pomaatomus saltatrix*) and striped bass (*Morone saxatilis*) were more successful when feeding on four species of pelagic prey fishes (CS = 20-95% for prey 20-30% of predator body length; Scharf et al. 1998, Scharf et al. 2003). We used a tank with a 2-18 greater experimental volume than those used in these previous studies, so it is not clear whether the differences in CS among studies were due to species differences or tank size. Together, our results support the conclusions of several field and modeling studies that piscivorous fishes consume far fewer prey fish than they encounter (Beauchamp et al. 1999, Jensen et al. 2006, Turesson and Bronmark 2007, Hansen et al. 2013a).

In combination with relatively low CS rates, other behavioral patterns revealed in this study likely limit the feeding rates of pelagic piscivores in natural environments. Salmon attempted multiple attacks on prey during only a small fraction (3%) of encounters, indicating they could not compensate for low CS by simply attacking repeatedly until they consumed a prey. Further, salmon consumed at most one prey from each encounter with a shoal, regardless of the number of prey per shoal, as previously reported for northern pike in Swedish lakes (Turesson and Bronmark 2004). An important implication is that if increasing prey density results in larger shoals, but no change in encounter rates with shoals, this could decouple predation rates from prey densities, as demonstrated for pike (Turesson and Bronmark 2007). Finally, salmon spent most of their time during encounters stalking prey, and this time was expended regardless of the success of the encounter. The stalking times we recorded (mean duration = 11 s / encounter) were probably insignificant compared to the time predators spend searching for prey in natural environments, but they could potentially limit predators that experience optimal feeding conditions during brief windows, such as crepuscular periods, changing tides, or chance encounters with ephemeral prey aggregations. If encounter rates become less limiting in these situations, this would magnify the relative importance of CS on feeding rates, with low CS potentially becoming the main factor limiting foraging on high-density prey (Grecay and Targett 1996). For example, a modeling analysis predicted short-tailed shearwaters (*Puffinus tenuirostris*) visually foraging on euphausiid swarms in the Bering Sea were predominantly limited by handling time and CS, rather than search (Lovvorn et al. 2001).

Our results supported the hypothesis that elevated turbidities reduce CS of piscivores, in addition to the previously documented effects of turbidity on piscivore reaction distance (Vogel and Beauchamp 1999, Mazur and Beauchamp 2003, Hansen et al. 2013b). CS declined 67% as turbidity increased from 0-2.3 beam attenuation / m (0-5.5 NTU). In comparison, Chinook salmon reaction distances to prey fish declined an estimated 61% over the same turbidity range in a previous study (Hansen et al. 2013b). Based on the cylinder model of pelagic visual foraging (Eggers 1977, Beauchamp et al. 1999), search volume and encounter rate are proportional to the square of reaction distance, so this implies an 85% reduction in encounter rate. Thus, our results indicate that turbidity limits feeding rates of piscivorous salmon more strongly than would be predicted based on encounter rates alone.

Field evidence from the Columbia River plume is consistent with our findings that elevated turbidity reduces juvenile Chinook salmon foraging on prey fish. Yearling Chinook salmon density was greater in the turbid plume than in adjacent, clearer oceanic waters, but although prey densities were relatively high, the stomach fullness of Chinook salmon tended to be lower in the plume (De Robertis et al. 2005, Morgan et al. 2005). Although piscivorous salmon face reduced foraging efficiency in turbid habitats, they may benefit from a reduced risk of predation by larger piscine and avian predators, as well as diminished tradeoffs between foraging and vigilance (Gregory 1993, Gregory and Levings 1998). Elevated turbidity may particularly benefit smaller, predominantly planktivorous juvenile salmon, whose foraging rates are not limited by turbidity across the range we tested (De Robertis et al. 2003).

Predator confusion limited the foraging efficiency of salmon, and this effect was evident only at a small spatial scale. The overall density of prey in the tank (5-m diameter) did not influence CS across an 80-fold range of prey density treatments. However, salmon achieved nearly three times greater CS when attacking solitary prey than when attacking shoals (generally 0.4-1.0 m diameter), regardless of prey density. Although the importance of predator confusion varies widely among fishes as well as other taxa (reviewed by Jeschke and Tollrian 2007), our results were consistent with previous studies of predation on clupeid fishes. For example, Chinook and coho (*O. kisutch*) salmon rarely captured prey when attacking shoals of alewife (*Alosa pseudoharengus*) and other freshwater forage fishes, but salmon aggressively pursued solitary prey fish and appeared to achieve greater CS, based on qualitative observations of tank experiments (Savitz and Bardygula-Nonn 1997). Similarly, *in-situ* observations indicated predator confusion limited four species of piscivorous marine fishes feeding on a large (>>100,000), stationary school of flat-iron herring (*Harengula thrissina*) in a nearshore habitat in the Gulf of California (Parrish 1993). Although few solitary herring separated from the school, predators quickly attacked these individuals and achieved nearly four-times greater CS than for attacks on the school. Predators achieved intermediate CS when attacking pseudopods, groups of ~100 herring that temporarily extended outwards from the main school (Parrish 1993). Our results quantify this effect for piscivorous salmonids feeding on smaller shoals of Pacific herring and show the process operates on a fine spatial scale.

Although the data did not support an interaction between turbidity and prey density, we could not rule it out because of methodological limitations. The analysis of individual attacks within trials revealed a significant effect of shoaling on CS; however, the outcomes of individual attacks could only be quantified under low-turbidity conditions. We could only use the coarser-grain trial-level data to test for an interaction between turbidity and overall prey density, potentially diminishing our ability to detect a biologically significant pattern. Future technological advances in acoustic tagging and acoustic cameras may provide better opportunities to test for potentially important interactions between visibility and the anti-predator effects of shoaling.

How realistic are the patterns reported in this study for application to wild predators? Our experiments used hatchery-origin salmon predators, and it is possible that wild salmon would display different CS. Hatchery salmon can differ from wild conspecifics in many traits, including size, agonistic behavior, the timing of ocean entry, and survival (e.g., Fenderson et al. 1968, Swain and Riddell 1990, Weber and Fausch 2003, Duffy et al. 2005, Larsson et al. 2011, Beamish et al. 2012), and it is possible that they achieve different CS rates as well. However, hatchery and wild salmon exhibit similar distribution, diet composition, gut fullness, feeding intensity, and growth rates during early marine residence (Armstrong et al. 2008, Daly et al. 2012). Due to these similarities as well as the difficulty of studying wild juvenile Chinook salmon, which are listed as endangered in our study region, we regard these results as a valuable step forward.

By necessity, we quantified predator-prey interactions in a spatially-restricted, artificial environment, and this may also have influenced our results. Predators sometimes appeared to avoid attacking prey near tank walls, as observed in other experiments (Savitz and Bardygula-Nonn 1997). The presence of walls is an unavoidable artifact of all tank experiments. However, as noted above our experimental arena was substantially larger than those used in previous predation studies (e.g., De Robertis et al. 2003, Mazur and Beauchamp 2003), which likely reduced artifacts due to interactions near the walls. The diameter of the tank was nearly 4-times the mean reaction distance (1.2 m) of Chinook salmon under fully illuminated, clear-water conditions (Hansen et al. 2013b). Thus, predators and prey encountered each other repeatedly, rather than remaining in continuous visual contact, as would be the case in smaller arenas. Further, most attacks occurred in the open portion of the arena, so CS was probably not heavily influenced.

The rate of attacks per encounter was probably more sensitive to tank effects, so we interpreted those results with caution. It is possible that piscivores in natural environments would be more likely to attack the prey they encountered, especially if encounter rates were low. Little is known about the rate of attacks per encounter for pelagic piscivores, likely due to the difficulty of observing these interactions in a natural environment and the logistical difficulty of measuring these processes experimentally. We reported only an overall mean rate of attacks per encounter due to the substantial time demands of quantifying encounters for free-swimming predators and prey, especially for the reduced visibility at high prey density treatments. Future research testing for effects of visibility and shoaling on attack rates would be valuable. Despite these potential limitations, this study clearly revealed the strong potential for post-encounter processes to limit piscivore foraging rates.

Implications for foraging models

Foraging models provide an approach for quantifying the relative foraging gain and predation risk of different habitats, and for explaining behavioral patterns such as the diel vertical migration (Clark and Levy 1988, Scheuerell and Schindler 2003, Hansen and Beauchamp 2015) and shoaling (Gjelland et al. 2009) of prey fishes, as well as the diet composition and predation rates of piscivores (Mazur and Beauchamp 2006, Hansen and Beauchamp 2014). Few empirical relationships are available to incorporate post-encounter processes into these models, with the exception of well-supported effects of predator-prey size ratios and prey morphology on CS (Scharf et al. 1998, Scharf et al. 2003). As a necessary result, many studies have assumed, sometimes implicitly, that predation rates (or predation risk for prey fish) were proportional to encounter rates (e.g., Clark and Levy 1988, Beauchamp et al. 1999, Jensen et al. 2006, Gjelland et al. 2009). If post-encounter factors limit predation rates and vary substantially with visibility and shoaling, as our results suggest, then this assumption deserves further scrutiny, and modeling studies should consider alternative hypotheses regarding how prey encounters translate into consumption rates (e.g., Mazur and Beauchamp 2006, Hansen and Beauchamp 2014).

As far as we are aware, this is the first study to measure the rate of attacks per encounter and CS of a salmonid piscivore, and the first to quantify continuous effects of turbidity and prey shoal size on CS of any pelagic piscivorous fish. In addition, we recently quantified the reaction distance of Chinook salmon as a function of light, turbidity, and prey size (Hansen et al. 2013b), so in combination these studies provide the most comprehensive foraging parameters for a pelagic piscivorous fish published to date. The effects of turbidity and shoaling on CS reported here (summarized in Table 2.4) can be readily applied in foraging models. Current approaches to estimating encounter rates already use turbidity data and hydroacoustics-derived prey densities (e.g., Jensen et al. 2006, Hansen et al. 2013a), so including a turbidity- and shoaling-dependent CS rate would not require additional field data. We found no support for an interaction between visibility and shoaling, suggesting these effects can be modeled independently. With these experimental results, we aim to facilitate visual foraging model applications in both marine and freshwater systems.

Fine-scale behavioral interactions between predators and prey can produce important emergent properties for food-web dynamics (Walters and Juanes 1993, Mittelbach and Osenberg 1994). Recent advances in foraging models have emphasized the importance of heterogeneous fine-scale prey densities for both predator search strategies and the strength of trophic interactions (Pitchford et al. 2003, Sims et al. 2008, Humphries et al. 2012). One recent theoretical approach incorporates patchiness into a pelagic foraging model as a two-step Poisson process by assuming that predators initially search for prey patches, and then search for individual prey within a patch (Anderson 2010). However, empirical data have previously been lacking to quantify the constraints on foraging interactions after a pelagic piscivorous fish encounters a patch of prey. This study offers a quantitative view of some of these constraints. Our results provide parameters for including visual and behavioral post-encounter constraints as well as patch dynamics in foraging models for pelagic piscivores.

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REFERENCES

Anderson, J. J. 2010. Ratio- and predator-dependent functional forms for predators optimally foraging in patches. American Naturalist **175**:240-249.

Armstrong, J. B. and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature **476**:84-87.

Armstrong, J. L., K. W. Myers, D. A. Beauchamp, N. D. Davis, R. V. Walker, J. L. Boldt, J. J. Piccolo, L. J. Haldorson, and J. H. Moss. 2008. Interannual and spatial feeding patterns of hatchery and wild juvenile pink salmon in the Gulf of Alaska in years of low and high survival. Transactions of the American Fisheries Society **137**:1299-1316.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Beamish, R., R. Sweeting, C. Neville, K. Lange, T. Beacham, and D. Preikshot. 2012. Wild Chinook salmon survive better than hatchery salmon in a period of poor production. Environmental Biology of Fishes **94**:135-148.

Beamish, R. J. and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography **49**:423-437.

Beauchamp, D. A. 1990. Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. Transactions of the American Fisheries Society **119**:475-482.

Beauchamp, D. A., C. M. Baldwin, J. L. Vogel, and C. P. Gubala. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences **56 Suppl. 1**:128-139.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Brechbühl, R., J. Casas, and S. Bacher. 2011. Diet choice of a predator in the wild: overabundance of prey and missed opportunities along the prey capture sequence. Ecosphere **2**:Article 133.

Brodeur, R., E. Daly, M. Sturdevant, T. Miller, J. Moss, M. Thiess, M. Trudel, L. Weitkamp, J. Armstrong, and E. Norton. 2007. Regional comparisons of juvenile salmon feeding in coastal marine waters off the West Coast of North America. Page 183 *in* C. B. Grimes, R. D. Brodeur, L. J. Halderson, and S. McKinnell, editors. The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. American Fisheries Society Bethesda, Maryland.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Casas, J. and T. Steinmann. 2014. Predator-induced flow disturbances alert prey, from the onset of an attack.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist:141-151.

Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviours: pre-versus postcapture constraints on size-dependent predator-prey interactions. Oikos **76**:368-380.

Churchill, J. H., C. D. Wirick, C. N. Flagg, and L. J. Pietrafesa. 1994. Sediment resuspension over the continental shelf east of the Delmarva Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography **41**:341-363.

Clark, C. W. and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist **131**:271-290.

Daly, E., R. Brodeur, J. Fisher, L. Weitkamp, D. Teel, and B. Beckman. 2012. Spatial and trophic overlap of marked and unmarked Columbia River Basin spring Chinook salmon during early marine residence with implications for competition between hatchery and naturally produced fish. Environmental Biology of Fishes **94**:117-134.

De Robertis, A., C. A. Morgan, R. A. Schabetsberger, R. W. Zabel, R. D. Brodeur, R. L. Emmett, C. M. Knight, G. K. Krutzikowsky, and E. Casillas. 2005. Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. Marine Ecology Progress Series **299**:33-44.

De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences **60**:1517-1526.

Dean, K. G., C. P. McRoy, K. Ahlnäs, and A. Springer. 1989. The plume of the Yukon River in relation to the oceanography of the Bering Sea. Remote Sensing of Environment **28**:75-84.

Domenici, P. 2001. The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. Comparative Biochemistry And Physiology A-Molecular & Integrative Physiology **131**:169-182.

Domenici, P., R. Batty, and T. Similä. 2000. Spacing of wild schooling herring while encircled by killer whales. Journal of Fish Biology **57**:831-836.

Duffy, E. J. and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences **68**:232-240.

Duffy, E. J., D. A. Beauchamp, and R. M. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. Estuarine Coastal and Shelf Science **64**:94-107.

Eggers, D. M. 1977. The nature of prey selection by planktivorous fish. Ecology **58**:46-59.

Elliott, J. P., I. M. Cowan, and C. Holling. 1977. Prey capture by the African lion. Canadian Journal of Zoology **55**:1811-1828.

Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998-2003:

Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Progress in Oceanography **68**:1-26.

Fenderson, O. C., W. H. Everhart, and K. M. Muth. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. Journal of the Fisheries Board of Canada **25**:1-14.

Flynn, A. J. and D. A. Ritz. 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. Journal of the Marine Biological Association of the United Kingdom **79**:487-494.

Gjelland, K. O., T. Bohn, J. K. Horne, I. Jensvoll, F. R. Knudsen, and P. A. Amundsen. 2009. Planktivore vertical migration and shoaling under a subarctic light regime. Canadian Journal of Fisheries and Aquatic Sciences **66**:525-539.

Grecay, P. A. and T. E. Targett. 1996. Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish *Cynoscion regalis*. Marine Ecology Progress Series **131**:11-16.

Gregory, R. S. 1993. Effect of turbidity on the predator avoidance behavior of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **50**:241-246.

Gregory, R. S. and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society **127**:275-285.

Grimes, C. B. and M. J. Kingsford. 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? Marine and Freshwater Research **47**:191-208.

Hansen, A. G. and D. A. Beauchamp. 2014. Effects of prey abundance, distribution, visual contrast and morphology on selection by a pelagic piscivore. Freshwater Biology 10.1111/fwb.12436:n/a-n/a.

Hansen, A. G. and D. A. Beauchamp. 2015. Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. Journal of Animal Ecology **84**:532-544.

Hansen, A. G., D. A. Beauchamp, and C. M. Baldwin. 2013a. Environmental constraints on piscivory: Insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout. Transactions of the American Fisheries Society **142**:300-316.

Hansen, A. G., D. A. Beauchamp, and E. R. Schoen. 2013b. Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. Transactions of the American Fisheries Society **142**:854-867.

Hillgruber, N. and C. E. Zimmerman. 2009. Estuarine ecology of juvenile salmon in Western Alaska: a review. Pages 183-199 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific Salmon: Ecology and Management of Western Alaska's Populations. American Fisheries Society Symposium, Bethesda, MD.

Howick, G. L. and W. J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Transactions of the American Fisheries Society **112**:508-516.

Hughes, N. F. and L. M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences **47**:2039-2048.

Humphries, N. E., H. Weimerskirch, N. Queiroz, E. J. Southall, and D. W. Sims. 2012. Foraging success of biological Lévy flights recorded in situ. Proceedings of the National Academy of Sciences **109**:7169-7174.

Jensen, O. P., T. R. Hrabik, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community II. Modeling trade-offs at an intermediate trophic level. Canadian Journal of Fisheries and Aquatic Sciences **63**:2296-2307.

Jeschke, J. M., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs **72**:95-112.

Jeschke, J. M. and R. Tollrian. 2007. Prey swarming: which predators become confused and why? Animal Behaviour **74**:387-393.

Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79-100 *in* D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, S.C.

Kimbell, H. S. and L. J. Morrell. 2015. Turbidity influences individual and group level responses to predation in guppies, Poecilia reticulata. Animal Behaviour **103**:179-185.

Kirk, J. 2010. Light and photosynthesis in aquatic ecosystems. 3rd edition. Cambridge University Press, Cambridge, UK.

Krueger, C. C., C. E. Zimmerman, and J. J. Spaeder. 2009. Ecology and managment of western Alaska Pacific salmon: Introduction to the proceedings. Pages 3-10 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific Salmon: Ecology and Management of Western Alaska's Populations. American Fisheries Society Symposium, Bethesda, MD.

Kruse, G. H. 1998. Salmon run failures in 1997-1998: A link to anomalous ocean conditions? Alaska Fishery Research Bulletin **5**:55-63.

Landeau, L. and J. Terborgh. 1986. Oddity and the 'confusion effect' in predation. Animal Behaviour **34**:1372-1380.

Larsson, S., T. Linnansaari, S. Vatanen, I. Serrano, and A. Haikonen. 2011. Feeding of wild and hatchery reared Atlantic salmon (Salmo salar L.) smolts during downstream migration. Environmental Biology of Fishes:1-9.

Lovvorn, J. R., C. L. Baduini, and G. L. Hunt. 2001. Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. Ecology **82**:2342-2356.

Mazur, M. M. and D. A. Beauchamp. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. Environmental Biology of Fishes **67**:397-405.

Mazur, M. M. and D. A. Beauchamp. 2006. Linking piscivory to spatial-temporal distributions of pelagic prey fishes with a visual foraging model. Journal of Fish Biology **69**:151-175.

McGill, B. J. and G. G. Mittelbach. 2006. An allometric vision and motion model to predict prey encounter rates. Evolutionary Ecology Research **8**:691-701.

McIntyre, J. K., D. H. Baldwin, D. A. Beauchamp, and N. L. Scholz. 2012. Low-level copper exposures increase visibility and vulnerability of juvenile coho salmon to cutthroat trout predators. Ecological Applications **22**:1460-1471.

Meager, J. J., P. Domenici, A. Shingles, and A. C. Utne-Palm. 2006. Escape responses in juvenile Atlantic cod Gadus morhua L.: the effects of turbidity and predator speed. Journal of Experimental Biology **209**:4174-4184.

Misund, O. A. 1993. Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat, and saithe schools. ICES Journal of Marine Science: Journal du Conseil **50**:145-160.

Mittelbach, G. G. and C. W. Osenberg. 1994. Using foraging theory to study trophic interactions. Pages 45–59 *in* D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, SC.

Morgan, C. A., A. De Robertis, and R. W. Zabel. 2005. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. Marine Ecology Progress Series **299**:19-31.

Moss, J. H. and D. A. Beauchamp. 2007. Functional response of juvenile pink and chum salmon: effects of consumer size and two types of zooplankton prey. Journal of Fish Biology **70**:610-622.

Nagelkerke, N. J. 1991. A note on a general definition of the coefficient of determination. Biometrika **78**:691-692.

Nakagawa, S. and H. Schielzeth. 2013. A general and simple method for obtaining r^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution **4**:133-142.

Nottestad, L. and B. E. Axelsen. 1999. Herring schooling manoeuvres in response to killer whale attacks. Canadian Journal of Zoology-Revue Canadienne De Zoologie **77**:1540-1546.

Parrish, J. K. 1993. Comparison of the hunting behavior of four piscine predators attacking schooling prey. Ethology **95**:233-246.

Petersen, J. and D. Gadomski. 1994. Light-mediated predation by northern squawfish on juvenile chinook salmon. Journal of Fish Biology **45**:227-242.

Pilskaln, C. H., J. H. Churchill, and L. M. Mayer. 1998. Resuspension of Sediment by Bottom Trawling in the Gulf of Maine and Potential Geochemical Consequences. Conservation Biology **12**:1223-1229.

Pitcher, T. J. and J. K. Parrish. 1993. Functions of shoaling behaviour in teleosts. Pages 363–439 *in* T. J. Pitcher, editor. Behaviour of Teleost Fishes. Chapman and Hall, London.

Pitchford, J. W., A. James, and J. Brindley. 2003. Optimal foraging in patchy turbulent environments. Marine Ecology Progress Series **256**:99-110.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Savitz, J. and L. Bardygula-Nonn. 1997. Behavioral interactions between coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus shawytscha*) and prey fish species. Ecology of Freshwater Fish **6**:190-195.

Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fisheries Oceanography **12**:523-540.

Scharf, F. S., J. A. Buckel, F. Juanes, and D. O. Conover. 1998. Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. Canadian Journal of Fisheries and Aquatic Sciences **55**:1695-1703.

Scharf, F. S., J. A. Buckel, P. A. McGinn, and F. Juanes. 2003. Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture. Journal of Experimental Marine Biology and Ecology **294**:41-59.

Scheuerell, M. D. and D. E. Schindler. 2003. Diel vertical migration by juvenile sockeye salmon: Empirical evidence for the antipredation window. Ecology **84**:1713-1720.

Shipley, L. A., D. E. Spalinger, J. E. Gross, N. T. Hobbs, and B. A. Wunder. 1996. The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. Functional Ecology **10**:234-244.

Sims, D. W., E. J. Southall, N. E. Humphries, G. C. Hays, C. J. A. Bradshaw, J. W. Pitchford, A. James, M. Z. Ahmed, A. S. Brierley, M. A. Hindell, D. Morritt, M. K. Musyl, D. Righton, E. L. C. Shepard, V. J. Wearmouth, R. P. Wilson, M. J. Witt, and J. D. Metcalfe. 2008. Scaling laws of marine predator search behaviour. Nature **451**:1098-U1095.

Stabeno, P., J. Schumacher, and K. Ohtani. 1999. The physical oceanography of the Bering Sea. Pages 1–28 *in* T. Loughlin and K. Ohtani, editors. Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, AK.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. Foraging: behavior and ecology. University of Chicago Press.

Swain, D. P. and B. E. Riddell. 1990. Variation in Agonistic Behavior between Newly Emerged Juveniles from Hatchery and Wild Populations of Coho Salmon, Oncorhynchus kisutch. Canadian Journal of Fisheries and Aquatic Sciences **47**:566-571.

Tomaro, L., D. Teel, W. Peterson, and J. Miller. 2012. When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Marine Ecology Progress Series **452**:237-252.

Turesson, H. and C. Bronmark. 2004. Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. Journal of Fish Biology **65**:363-375.

Turesson, H. and C. Bronmark. 2007. Predator-prey encounter rates in freshwater piscivores: effects of prey density and water transparency. Oecologia **153**:281-290.

Vogel, J. L. and D. A. Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Canadian Journal of Fisheries and Aquatic Sciences **56**:1293-1297.

Wahl, D. H. and R. A. Stein. 1988. Selective predation by 3 esocids: The role of prey behavior and morphology. Transactions of the American Fisheries Society **117**:142-151.

Walters, C. J. and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences **50**:2058-2070.

Weber, E. D. and K. D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences **60**:1018-1036.

Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics **15**:393-425.

Woodson, L. E., B. K. Wells, P. K. Weber, R. B. MacFarlane, G. E. Whitman, and R. C. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Marine Ecology Progress Series **487**:163-175.

TABLES

Table 2.1. Model selection results evaluating the effects of turbidity, size ratio (mean predator fork length / mean prey fork length), and date on the capture success (prey consumed / attack) of Chinook salmon foraging on Pacific herring.

Model	k	$-2l$	AIC_c	ΔAIC_c	w_i	pseudo-r^2
Turbidity	*2*	62.1	66.7	0	0.48	0.27
Turbidity + Day	*3*	61.4	68.8	2.1	0.17	0.29
Turbidity + Size ratio	*3*	61.9	69.3	2.6	0.13	0.28
Intercept only	*1*	68.4	70.6	3.9	0.07	0.00
Size ratio	*2*	66.7	71.4	4.6	0.05	0.08
Day	*2*	66.7	71.4	4.7	0.05	0.08
Turbidity + Day + Size ratio	*4*	61.4	71.9	5.2	0.04	0.30
Day + Size ratio	*3*	66.3	73.7	7.0	0.01	0.10

Notes: Values shown for each model include the number of parameters k, the log likelihood l, the corrected Akaike's information criterion (AIC_c), the differences in AIC_c among models (ΔAIC_c), Akaike weights (w_i), and the adjusted coefficient of determination for generalized linear models (pseudo-r^2).

Table 2.2. Model selection results evaluating the effects of prey density, turbidity, size ratio (mean predator fork length / mean prey fork length), and date on the capture success (prey consumed / attack) of Chinook salmon foraging on Pacific herring.

Model	k	$-2l$	AIC$_c$	ΔAIC$_c$	w_i	pseudo-r^2
Intercept only	1	84.7	86.9	0.0	0.28	0.00
log(Prey density)	2	83.5	88.1	1.2	0.15	0.05
Turbidity	2	84.2	88.8	1.9	0.10	0.02
Size ratio	2	84.6	89.2	2.4	0.08	0.00
Date	2	84.7	89.3	2.4	0.08	0.00
log(Prey density) + Size ratio	3	83.0	90.3	3.4	0.05	0.07
log(Prey density) + Date	3	83.0	90.3	3.4	0.05	0.07
log(Prey density) + Turbidity	3	83.1	90.4	3.5	0.05	0.07
Turbidity + Size ratio	3	84.2	91.5	4.6	0.03	0.02
Turbidity + Date	3	84.2	91.5	4.6	0.03	0.02
Date + Size ratio	3	84.6	91.9	5.0	0.02	0.00
log(Prey density) + Date + Size ratio	4	82.0	92.2	5.4	0.02	0.11
log(Prey density) + Turbidity + Date	4	82.7	92.9	6.0	0.01	0.09
log(Prey density) + Turbidity + Size ratio	4	82.7	92.9	6.0	0.01	0.09
log(Prey density) * Turbidity	4	82.9	93.1	6.2	0.01	0.08
Turbidity + Date + Size ratio	4	84.2	94.4	7.5	0.01	0.02
log(Prey density) + Turbidity + Date + Size	5	81.8	95.3	8.4	0.00	0.12
log(Prey density) * Turbidity + Date	5	82.5	96.0	9.1	0.00	0.09
log(Prey density) * Turbidity + Size ratio	5	82.6	96.1	9.3	0.00	0.09
log(Prey density) * Turbidity + Date + Size	6	81.7	99.0	12.1	0.00	0.12

Notes: Values shown for each model include the number of parameters k, the log likelihood l, the corrected Akaike's information criterion (AIC$_c$), the differences in AIC$_c$ among models (ΔAIC$_c$), the Akaike weights (w_i), and the adjusted coefficient of determination for generalized linear models (pseudo-r^2). Asterisks between model terms signify inclusion of both individual terms and their interaction.

Table 2.3. Model selection results evaluating the effects of shoaling (a categorical variable indicating whether attacks targeted solitary prey or shoals), shoal size (a continuous variable indicating the number of prey attacked, with solitary prey assigned a shoal size of 1), size ratio (mean predator fork length / mean prey fork length), and date on the capture success of Chinook salmon foraging on Pacific herring in low-turbidity trials (0-0.3 / m beam attenuation). All models included a random effect of trial.

Model	k	$-2l$	AIC$_c$	ΔAIC$_c$	w_i	$r^2_{\mathrm{GLMM(m)}}$
Shoaling + Trial	3	206.6	212.6	0	0.31	0.093
log(Shoal size) + Trial	3	207.8	213.9	1.26	0.17	0.090
Shoaling + Date + Trial	4	205.9	214.1	1.43	0.15	0.100
Shoaling + Size ratio + Trial	4	206.6	214.7	2.05	0.11	0.093
log(Shoal size) + Date + Trial	4	206.8	214.9	2.26	0.10	0.095
log(Shoal size) + Size ratio + Trial	4	207.8	215.9	3.29	0.06	0.090
Date + Trial	3	210.7	216.8	4.11	0.04	0.068
log(Prey density) + Date + Trial	4	209.9	218.0	5.4	0.02	0.067
log(Prey density) + Trial	3	212.4	218.5	5.85	0.02	0.044
log(Prey density) + Size ratio + Trial	4	212.3	220.4	7.78	0.01	0.044
Trial	2	216.5	220.6	7.94	0.01	0.000
Size ratio + Trial	3	214.9	221.0	8.36	0.00	0.022

Notes: Values shown for each model include the number of parameters k, the log likelihood l, the differences of the corrected Akaike's information criterion among models (ΔAIC$_c$), and Akaike weights (w_i), and the marginal coefficient of determination for generalized linear mixed models ($r^2_{\mathrm{GLMM(m)}}$).

Table 2.4. Parameterized logistic equations predicting capture success (prey consumed / attack) from turbidity (in beam attenuation or nephelometric turbidity units [NTU]), shoaling (categorical variable) or prey shoal size (continuous variable). Error estimates are shown for all parameters.

Explanatory variable	Model	pseudo-r^2 or $r^2_{\mathrm{GLMM(m)}}$	Parameter estimates		
			Parameter	Estimate	SE
Turbidity (c: beam attenuation / m)	$\mathrm{CS} = \frac{e^{(\beta_0 + \beta_1 c)}}{1 + e^{(\beta_0 + \beta_1 c)}}$	0.27	β_0 β_1	-2.53 -0.504	0.209 0.210
Turbidity (NTU)	$\mathrm{CS} = \frac{e^{(\beta_0 + \beta_1 \mathrm{NTU})}}{1 + e^{(\beta_0 + \beta_1 \mathrm{NTU})}}$	0.27	β_0 β_1	-2.56 -0.203	0.201 0.084
Shoaling (s)	$\mathrm{CS} = \frac{e^{(\beta_0 + \beta_1 s)}}{1 + e^{(\beta_0 + \beta_1 s)}}$	0.093	β_0 β_1	-1.39 -1.18	0.23 0.38
Shoal size (SS)	$\mathrm{CS} = \frac{e^{(\beta_0 + \beta_1 \mathrm{SS})}}{1 + e^{(\beta_0 + \beta_1 \mathrm{SS})}}$	0.090	β_0 β_1	-1.44 -0.285	0.23 0.099

Notes: Categorical "shoaling" variable coded as 0 for solitary prey and 1 for shoals of ≥ 2 prey. For turbidity equations, pseudo-r^2 values indicate the explanatory power for predicting the CS rates of experimental trials. For shoaling and shoal size equations, $r^2_{\mathrm{GLMM(m)}}$ values indicate the explanatory power for predicting the success of individual attacks within trials.

FIGURES

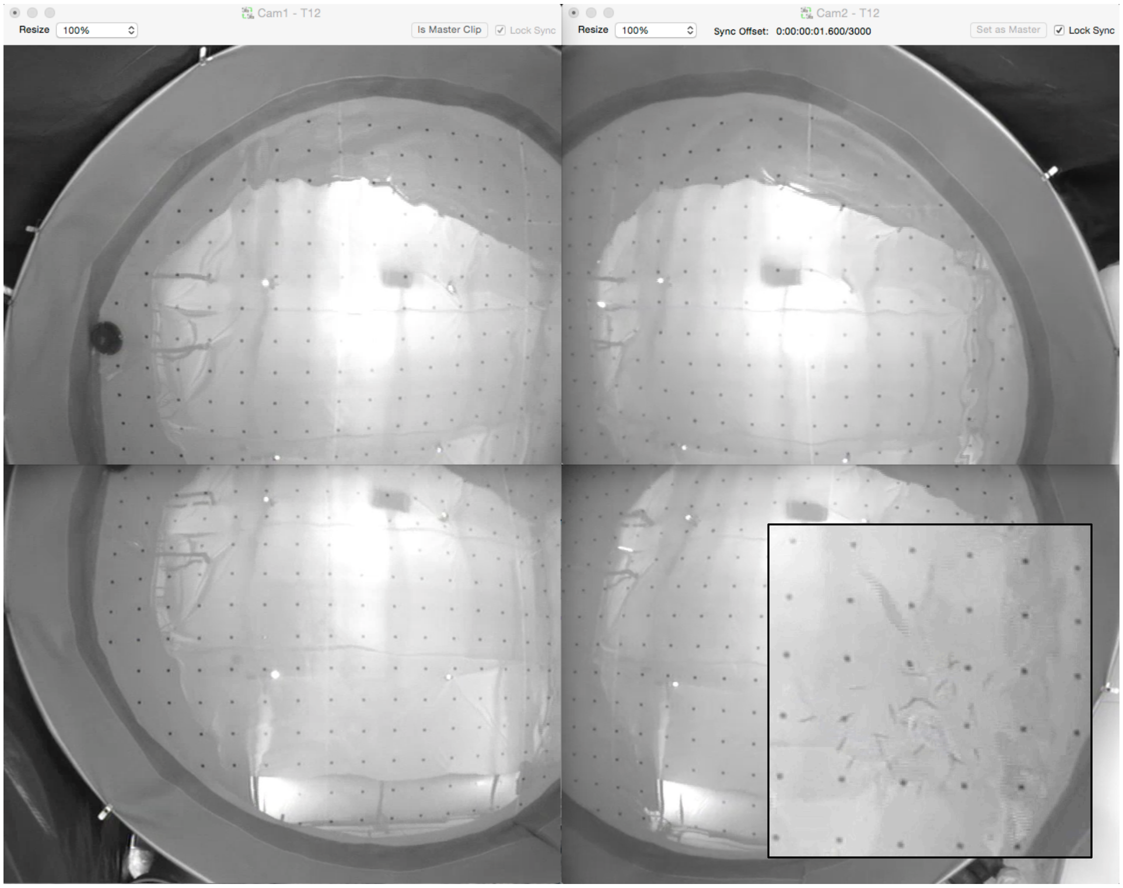

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Figure 2.1. Screenshot image of an experimental trial viewed in VidSync software. The four overlapping camera views of the 4.6 m diameter experimental arena are shown. The 20 cm measurement grid is visible on the tank bottom, and the fine-mesh drain cover is visible at left. The inset shows a Chinook salmon attacking a school of Pacific herring.

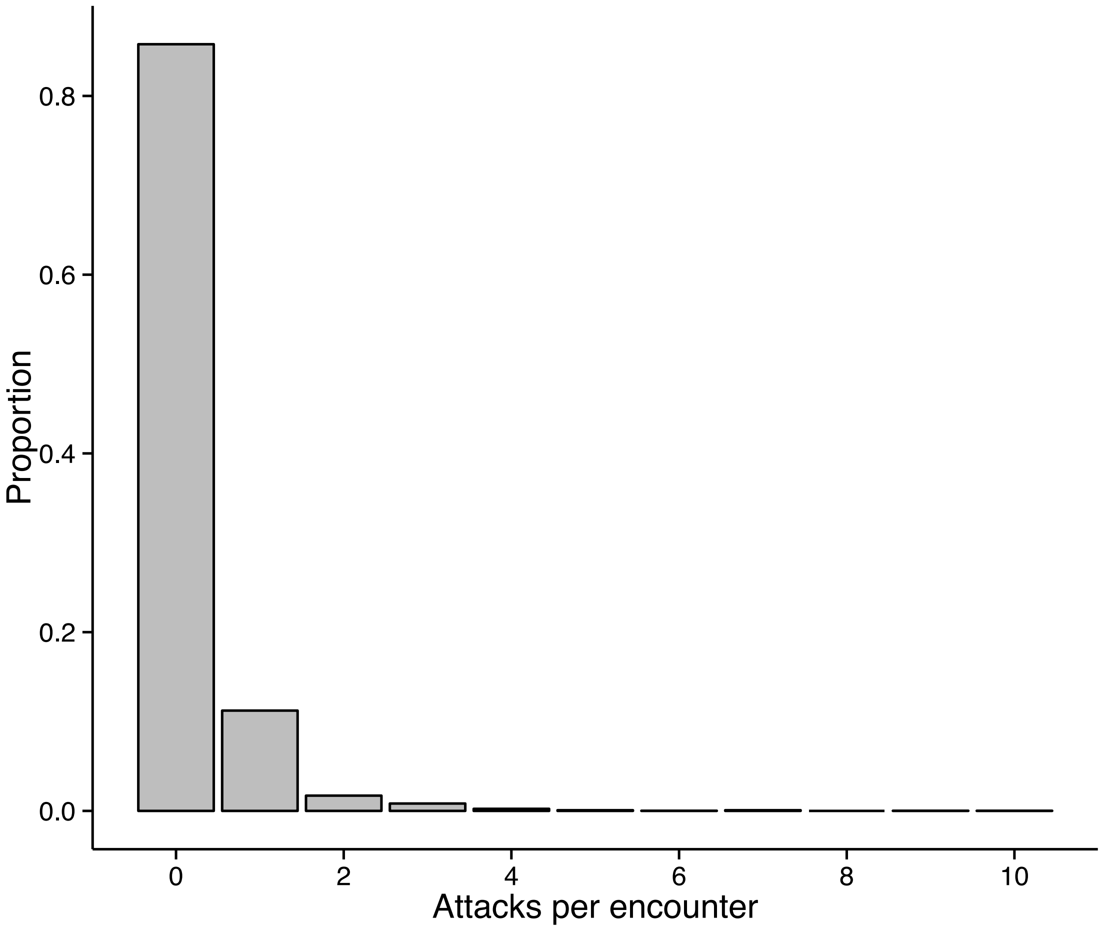

Figure 2.2. The proportional frequency distribution of Chinook salmon attack rate (attacks / encounter) with prey fish across all experiments.

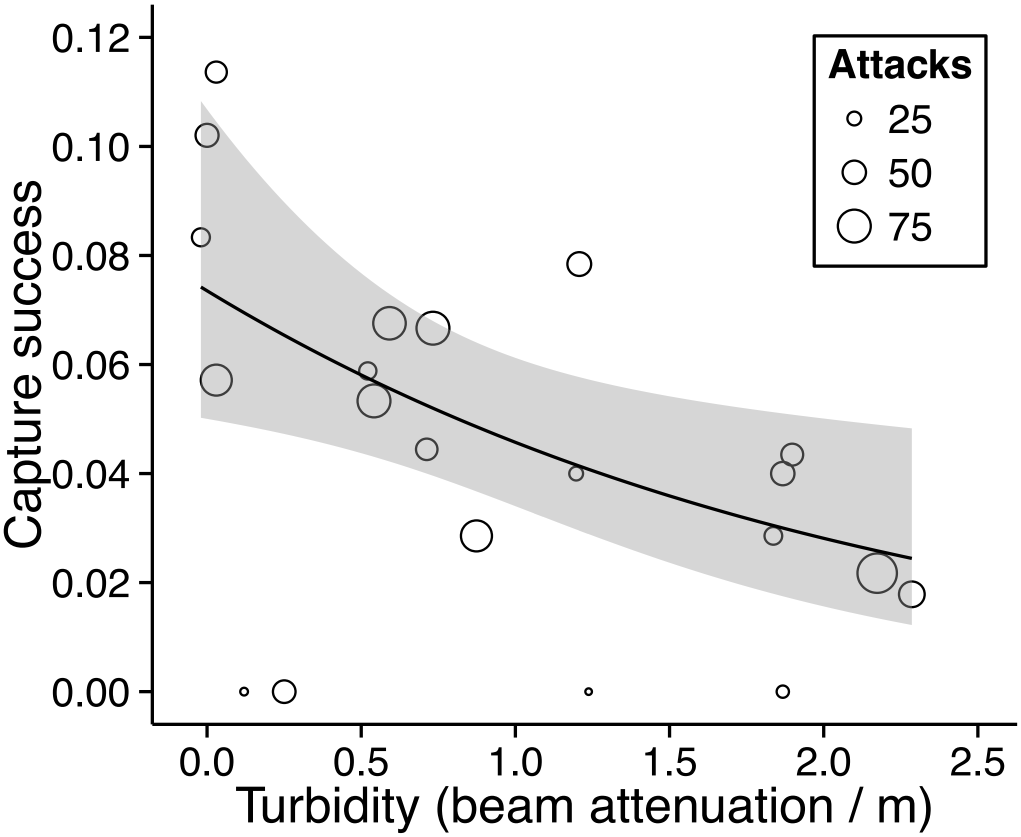

Figure 2.3. The capture success (prey consumed per attack) of salmon declined by two-thirds with increasing turbidity. Symbol size indicates the number of attacks per trial, and the curve represents a logistic regression fit to the data with a 95% confidence region. The beam attenuation range of 0-2.3/m corresponded to 0-5.5 nephelometric turbidity units.

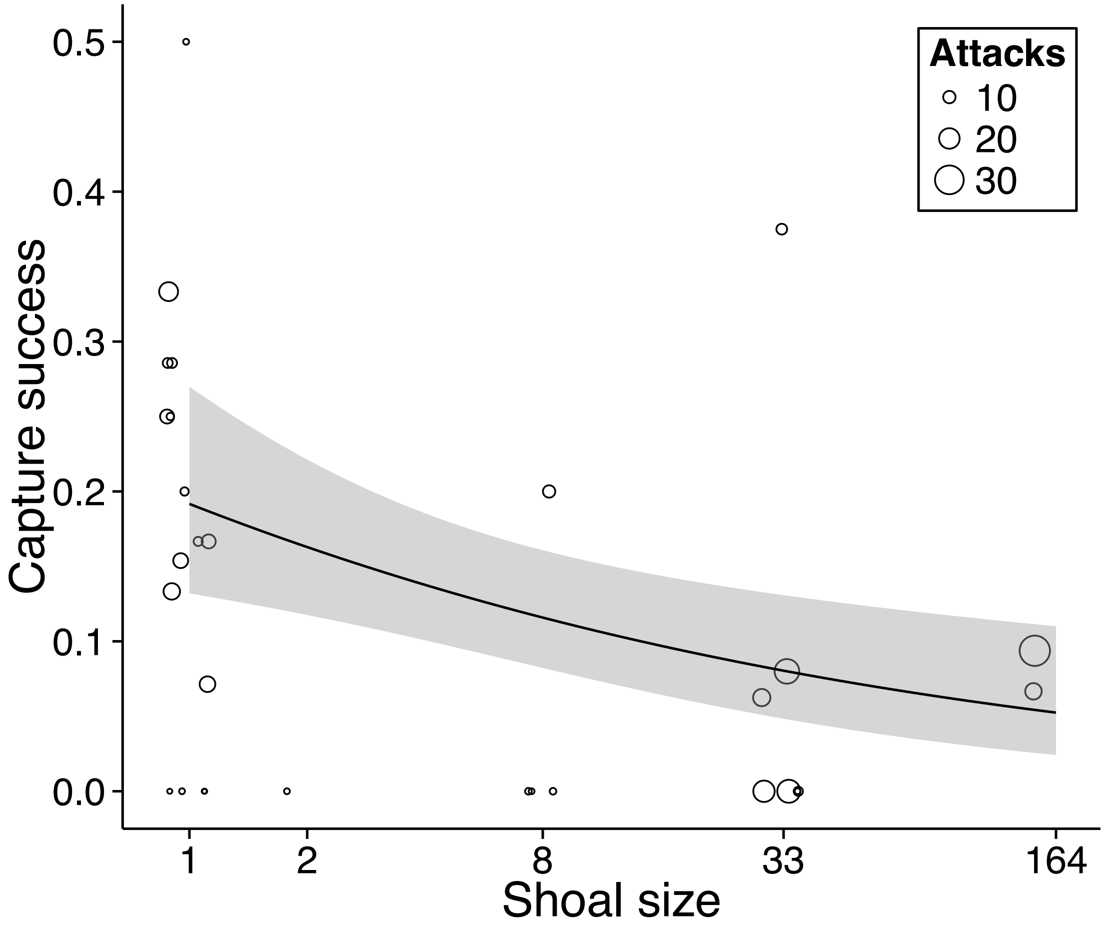

Figure 2.4. The capture success of Chinook salmon declined by 73% as they attacked larger groups of herring, ranging from individual herring (shoal size = 1) to shoals of 164 herring. Symbols represent means for each combination of trial and shoal size, symbol size represents the number of attacks, and x-values are jittered slightly to reduce over-plotting. The curve represents a logistic model fit to the data, and the shaded band represents a 95% confidence region.

Chapter 3. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee

(Schoen, E.R., Beauchamp, D.A., and Overman, N.C. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society **141**(5): 1191-1206.)

ABSTRACT

Introduced long-lived predators often cause significant impacts on their prey, but these impacts can be masked from detection due to high "predatory inertia": time lags in population growth and dietary ontogeny. We asked whether predation by introduced lake trout *Salvelinus namaycush* could explain an 88% decline in kokanee *Oncorhynchus nerka* escapement during 2005-2009 in Lake Chelan, Washington. We quantified the strength and trend of predation impacts with field sampling, a hydroacoustic assessment of kokanee production, and bioenergetics and age-structured population models of lake trout. Lake trout consumption of kokanee exceeded kokanee production, indicating strong predation impacts at the start of the decline. Fully piscivorous lake trout > 550 mm fork length were responsible for 83% of this predation. The population model predicted that a pulse of strong stocked cohorts crossed this size threshold, causing the biomass of fully piscivorous lake trout to expand by roughly 70-300% during 2004-2009 and driving predation pressure to peak levels. Together, these results suggested that lake trout predation was a large and growing source of kokanee mortality during the decline. Counterintuitively, predation pressure was projected to increase even if the numbers of harvestable lake trout declined, as strong cohorts grew to piscivorous size while succumbing to mortality. Angler catch rates of lake trout declined by 40% during 2004-2007, as predicted by

the population model; this masked the rise in predation pressure. This analysis demonstrates the potential for introduced predators exhibiting high predatory inertia to cause strong, latent impacts on prey that would be unexpected based on harvest trends and prior dynamics alone. Forward-looking monitoring and modeling analyses are clearly advantageous if managers attempt to maintain ecosystems in long-term "balance" by detecting and reversing incipient changes in predation.

INTRODUCTION

Introductions of long-lived predators often cause dramatic change to freshwater ecosystems, but these impacts can be difficult to predict and quantify (Eby et al. 2006, Martinez et al. 2009). While piscivores such as lake trout *Salvelinus namaycush*, northern pike *Esox lucius*, and walleye *Sander vitreus* can reduce or extirpate prey fish populations (He and Kitchell 1990, Bowles et al. 1991, McMahon and Bennett 1996, Patankar et al. 2006, Bystrom et al. 2007, Ellis et al. 2011), these species also appear to interact weakly with the same prey taxa in other systems (Richards et al. 1991, McMahon and Bennett 1996, Martinez et al. 2009, Ellis et al. 2011), and the conditions underlying these differences are poorly understood. Studies using before-after comparisons to evaluate impacts are often confounded by other processes such as habitat alteration (Dextrase and Mandrak 2006), eutrophication (Vander Zanden et al. 2003), or climate change (Rahel and Olden 2008, Sharma et al. 2009). Complicating matters, many long-lived predators exhibit traits such as lengthy generation times and dietary ontogenies that delay their maximum impacts for years after they are introduced. These traits have been termed "high predatory inertia" in the context of manipulating predator populations to control non-native prey fish (Stewart et al. 1981). Here we explore how high predatory inertia may also inhibit efforts to evaluate the ecological impacts of introduced piscivores, by making latent strong interactions difficult to distinguish from persistent weak interactions.

High predatory inertia complicates standard approaches to quantifying food web patterns and dynamics. Strong predation interactions are most convincingly identified with direct experimental manipulation (Paine 1980, Schindler 1998, Carpenter et al. 2001), but controlled experiments are often impractical in large or unique systems, especially when the effects of predators develop slowly. More commonly, predation impacts are evaluated indirectly using either bioenergetics or population dynamics models, and a combination of these approaches can be useful for quantifying the impacts of long-lived predators (e.g., Stewart et al. 1981, Luecke et al. 1994, Schindler et al. 1998). Bioenergetic analysis provides quantitative estimates of predation rates, but requires intensive sampling that is generally practical only for relatively short periods and does not predict future dynamics in changing systems (Ney 1993, Beauchamp et al. 2007, Chipps and Wahl 2008). Population models can incorporate dynamics on longer temporal scales, but do not identify mechanisms of interaction, and are sensitive to confounding events and ecological time lags (Stenseth et al. 1997, White et al. 2006, Peckarsky et al. 2008).

Despite these challenges, strong interactions by long-lived predators are particularly important to identify in advance because of the time lags involved with detecting and responding to their impacts. For example, juvenile lake trout are difficult to sample, so an increase in recruitment may go unnoticed for 4-7 years, until fish become fully vulnerable to angling or other sampling gear (Shuter et al. 1998). Another two or more years may pass before harvestable lake trout become fully piscivorous (Ruzycki et al. 2003), and an upsurge in predation may remain undetected until the affected prey cohort reaches the fishery or spawning grounds (Ellis et al. 2011). Finally, these predators are slow to respond to changes in stocking or harvest (Stewart et al. 1981), so management efforts to mitigate predation impacts may require several additional years to become effective.

A recent decline in kokanee *Oncorhynchus nerka* abundance in Lake Chelan, Washington raised concerns about lake trout predation (Martinez et al. 2009), but abundance trends did not suggest an obvious link between the lake trout introduction and the kokanee decline. Lake trout were first introduced to the lake in 1980 and were stocked heavily from 1990-2000 to establish a trophy fishery (Figure 3.1; Washington Dept. Fish and Wildlife data). Stocking was terminated following this 11-year pulse, and harvest limits were liberalized to reduce potential predation impacts (Martinez et al. 2009). Natural reproduction of lake trout was first documented in 2000 (Duke Engineering and Services 2000). Interestingly, kokanee escapement increased roughly four-fold from the early 1990s to the mid-2000s, as lake trout became established. From this peak, kokanee escapement declined by 88% during 2005-2009, before partially recovering (Figure 1; Keesee and Keller 2012). Reports from the fishery indicated that lake trout harvest rates mirrored these trends, increasing substantially during the 1990s to mid-2000s (Chelan County Public Utility District 2007, Martinez et al. 2009) before declining from 2005-2008 (A. Jones, Darrell and Dad's Family Guide Service, personal communication). Positively correlated densities of predators and prey generally suggest that top-down control is weak (e.g., Worm and Myers 2003, Ware and Thomson 2005); therefore, one obvious interpretation of these synchronized abundance trends was that lake trout predation had weak impacts on kokanee. However, unlike many previously studied lake trout populations (e.g., Stewart et al. 1981, Luecke et al. 1994, Ruzycki et al. 2003), the population in Lake Chelan had an irregular stocking history, and stable recruitment patterns could not be assumed. An unstable age structure could decouple the trends of harvest and prey consumption, potentially masking a strong predation interaction.

Do lake trout interact weakly with kokanee in Lake Chelan, or can strong latent impacts explain the recent kokanee decline? Our objectives were: 1) to quantify the predation rate of lake trout on kokanee at the beginning of the decline in 2005; 2) to determine the impact of this predation rate by comparing it with the production rate and biomass of the kokanee population in 2005; and 3) to determine whether the timing of longer-term trends in lake trout and kokanee population dynamics were consistent with a strong predation interaction during the decline.

STUDY AREA

Lake Chelan is a deep (mean depth 144 m, maximum depth 453 m), glacially-formed lake located in the Cascade Range in north-central Washington (48° N, 120° W; Figure 3.2). The lake is long and narrow (length 81 km, maximum width < 3 km), and is composed of two basins, Lucerne Basin in the northwest and Wapato Basin in the southeast (Kendra and Singleton 1987). The lake is ultra-oligotrophic (total phosphorus averages 3.2 µg/L) and monomictic. Native fish species include bridgelip sucker *Catostomus columbianus*, burbot *Lota lota*, largescale sucker *C. macrocheilus*, northern pikeminnow *Ptychocheilus oregonensis*, peamouth *Mylocheilus caurinus*, slimy sculpin *Cottus cognatus*, threespine stickleback *Gasterosteus aculeatus*, and westslope cutthroat trout *O. clarki lewisi*. Native bull trout *S. confluentus* were extirpated from the lake circa 1950. Many nonnative fish and invertebrate species have been introduced to the lake, primarily to enhance sport fisheries, including lake-resident Chinook salmon *O. tshawytscha*, kokanee, lake trout, opossum shrimp *Mysis diluviana*, rainbow trout *O. mykiss*, and smallmouth bass *Micropterus dolomieu* (Brown 1984, Wydoski and Whitney 2003).

Chinook salmon, kokanee, rainbow trout, and westslope cutthroat trout are currently stocked annually.

Kokanee were introduced to Lake Chelan in 1917 and have supported a popular fishery for decades (Brown 1984, Hagen 1997, Duke Engineering and Services 2000). Most kokanee in Lake Chelan exhibit a 3- or 4-year egg-to-egg life cycle (Truscott and Peven 1988, Peven 1989, 1990). Over 90% of kokanee spawning takes place in the Stehekin River and its tributaries at the north end of the lake during September and October (Peven 1990, Keesee and Keller 2012). The kokanee population declined substantially during the late 1970s following introductions of *Mysis* and Chinook salmon (Brown 1984), but recovered during the 1980s and 1990s. Spawner surveys have been conducted in major tributaries annually since 1981. Escapement is estimated using the area-under-the-curve method (Neilson and Geen 1981), assuming a spawner residence time of 15 days (Brown 1984). These surveys are considered to indicate the escapement trend, but not the complete number of spawners (Chelan County Public Utility District 2007). Harvest removes only a small fraction of kokanee escapement (Brown 1984). Kokanee are stocked directly into the lake in the Wapato Basin, but it is unclear whether these fish contribute to the fishery or spawning population (Duke Engineering and Services 2000).

METHODS

We used field data and a bioenergetics model to quantify ontogenetic and seasonal patterns in prey consumption by lake trout. We compared these consumption values to the estimated kokanee biomass and production rate from a hydroacoustics survey to determine the impact of lake trout predation on the kokanee population. Finally, using stocking records and a population model, we reconstructed the past abundance and age structure of lake trout and then projected these trends into the future to characterize likely changes in predation pressure under different scenarios of natural reproduction.

Field sampling

We conducted standardized sampling every three months from August 2004 through May 2006 to quantify the seasonal diet, distribution, and growth pattern of lake trout. Lake trout were captured with horizontal sinking gill nets fished overnight at five fixed sites (Figure 3.2). At each sampling site, four depth strata were sampled with one small-mesh net (2.5, 3.2, 3.8, 5.1, 6.4, and 7.6 cm stretched mesh) and one large-mesh net (8.9, 10.2, 11.4, 12.7, and 15.2 cm stretched mesh). The depth strata (0-15, 15-30, 30-50, and 50-70 m) corresponded with the epilimnion, metalimnion, and two depths in the hypolimnion during late summer. Kokanee were sampled opportunistically by angling and with horizontal midwater gill nets and large "curtain" gill nets (Beauchamp et al. 2009).

Fork length (FL; mm), wet weight (g), and sex of captured fish were recorded in the field. Lake trout stomachs were collected and frozen immediately, and gonads were weighed to determine reproductive investment. For age and growth analysis, opercles and otoliths were collected from lake trout, and scales were collected from kokanee. Vertical thermal profiles were collected with a Hydrolab Datasonde (Hach Environmental) at each sampling site.

Hydroacoustic surveys

To quantify the biomass of kokanee, a hydroacoustic survey was conducted during moonless nights on 30-31 August 2005, during late-summer thermal stratification when schooling behavior was minimized (Luecke and Wurtsbaugh 1993). The survey consisted of 22 transects in a zig-zag pattern (Figure 3.2). We stratified the survey into three ecologically distinct lake regions: the Stehekin River area (two transects), the remainder of Lucerne Basin (16 transects), and Wapato Basin (four transects). All transects were conducted in the pelagic portion of the lake, which was defined as areas with water depths $\geq$ 15 m and comprised > 90% of the total lake surface area. Hydroacoustic sampling was conducted from a 7-m boat with a 200-kHz echosounder (model DE 6000, Biosonics). A 6.7° split-beam transducer was mounted on a tow body facing downward at a depth of 1 m and towed at 8-10 km/h. Data were acquired using a minimum target strength threshold of -55 dB, a 0.4 ms pulse width, and a ping rate of 1 ping/s. Data were analyzed using Echoview version 4.2 software (Myriax Pty).

Kokanee density was estimated by echo counting single acoustic targets, and density was converted to an estimate of total biomass using data on body weight and lake bathymetry. The density of targets was relatively low (0-5 targets / 1,000 m^3), and no schools were observed on echograms. We assumed that all small (< 330 mm fork length), pelagic targets were kokanee, because kokanee comprised 95% of the mid-water gill net catch, and modal sizes of acoustic targets corresponded with the size distribution of kokanee. We converted target strength values to fork lengths using Love's (1971) equation and a total length to fork length relationship for kokanee (FL = 0.939 TL; Hyatt and Hubert 2000). Fork length estimates (mm) were converted to weight (W, g) using a relationship developed from kokanee sampled during this study (r^2 = 0.99, N = 93, P < 0.0001):

$$W = 0.00000402 \bullet \mathrm{FL}^{3.20} \qquad (3.1)$$

We aged kokanee scales to determine the size-at-age relationship and used size modes of hydroacoustic targets to assign targets to age classes (age 0: 30-100 mm FL; age 1: 100-200 mm FL; ages 2-4: 200-330 mm FL). The estimated body weights of individual targets were added to determine the biomass of each age class sampled in 2-m depth intervals (from 2-200 m) within each transect. Kokanee biomass density (kg / 1,000 m^3) was calculated for each interval within each transect by dividing the biomass detected by the volume acoustically sampled. These depth-specific volumetric densities were multiplied by the total volume of the depth stratum within the corresponding lake region (Kendra and Singleton 1987) and summed across all depths, and the sum was divided by the surface area of the lake region to yield the areal biomass density (kg / ha) for each transect. We calculated the mean areal biomass density of each kokanee age class in each lake region, expanded these values by the surface area of each region (Table 4 in Kendra and Singleton 1987), and summed them to estimate the total biomass. The production rate (metric tons / year) of the kokanee population was calculated using the instantaneous growth-rate method (Ney 1993, Hayes et al. 2007).

Diet analysis

We analyzed diets of lake trout for input to the bioenergetics model. Stomach contents were identified to species for prey fishes and to order and life stage for invertebrates, and the blotted wet weight of each prey type was recorded. The lengths of prey fish were measured or estimated from the lengths of diagnostic bones when possible (see Schoen and Beauchamp 2010). A subset of salmonid prey specimens (n = 21) were unidentifiable to the species level based on bone morphology and were analyzed genetically by the Molecular Genetics Facility at the University of Washington, School of Aquatic and Fishery Sciences. Prey DNA samples were extracted, amplified using polymerase chain reaction, and sequenced following the methods of Buser et al. (2009), with modifications described by Schoen and Beauchamp (2010). Phylogenetic relationships were assigned using MEGA4 software (Tamura et al. 2007).

We calculated diet proportions by weight (Chipps and Garvey 2007) for four size classes of lake trout, subdivided by season. Within these groups, diet composition differed between the two lake basins (Schoen and Beauchamp 2010) so we estimated lake-wide diet proportions as the mean of the diet proportions in each basin, weighted by the relative abundance of lake trout in each basin. We assumed that the density of each lake trout size class was proportional to the catch per unit effort (CPUE) of that size class in sinking gill nets. We scaled these estimates to the area of benthic slope zone habitat available in each basin (Lucerne Basin, 1728 ha; Wapato Basin, 1767 ha) at depths of 15-70 m typically occupied by lake trout (Hansen et al. 1995) to estimate the proportion of the lake trout population in each basin.

Lake trout size distribution, growth, and survival

We used field data to characterize the size distribution and the growth and survival rates of lake trout. Lake trout captured in gill nets ranged from 182-846 mm FL (n = 504), and the size distribution showed no obvious change between the two years of sampling (Figure 3.3). We aged the lake trout using opercles (Sharp and Bernard 1988) because sagittal otoliths did not exhibit clear annual marks. Growth in length was characterized by fitting the von Bertalanffy model parameterization of Gallucci and Quinn (1979):

$$\mathrm{FL}_t = L_\infty \left(1 - e^{-(\omega/L_\infty)t}\right) \ , \tag{3.2}$$

where FL_t is fork length (mm) at age t (years), L_∞ is the asymptotic maximum length (mm), and ω is the growth rate of young fish (mm/year), to empirical length and age data from the subset of fish that were aged (n = 188) using maximum likelihood estimation (Isely and Grabowski 2007). Fork length was converted to wet weight (W, g) using a relationship developed from lake trout sampled during this study ($r^2 = 0.92$, N = 504, P < 0.0001):

$$W = 0.00000799 \bullet \mathrm{FL}^{3.07} \tag{3.3}$$

We estimated the survival rate of lake trout using the catch curve method (Miranda and Bettoli 2007). To satisfy the assumption of stable recruitment among years, we included only the cohorts stocked in roughly equal numbers from 1990-2000 in this analysis (this assumption is addressed in the Discussion). The age frequency distribution of captured lake trout was corrected for gill net size selectivity (Hansen et al. 1997) and for inequalities in effort among mesh sizes (Ruzycki et al. 2003).

Per-capita consumption by lake trout

Per-capita consumption rates of lake trout were estimated with a bioenergetics model developed by Stewart et al. (1983), with physiological parameters modified by Luecke et al. (1999). Simulations were run for 2-16 year old fish using a daily time step, with model day 1 representing 1 May. Model inputs included annual growth (weight at age), seasonal diet composition, the water temperature experienced by the consumer ("thermal experience"), the energy densities of prey organisms, and energy losses due to spawning.

Growth inputs for lake trout were generated from the age-length and length-weight relationships derived above (Table 3.1). Seasonal diet composition was determined from stomach content data (Table 3.2). For simplicity, prey were grouped into 10 categories for analysis. The seasonal thermal experience of each lake trout size class was estimated using thermal profiles and depth distribution patterns (Table 3.2; Beauchamp et al. 2007). Thermal experiences were calculated separately for each lake basin and values were pooled following the method used for diet composition. We used prey energy density values from the literature (Table 3.3) and assumed that prey indigestibility was 3% for fishes and 17% for invertebrates (Beauchamp et al. 2007). We simulated spawning losses by reducing body mass by 6.8% on 15 November for lake trout > 400 mm in fork length (Stewart et al. 1983; E. R. S. unpubl. data).

To compare consumption rates among seasons and size classes of lake trout during the focal 2004-2006 period, we also took the observed age structure into account. Daily estimates of consumption by individual lake trout were expanded into aggregate seasonal and annual consumption estimates for an age-structured population unit of 1,000 lake trout (age 2-16 years), with the proportion of individuals at each age determined by the observed survival rate (Table 3.1). The number of juvenile lake trout consumed was estimated by dividing the biomass consumed by the geometric mean weights of 1- and 2-year-old lake trout as estimated by the growth model.

Lake trout population dynamics

We simulated trends in lake trout abundance and size structure with a deterministic, age-structured population model. The numbers of lake trout N_{jt} at age j in year t were projected forward to indicate the numbers $N_{j+1,t+1}$ at age $j + 1$, in year $t + 1$, according to the instantaneous annual mortality rate Z (Hilborn and Walters 1992):

$$N_{j+1,\ t+1} = N_{jt}\, e^{-Z} \tag{3.4}$$

Age-1 recruits were added to the population through stocking and natural reproduction. Natural reproductive rates were unknown, so we bracketed this uncertainty by simulating three scenarios representing the range of possibilities: no reproduction, “replacement” (a reproductive rate sufficient to offset mortality losses over the long term), and a rapid reproductive rate derived from literature values. For each scenario, the numbers of age-0 fish stocked in each year were multiplied by the survival rate S to estimate the numbers surviving to age 1 in the following year. For the replacement and rapid reproduction scenarios, spawning also contributed to recruitment. The numbers of naturally spawned age-1 recruits $N_{1,\ t+1}$ in year $t + 1$ were estimated as:

$$N_{1,\ t+1} = F_t\, S_0 \tag{3.5}$$

where F_t is the population fecundity (total number of eggs) produced in the previous year t and S_0 is egg-to-age-1 survival. We used an estimate of individual fecundity f (eggs / mature female) reported for an introduced, low-density lake trout population (Ruzycki et al. 2003):

$$f = 0.03\ W^{1.48} \tag{3.6}$$

where W is female body weight (g). We calculated F in each year as the sum of f for all females in each reproductively mature cohort (age ≥ 7 years), assuming a sex ratio of 1:1. For the rapid reproduction scenario, we used an S_0 value of 0.0043 estimated for low-density lake trout populations (Shuter et al. 1998). For the replacement scenario, we iteratively adjusted S_0 downward until the projected long-term annual population growth rate λ equaled 1, meaning that natural reproduction was exactly sufficient to balance mortality over time.

We simulated the numbers of lake trout at each age for ages 1-30, in each year from 1980-2015, under each scenario. Although the population was young during our 2004-2006 sampling period (oldest fish aged = 19 years), we assumed that older age classes would be represented in later years as the population matured, according to the observed mortality rate. To predict how population trends would influence lake trout harvest rates, we estimated the numbers of lake trout vulnerable to harvest by calculating the length at 50% vulnerability to harvest, L_c, for lake trout fisheries free of size restrictions on harvest (Shuter et al. 1998) as:

$$L_c = 0.853\ \omega^{0.421}\ L_\infty^{0.669}, \tag{3.7}$$

assuming a knife-edged transition to full vulnerability. We presented the population model results as the total population size (including fish ≥ 1 years old), the numbers of lake trout vulnerable to harvest (age ≥ 5 years), and the biomass of large piscivorous lake trout (age ≥ 9 years). We intended these simulations to illustrate the potential range of population trajectories given the known demographic constraints, rather than to predict the true values exactly.

Lake trout harvest trends

We analyzed harvest records from the lake trout fishery to characterize trends in catch per unit effort (CPUE). The lake trout fishery was confined to the Wapato Basin and a small adjacent portion of the Lucerne Basin. Four of the five primary charter guides on Lake Chelan provided harvest records for a subset of their trips during 2004-2007. Harvest records consisted of standardized questionnaire forms completed by guided anglers indicating the duration of the charter (full day or half day) and the numbers of each fish species harvested. Harvest records with usable data were collected on 445 trips, including 53% of all trips by the participating guides during 2005-2007, the years for which the total numbers of trips were known, and records were well distributed across seasons and years. We calculated the annual mean CPUE, with effort defined as the number of full-day equivalent charters per year. Mean harvest on half-day trips was 57.7% of harvest on full-day trips, so we counted half-day trips as 0.577 days of effort.

Predation impacts of lake trout on kokanee

To estimate the impact of lake trout predation on kokanee in 2005, the year of the hydroacoustics survey, we expanded the per-capita kokanee consumption of each lake trout age class by the abundance of that age during 2005, as estimated by the population model. We compared this population-level consumption estimate to the estimates of kokanee biomass and production from the hydroacoustics survey. We restricted this comparison to the biomass and production of kokanee aged 1 and greater because lake trout diets contained almost no age-0 kokanee.

Finally, to illustrate the likely consequences of lake trout population dynamics for kokanee, we simulated the trend in lake trout predation pressure on kokanee over time. We expanded the annual per-capita kokanee consumption of each lake trout age class by the abundance of that age during each year 1980-2015, as estimated by the population model. We interpreted this projected trend as a relative index of predation pressure (i.e., lake trout demand for kokanee prey) because predicting actual consumption rates would require yearly diet composition data, which were only available for 2004-2006.

Statistical analyses were performed using R version 2.10.0 (Ihaka and Gentleman 1996).

RESULTS

Kokanee biomass and production

Lake Chelan supported a kokanee biomass of approximately 43.1 metric tons during August 2005, based on a quantitative hydroacoustic survey of the lake. Age-0 kokanee accounted for less than 2% of this biomass (823 ± 67 kg; mean ± 1 SE). The biomass of age-1 kokanee represented 12% of the total biomass (5.29 ± 532 metric tons). Kokanee aged 2 and older represented 86% of the total (37.0 ± 4.0 metric tons). Densities of all kokanee age classes were greatest near the Stehekin River, with lower densities distributed throughout the rest of the lake (Table 3.4). Production by the kokanee population was an estimated 32.3 metric tons / year, including 22.2 metric tons / year by kokanee age 1 and greater.

Lake trout diet, growth, and survival

The diet of lake trout shifted from *Mysis* to fish as lake trout grew, and salmonid prey were particularly important for the largest lake trout (Table 3.2). *Mysis* represented 73% of the annual diet of the smallest lake trout (180-450 mm fork length), but only 20% of the diet of the largest lake trout (551-850 mm FL). All size classes of lake trout consumed substantial proportions of cyprinids during May, before thermal stratification forced lake trout into deep water, which spatially segregated them from these prey (Table 3.2). Lake trout began consuming kokanee and other salmonids after exceeding 450 mm FL, and kokanee comprised 30% of the annual diet of the largest lake trout. Kokanee were most prevalent in diets of the largest lake trout during February (91% of diet; Table 3.2). Over ninety percent of kokanee in lake trout diets were age 1 or older (> 100 mm FL; Figure 3.4). The largest lake trout also consumed juvenile lake trout (ages 1-2), mostly during August (Table 3.2). The lengths of all ingested prey fishes were ≤ 41% of lake trout lengths (n = 62; Figure 3.4).

The growth rate of young lake trout ω was 0.186 mm / year, and the asymptotic maximum fork length L_∞ was 671 mm. The instantaneous annual mortality rate *Z* for lake trout was 0.2843 (*n* = 123 fish ages 7-12 years, $r^2 = 0.55$). This corresponded to an annual survival rate *S* of 75%.

Age-structured consumption rates of lake trout

To compare consumption rates among size classes of lake trout and seasons during the focal 2004-2006 period, we expanded per-capita consumption rates according to the observed age structure. An age-structured population unit of 1,000 lake trout (ages 2-16) consumed an estimated 3,419 kg of prey annually, including 2,079 kg of *Mysis* and 1,264 kg of fish (Figure 3.5). Less than 30% of the fish biomass consumed was salmonid prey, including 177 kg of kokanee, 164 kg of lake trout, 1.5 kg of Chinook salmon, and 1.7 kg of unidentified salmonids. The biomass of juvenile lake trout consumed represented approximately 4,038 age-1 or 979 age-2 lake trout individuals consumed annually per 1,000 adult lake trout if predation were focused solely on those respective age classes. The smallest lake trout size class was responsible for 52% of total prey consumption, but only 33% of fish consumption. The largest lake trout size class

(551-850 mm FL) was responsible for 83% of predation on kokanee, despite representing only 13% of the population numerically.

Lake trout showed strong seasonal patterns in prey consumption (Figure 3.5). Consumption rates were generally greatest during July-December, when lake trout experienced higher water temperatures (Table 3.2). Seasonal changes in predation on different prey taxa mirrored seasonal diet composition patterns, with lake trout preying heavily on kokanee during January-March, cyprinids during April-June, and smaller lake trout during July-September.

Lake trout population dynamics and harvest trends

The simulated trend in total lake trout abundance declined under the no reproduction scenario but increased under the replacement and rapid reproduction scenarios following the 2004-2006 sampling period (Figure 3.6A). While lake trout were originally introduced to the lake during 1980-1982, these early cohorts and their offspring were far outnumbered by the cohorts stocked during the 1990s, under all reproductive scenarios. After initial stocking in 1980-1982, the simulated lake trout population ($\geq$ age 1) remained low during the 1980s. The simulated population grew substantially with heavy stocking during the 1990s, and population growth slowed in all scenarios after stocking ceased. Under the no reproduction scenario, abundance reached a maximum in 2001 and then declined ($\lambda = 0.75$). Under the replacement scenario, lake trout numbers declined from 2001-2005, then increased and oscillated towards equilibrium. Under the rapid reproduction scenario, population growth slowed from 2001-2004 and returned to rapid annual growth ($\lambda > 1.1$) in 2005.

The simulated abundance of lake trout vulnerable to harvest declined under the no reproduction and replacement scenarios but increased under the rapid reproduction scenario after the 2004-2006 sampling period (Figure 3.6B). These trends followed the trends in total abundance after a developmental lag as successive cohorts became vulnerable to anglers. The predicted size of 50% vulnerability L_c was 412 mm FL, corresponding to an age of 5.1 years. The numbers of lake trout vulnerable to harvest increased substantially from 1994 to 2005 under all scenarios, but the trajectories diverged after the last stocked cohort became vulnerable: harvestable lake trout increased under the rapid reproduction scenario, but declined under both the replacement and no-reproduction scenarios (Figure 3.6B). Based on harvest records, lake trout CPUE by the charter fishery declined from 12.6 ± 0.6 (mean ± 1 SE) fish per full-day charter in 2004 to 8.7 ± 0.5 in 2005, 8.8 ± 0.5 in 2006, and 7.2 ± 0.3 in 2007 (Figure 3.6B).

The simulated biomass of large, highly piscivorous lake trout (FL > 550 mm; age ≥ 9.2 years) expanded rapidly under all reproductive scenarios beginning in 1999 and continued to grow after the 2004-2006 sampling period as successive stocked cohorts grew into the size range of effective kokanee predators (Figure 3.6C). From 2004 to 2009, the biomass of large lake trout increased 70% under the no reproduction scenario, 201% under the replacement scenario, and 296% under the rapid reproduction scenario. After 2009, the simulated biomass of large lake trout then began to decline under the no reproduction and replacement scenarios but continued to increase under the rapid reproduction scenario.

Predation impacts of lake trout on kokanee

Lake trout consumed a large proportion of the standing stock biomass and production of the kokanee population in 2005. The population-level lake trout consumption of kokanee ranged from an estimated 33.9 metric tons (no reproduction scenario) to 36.3 metric tons (replacement scenario, and 46.8 metric tons (rapid reproduction scenario). Consumption estimates exceeded (153-211%) the estimated annual production rate of age-1 and older kokanee and represented 53-73% of the production plus the standing stock biomass of these kokanee in 2005.

The index of simulated lake trout predation pressure on kokanee generally mirrored the trend of simulated large lake trout biomass (Figure 3.6C,D). Under all scenarios, simulated predation pressure increased roughly 6-fold from 1998 to 2006. Under the no reproduction scenario, simulated predation pressure reached a plateau during 2006-2008 and began to decline substantially in 2009. Under the replacement scenario, simulated predation pressure rose to a peak in 2009 and declined for the following six years. Under the rapid reproduction scenario, simulated predation pressure increased continuously. All three scenarios predicted that predation pressure was greater during the kokanee decline (2005-2009) than in any previous year (Figure 3.6D).

DISCUSSION

Impacts of lake trout predation on kokanee

Lake trout predation likely contributed substantially to the 88% decline in kokanee escapement between 2005 and 2009. In 2005, when kokanee were acoustically surveyed, our simulations indicated that lake trout consumed a large proportion of kokanee production and biomass, and predation pressure reached its greatest level since lake trout were introduced to the lake. Predation pressure was projected to remain at or above this level through at least 2009. Despite abundance and harvest trends that suggested a synchronous rise and fall of predator and prey populations, this analysis suggested that predation caused strong and growing impacts on the declining prey population.

The bioenergetics analysis revealed that lake trout predation imposed strong impacts on the kokanee population in 2005. Annual lake trout consumption of kokanee exceeded the annual production of age-1 and older kokanee and claimed more than half the sum of annual production and standing stock biomass of these kokanee cohorts. This predation rate was likely unsustainable (Ney 1990, Beauchamp et al. 2007), suggesting that predation contributed to sharp declines in kokanee escapement beginning in 2006. Although they represented less than 15% of the population, the largest size class of lake trout (>550 mm FL) was responsible for most (83%) predation on kokanee during the focal sampling period of 2004-2006. This was consistent with studies from other lakes finding that the largest lake trout consume more salmonid prey than smaller lake trout, although they may be relatively few in number (Johnson and Martinez 2000, Ruzycki et al. 2003, Beauchamp et al. 2007). The full impacts of lake trout were likely even greater because we did not estimate non-consumptive effects, which may have reduced kokanee productivity through behavioral changes (Werner and Peacor 2003, Hardiman et al. 2004).

The trends and timing of lake trout population dynamics were consistent with strong predation impacts on kokanee during the 2005-2009 population decline. The population model predicted a 70-296% increase in the biomass of the largest size class of lake trout from 2004-2009, driving predation pressure on kokanee to all-time peak levels. The trends in large lake trout biomass and predation pressure were predicted to lag behind the trend in lake trout harvest by roughly four years. These trends were consequences of the pulsed stocking history of lake trout, observed growth and mortality rates, and three scenarios representing the range of potential reproduction rates. Until 2009, the projected trends were similar for all three reproductive scenarios because the largest lake trout size class was dominated by stocked fish. After 2009, the trajectories of the scenarios diverged, indicating that the biomass of large lake trout and predation pressure could either continue to increase, stabilize, or decrease, depending on natural reproductive rates. For this reason, quantifying the natural recruitment of lake trout should become a critical priority.

Although the population analysis depended on several important assumptions, we limited the interpretation of model results to key conclusions that were strongly supported by data. We primarily used model output to project the broad trends and timing of population dynamics and predation pressure, and only used numerical estimates of abundance in further analyses for the 2005 model year, when field data were collected (e.g., diet composition and thermal experience). The mortality analysis likely produced conservative estimates of both the predatory inertia of lake trout and impacts on kokanee. Although catch curve analysis relies on the assumption of equal recruitment among years, stocking rates actually increased slightly (mean annual increase = 4.3%) during the 1993-1999 period corresponding to the cohorts in the analysis. Natural reproduction also likely added a small number of recruits to the 1998 and 1999 cohorts. This inflated the relative abundance of young fish in the catch and led us to overestimate mortality slightly. Therefore, the model likely underestimated the demographic importance of older, more piscivorous lake trout in the simulations, resulting in conservative estimates of predation on salmonids and the time lag before each cohort achieved its maximum predatory impact.

Unstable predator age-structure produces unexpected dynamics

The no-reproduction and replacement scenarios of the population model illustrated a counterintuitive possibility: the numbers of harvestable lake trout may have declined during the mid-to-late 2000s while consumption of kokanee actually rose. This was possible because of high predatory inertia combined with an unstable age structure due to the irregular stocking history. The 11 years of heavy stocking produced a "baby boom" effect, with a pulse of strong, aging cohorts dominating the demographics of the population. Each cohort became vulnerable to harvest roughly four years before achieving full piscivory, causing the harvestable population to peak and begin declining while predation pressure continued to rise. An important consequence of this prediction is that the latent strong predation interaction was initially concealed from researchers and managers because harvest was more easily monitored than predation, and lake trout harvest varied synchronously with kokanee escapement.

Consistent with this prediction of the population model, two lines of empirical evidence suggest that the numbers of harvestable lake trout in fact did decline during the mid-to-late 2000s. First, catch per unit effort of the charter fishery declined by over 40% from 2004 to 2007. Trends in CPUE for lake trout fisheries are often hyperstable, biased in a positive direction relative to actual abundance trends, because angler expertise generally improves over time (Shuter et al. 1998). Thus, the harvestable population may have actually declined faster than suggested by the catch rate. Informal reports suggested that catch rates continued to decline until 2008, before increasing during 2009-2011 (A. Jones, personal communication). Second, a comparison of gill net catch curves suggested that lake trout < 400 mm FL were underrepresented by roughly 50% in the Lake Chelan population relative to an established, self-sustaining population sampled with similar methods in Lake Tahoe, California-Nevada (E. R. Schoen, unpublished; Thiede 1997). This pattern suggests that natural reproduction in Lake Chelan did not produce as many recruits during the early 2000s as necessary to replace the cohorts stocked during the 1990s. These weaker cohorts would be expected to reach harvestable size during 2005-2009. The bioenergetics analysis revealed a substantial rate of cannibalism by lake trout, which can limit recruitment in fluctuating, age-structured predator populations (Wissinger et al. 2010).

Of the three scenarios bracketing the range of potential lake trout reproductive rates, the replacement scenario appeared to match observed trends best. Both the no-reproduction and replacement scenarios predicted the observed decline of harvestable lake trout during the mid-to-late 2000s, as noted above. However, lake trout were observed spawning in Lake Chelan as early as 2000 (Duke Engineering and Services 2000), and we captured a number of fish that were too young to have been stocked. So we considered the no-reproduction scenario to be an extreme lower bound, rather than a likely outcome. Conversely, the constantly increasing trend in harvestable lake trout numbers predicted by the rapid reproduction scenario did not fit the observed decline in catch rates. This scenario used the fecundity rate reported for a rapidly expanding lake trout population in Yellowstone Lake (Ruzycki et al. 2003), which was near the low end of a range of estimates of lake trout fecundity from other low-density, fast growing populations (Shuter et al. 1998). The rapid reproduction scenario predicted a mean annual population growth rate (λ) of 1.13 after stocking ceased, well below a value recently reported for lake trout in Lake Pend Oreille ($\lambda = 1.63$; Hansen et al. 2008). Therefore, lake trout in Lake Chelan appeared to reproduce at a slower rate than the fastest growing populations reported in other studies, but either moderate positive or negative population growth was possible.

Disentangling predation from confounding factors

Aside from predation by lake trout, other factors may also have contributed to the kokanee decline. Floods in key spawning streams during October 2003 probably limited kokanee returns during 2006 and 2007 (Keesee and Keller 2012). A one-year suspension of kokanee stocking in 2006 may also have contributed to low escapements in 2008 and 2009; however, hatchery kokanee fry are heavily consumed by lake trout immediately after stocking in Lake Chelan (E.R.S., unpublished), and it is unclear whether hatchery fish contribute to the spawning population (Duke Engineering and Services 2000). Brown (1984) estimated that harvest reduced kokanee escapement by < 5% in 1982; if harvest remained at this order of magnitude it was unlikely to cause the recent decline. We did not estimate kokanee harvest in this study because many unguided anglers participated in the kokanee fishery, and our data only covered the charter fleet. It is possible that harvest limits kokanee in years of low abundance, especially if compensatory growth increases body size and vulnerability to harvest (Martinez and Wiltzius 1995, Rieman and Maiolie 1995). Previous studies indicated that kokanee were not strongly limited by food supply or competition with *Mysis* (Schoen 2007), or by predation from other piscivores such as northern pikeminnow or Chinook salmon (Schoen and Beauchamp 2010) during the 2005-2009 decline.

Disentangling the impacts of high predatory inertia and confounding factors is an important step towards prioritizing limited resources for conservation. The complementary analyses presented in this study offer a useful approach for overcoming these challenges. While population dynamics analysis alone predicted increasing predation pressure, this was insufficient to determine whether predation contributed to the kokanee decline because of confounding events and the past volatility of kokanee escapement. Bioenergetics analysis predicted that the absolute impacts of predation were strong during a critical snapshot in time, at the beginning of the decline, but did not provide any long-term context or predictive power outside of this period. Conclusions based on the bioenergetics results alone would have been particularly short-lived for this system because of the unstable age distribution of predators. Together, this combined approach revealed strong and growing predation impacts during the kokanee decline.

Could prey switching reduce impacts on kokanee?

We interpreted the rapidly increasing biomass of large lake trout during 1999-2009 as evidence of increasing predation on kokanee. However, lake trout are opportunistic predators and may instead have switched to other prey as the kokanee population declined from its peak abundance after the 2004-2006 diet-sampling period. Evidence for such diet switching in other systems is limited. Lake trout in Lake Tahoe have shown great interannual variability in the proportion of fish in the diet (Richards et al. 1991), and consumed more kokanee in years when kokanee densities were greater (Thiede 1997). However, lake trout in the Great Lakes sustained high consumption rates across an 100-fold range of prey fish densities, suggesting the capability to severely reduce fish populations without switching to alternative prey (Eby et al. 1995). Similarly, lake trout diets in Flathead Lake and bull trout and rainbow trout diets in Lake Pend Oreille continued to be dominated by kokanee despite 80-90% declines in kokanee density in each lake (Clarke et al. 2005, Beauchamp et al. 2007). Thus, while prey switching may have somewhat reduced lake trout per-capita predation on kokanee, this effect was uncertain and very unlikely to compensate for the substantial increase in large lake trout biomass between 1999 and 2009. In the absence of long-term diet data (e.g., Eby et al. 1995, Scheuerell et al. 2005), piscivore foraging models (Breck 1993, Beauchamp et al. 1999, Mazur and Beauchamp 2006) could predict whether a lake trout prey-switching threshold is likely in this system by comparing the expected energy gains associated with alternative foraging strategies.

Management implications

Aside from its predation impacts, the lake trout population in Lake Chelan has become a valuable resource that supports a popular fishery. If management goals include sustaining this fishery, then unchecked population growth is undesirable because the body size of lake trout would likely decline dramatically without abundant kokanee prey (Bowles et al. 1991, Stafford et al. 2002, Martinez et al. 2009). We recommend assessment of natural lake trout recruitment, which will strongly influence future predation rates as the pulse of stocked cohorts is replaced. If the population is growing, more than a decade after stocking ceased, then lake trout reduction measures may be necessary to sustain kokanee, restore native westslope cutthroat trout, or maintain the trophy value of the lake trout fishery. Alternatively, if reproduction is slower than past stocking rates, then the lake trout catch rate may continue to decline before stabilizing at a reduced level as the strong stocked cohorts are eventually lost from the population.

When introduced predatory game fishes support valuable fisheries, this presents a challenging management dilemma. Allowing these populations to expand risks uncertain but potentially serious harm to prey and ecosystem processes, while piscivore reduction programs impose certain monetary and social costs on established recreational fisheries (Eby et al. 2006, Martinez et al. 2009). Given these incentives, indecision is a tempting choice for managers (Walters and Martell 2004: 10), who may choose to wait and see how severe the predation impacts become. However, this approach carries substantial risk, given the many examples of the ecological impacts of non-native lake trout and the time lags associated with detecting and successfully reversing their impacts. Due to unanticipated surges in lake trout density and high predatory inertia, kokanee were extirpated from Flathead Lake, Montana and Priest Lake, Idaho before managers could act (Beattie and Clancey 1991, Bowles et al. 1991, Ellis et al. 2011). While more gradual prey declines allowed time for predator suppression in Yellowstone Lake, Wyoming and Lake Pend Oreille, Idaho, several years elapsed before these programs were developed and implemented (Bigelow et al. 2003, Hansen et al. 2008, Martinez et al. 2009). While less intensive precautionary steps such as cessation of stocking and removal of harvest limits are common (Martinez et al. 2009), our results demonstrate that these can be insufficient for reducing predation pressure on a 5-10 year time-scale, even if reproductive rates are moderate or low.

Understanding the processes that control the strength and timing of impacts by long-lived predators is an important step toward effectively managing affected ecosystems. Past coexistence or synchronized abundance trends of predators and prey should not be interpreted as evidence of a weak predation interaction without careful consideration of predator demography and dietary ontogeny. Managers should consider implementing monitoring programs to allow early detection of changing impacts, such as regular assessment of predator recruitment and in-lake monitoring of prey fishes with hydroacoustics or gill nets. Advance knowledge of predator demographics, distribution, and spawning locations may facilitate rapid and effective removal programs if these become necessary (Ruzycki et al. 2003, Hansen et al. 2010, Dux et al. 2011). Forward-looking field sampling and modeling analyses are clearly advantageous if managers attempt to maintain introduced piscivores in long-term "balance" with their prey by detecting and reversing incipient changes in predation impacts.

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REFERENCES

Adare, K. I. and D. C. Lasenby. 1994. Seasonal changes in the total lipid content of the opossum shrimp, *Mysis relicta* (Malacostraca, Mysidacea). Canadian Journal of Fisheries and Aquatic Sciences 51:1935-1941.

Beattie, W. D. and P. T. Clancey. 1991. Effects of *Mysis relicta* on the zooplankton community and kokanee population of Flathead Lake, Montana. Pages 39-48 *in* T. P. Nesler and E. P. Bergersen, editors. Mysids in fisheries: Hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, Maryland.

Beauchamp, D. A., C. M. Baldwin, J. L. Vogel, and C. P. Gubala. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences 56 Suppl. 1:128-139.

Beauchamp, D. A., D. Parrish, and R. A. Whaley. 2009. Salmonids/coldwater species in large standing waters. Pages 97-117 *in* S. Bonar, D. W. Willis, and W. A. Hubert, editors. Standard Sampling Methods for North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

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.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Bigelow, P., T. Koel, D. Mahony, B. Ertel, B. Rowdon, and S. Olliff. 2003. Protection of native Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park, Wyoming. Technical report NPS/NRWRD/NRTR-2003/314. National Park Service, Water Resources Division, Fort Collins, Colorado.

Bowles, E. C., B. E. Rieman, G. R. Mauser, and D. H. Bennett. 1991. Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. American Fisheries Society Symposium 9:65-74.

Breck, J. E. 1993. Foraging theory and piscivorous fish: Are forage fish just big zooplankton? Transactions of the American Fisheries Society 122:902-911.

Brown, L. G. 1984. Lake Chelan fishery investigations. Chelan County Public Utility District No. 1 and Washington Department of Game, Olympia.

Buser, T., N. Davis, I. Jiménez-Hidalgo, and L. Hauser. 2009. Genetic techniques provide evidence of Chinook salmon feeding on walleye pollock offal. North Pacific Anadromous Fish Commission Bulletin 5:225-229.

Bystrom, P., J. Karlsson, P. Nilsson, T. Van Kooten, J. Ask, and F. Olofsson. 2007. Substitution of top predators: effects of pike invasion in a subarctic lake. Freshwater Biology 52:1271-1280.

Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecological Monographs 71:163-186.

Chelan County Public Utility District. 2007. Lake Chelan fishery plan. Wenatchee, Washington.

Chipps, S. R. and J. E. Garvey. 2007. Quantitative assessment of food habits and feeding patterns. Pages 473-514 *in* C. S. Guy and M. L. Brown, editors. Analysis and

Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Chipps, S. R. and D. H. Wahl. 2008. Bioenergetics modeling in the 21st century: Reviewing new insights and revisiting old constraints. Transactions of the American Fisheries Society 137:298-313.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267-277.

Dextrase, A. and N. Mandrak. 2006. Impacts of alien invasive species on freshwater fauna at risk in Canada. Biological Invasions 8:13-24.

Duke Engineering and Services. 2000. Lake Chelan Fisheries Investigation, Lake Chelan Hydroelectric Project No. 637., Prepared for Chelan County Public Utility District No. 1, Bellingham, Washington.

Dux, A. M., C. S. Guy, and W. A. Fredenberg. 2011. Spatiotemporal distribution and population characteristics of a nonnative lake trout population, with implications for suppression. North American Journal of Fisheries Management 31:187-196.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends In Ecology & Evolution 21:576-584.

Eby, L. A., L. G. Rudstam, and J. F. Kitchell. 1995. Predator responses to prey population dynamics: An empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1564-1571.

Ellis, B., J. Stanford, D. Goodman, C. Stafford, D. Gustafson, D. Beauchamp, D. Chess, J. Craft, M. Deleray, and B. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108:1070-1075.

Gallucci, V. F. and T. J. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. Transactions of the American Fisheries Society 108:14-25.

Hagen, J. E. 1997. An Evaluation of a Trout Fishery Enhancement Program in Lake Chelan. Master's thesis. University of Washington, Seattle.

Hansen, M., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator–prey dynamics in Lake Pend Oreille, Idaho, USA. Hydrobiologia 650:85-100.

Hansen, M. J., N. J. Horner, M. Liter, M. P. Peterson, and M. A. Maiolic. 2008. Dynamics of an increasing lake trout population in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management 28:1160-1171.

Hansen, M. J., C. P. Madenjian, J. H. Selgeby, and T. E. Helser. 1997. Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 54:2483-2490.

Hansen, M. J., J. W. Peck, R. G. Schorfhaar, J. H. Selgeby, D. R. Schreiner, S. T. Schram, B. L. Swanson, W. R. MacCallum, M. K. Burnham-Curtis, and G. L. Curtis. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. Journal of Great Lakes Research 21:152-175.

Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society 133:1366-1378.

Hayes, D., J. Bence, T. Kwak, and B. Thompson. 2007. Abundance, biomass, and production. Pages 327-374 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

He, X. and J. Kitchell. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. Transactions of the American Fisheries Society 119:825-835.

Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Kluwer Academic Publishers, Norwell, Massachussetts.

Hyatt, M. H. and W. A. Hubert. 2000. Proposed standard-weight (W_s) equations for kokanee, golden trout and bull trout. Journal of Freshwater Ecology 15:559-563.

Ihaka, R. and R. Gentleman. 1996. R: A language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299-314.

Isely, J. and T. Grabowski. 2007. Age and Growth. Pages 187–228 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Johnson, B. M. and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

Johnson, T. B., D. M. Mason, S. T. Schram, and J. F. Kitchell. 1999. Ontogenetic and seasonal patterns in the energy content of piscivorous fishes in Lake Superior. Journal of Great Lakes Research 25:275-281.

Keesee, B. G. and L. M. Keller. 2012. Lake Chelan Kokanee Spawning Ground Surveys 2011. Final Report., Chelan County Public Utility District, Wenatchee, WA.

Kendra, W. and L. R. Singleton. 1987. Morphometry of Lake Chelan. Water Quality Investigations Section, Washington State Dept. of Ecology, Olympia.

Lasenby, D. C. 1971. The ecology of *Mysis relicta* in an arctic and a temperate lake. Doctoral dissertation. University of Toronto, Toronto.

Love, R. 1971. Dorsal aspect target strength of an individual fish. The Journal of the Acoustical Society of America 49:816.

Luecke, C., T. Edwards, M. Wengert, S. Brayton, and R. Schneidervin. 1994. Simulated changes in lake trout yield, trophies, and forage consumption under various slot limits. North American Journal of Fisheries Management 14:14-21.

Luecke, C., M. W. Wengert, and R. W. Schneidervin. 1999. Comparing results of a spatially explicit growth model with changes in the length-weight relationship of lake trout (*Salvelinus namaycush*) in Flaming Gorge Reservoir. Canadian Journal of Fisheries and Aquatic Sciences 56:162-169.

Luecke, C. and W. A. Wurtsbaugh. 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. Transactions of the American Fisheries Society 122:112-120.

Martinez, P., P. Bigelow, M. Deleray, W. Fredenberg, B. Hansen, N. Horner, S. Lehr, R. Schneidervin, S. Tolentino, and A. Viola. 2009. Western lake trout woes. Fisheries 34:424-442.

Martinez, P. J. and W. J. Wiltzius. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management 15:220-228.

Mazur, M. M. 2004. Linking visual foraging with temporal prey distributions to model trophic interactions in Lake Washington. Doctoral dissertation. University of Washington, Seattle.

Mazur, M. M. and D. A. Beauchamp. 2006. Linking piscivory to spatial-temporal distributions of pelagic prey fishes with a visual foraging model. Journal of Fish Biology 69:151-175.

McMahon, T. E. and D. H. Bennett. 1996. Walleye and northern pike: Boost or bane to Northwest fisheries? Fisheries 21:6-13.

Miranda, L. E. and P. W. Bettoli. 2007. Mortality. Pages 229-277 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Neilson, J. D. and G. H. Geen. 1981. Enumeration of spawning salmon from spawner residence time and aerial counts. Transactions of the American Fisheries Society 110:554-556.

Ney, J. J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. Reviews In Aquatic Sciences 2:55-81.

Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122:736-748.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure - the 3rd Tansley lecture. Journal of Animal Ecology 49:667-685.

Patankar, R., F. A. von Hippel, and M. A. Bell. 2006. Extinction of a weakly armoured threespine stickleback (*Gasterosteus aculeatus*) population in Prator Lake, Alaska. Ecology of Freshwater Fish 15:482-487.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416-2425.

Peven, C. M. 1989. Lake Chelan Spawning Ground Surveys - 1989. Chelan County Public Utility District, Wenatchee, WA.

Peven, C. M. 1990. Lake Chelan Spawning Ground Surveys - 1990. Chelan County Public Utility District, Wenatchee, WA.

Rahel, F. J. and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521-533.

Richards, R., C. Goldman, E. Byron, and C. Levitan. 1991. The mysids and lake trout of Lake Tahoe: A 25-year history of changes in the fertility, plankton, and fishery of an alpine lake. Pages 30-38 *in* T. P. Nesler and E. P. Bergersen, editors. Mysids in fisheries: Hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, Maryland.

Rieman, B. E. and M. A. Maiolie. 1995. Kokanee population density and resulting fisheries. North American Journal of Fisheries Management 15:229-237.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Scheuerell, J. M., D. E. Schindler, M. D. Scheuerell, K. L. Fresh, T. H. Sibley, A. H. Litt, and J. H. Shepherd. 2005. Temporal dynamics in foraging behavior of a pelagic predator. Canadian Journal of Fisheries and Aquatic Sciences 62:2494-2501.

Schindler, D. E., J. F. Kitchell, and R. Ogutu-Ohwayo. 1998. Ecological consequences of alternative gill net fisheries for Nile perch in Lake Victoria. Conservation Biology 12:56-64.

Schindler, D. W. 1998. Replication versus realism: The need for ecosystem-scale experiments. Ecosystems 1:323-334.

Schoen, E. R. 2007. Pelagic trophic interactions in contrasting basins of Lake Chelan. Master's thesis. University of Washington, Seattle.

Schoen, E. R. and D. A. Beauchamp. 2010. Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management. Washington Cooperative Fish and Wildlife Research Unit, US Geological Survey, University of Washington, Seattle.

Sharma, S., D. A. Jackson, and C. K. Minns. 2009. Quantifying the potential effects of climate change and the invasion of smallmouth bass on native lake trout populations across Canadian lakes. Ecography 32:517-525.

Sharp, D. and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management 8:367-372.

Shuter, B. J., M. L. Jones, R. M. Korver, and N. P. Lester. 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55:2161-2177.

Stafford, C. P., J. A. Stanford, F. R. Hauer, and E. B. Brothers. 2002. Changes in lake trout growth associated with *Mysis relicta* establishment: A retrospective analysis using otoliths. Transactions of the American Fisheries Society 131:994-1003.

Stenseth, N., W. Falck, O. Bjørnstad, and C. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx.

Proceedings of the National Academy of Sciences of the United States of America 94:5147.

Stewart, D. J. and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Canadian Journal of Fisheries and Aquatic Sciences 48:909-922.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110:751-763.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout (*Salvelinus namaycush*): application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681-698.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24:1596-1599.

Thiede, G. P. 1997. Impact of lake trout predation on prey populations in Lake Tahoe: a bioenergetics assessment. Master's thesis. Utah State University, Logan.

Truscott, K. B. and C. M. Peven. 1988. Lake Chelan Spawning Ground Surveys, 1988. Chelan County Public Utility District, Wenatchee, WA.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6:274-288.

Walters, C. and S. Martell. 2004. Fisheries Ecology and Management. Princeton University Press, Princeton, New Jersey.

Ware, D. M. and R. E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science 308:1280-1284.

Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.

White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. Diversity and Distributions 12:443-455.

Wissinger, S. A., H. H. Whiteman, M. Denoël, M. L. Mumford, and C. B. Aubee. 2010. Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations. Ecology 91:549-559.

Worm, B. and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84:162-173.

Wydoski, R. S. and R. R. Whitney. 2003. Inland fishes of Washington. 2nd edition. University of Washington Press, Seattle.

TABLES

Table 3.1. Growth, size class, age structure, and proportion of physiological maximum consumption rate ($C_{\max}$) values used for bioenergetics simulations of lake trout.

Age[a] (years)	Wet weight (g)	Size class[b] (FL, mm)	Age structure[c]	Proportion of $C_{\max}$
2	103	180-450	251.0	0.80
3	275	180-450	188.9	0.76
4	515	180-450	142.1	0.72
5	798	180-450	107.0	0.72
6	1100	451-500	80.5	0.65
7	1404	501-550	60.6	0.61
8	1696	501-550	45.6	0.61
9	1966	551-850	34.3	0.45
10	2212	551-850	25.8	0.43
11	2432	551-850	19.4	0.43
12	2625	551-850	14.6	0.42
13	2792	551-850	11.0	0.42
14	2937	551-850	8.3	0.41

15	3061	551-850	6.2	0.41
16	3167	551-850	4.7	0.41
17	3256	551-850		

[a] Consumption was estimated for lake trout growing from wet weight at age t to $t+1$ for ages 2-16. May 1st represented day 1 of the simulations.

[b] Size classes were used to assign diet and thermal experience inputs to lake trout in the model. Values indicate the size class on model day 1 at each age.

[c] Expected numbers of lake trout at each age, in a unit population of 1,000 fish of age ≥ 2 years with the observed mortality rate. Numbers at age were adjusted on a daily time step in simulations but are represented here on an annual basis for simplicity. Values indicate the numbers at age on model day 1.

Table 3.2. Seasonal thermal experience and diet composition of four size classes of lake trout. Diet proportions of 0.10 or more are indicated with bold type.

				Diet proportions by weight									
Size class (FL; mm)	Month	Thermal experience (˚C)	n (non-empty stomachs)	Burbot	Chinook salmon	Cyprinids	Kokanee	Lake trout	Threespine stickleback	Unidentified salmonids	Other fish	*Mysis diluviana*	Other invertebrates
180-450	Feb	5.3	10	0	0	0	0	0	0.032	0	0	**0.968**	0
	May	6.8	16	0	0	**0.483**	0	0	0.066	0	0	**0.447**	0.004
	Aug	11.1	9	0.065	0	0	0	0	0.037	0	0.037	**0.759**	**0.102**
	Nov	8.7	29	0	0	0	0	0	**0.184**	0	0.048	**0.762**	0.006
451-500	Feb	5.3	22	0	0	0.016	0.043	0	0.018	0	0	**0.896**	0.027
	May	7.0	33	0	0	**0.731**	0	0.014	0	0	0	**0.252**	0.003
	Aug	11.0	15	0	0	0	0	0	0	0	**0.153**	**0.844**	0.002
	Nov	9.4	27	0	0	0	0.039	0	**0.270**	0	0.015	**0.650**	0.026
501-550	Feb	5.4	12	0	0	0	0.027	0	0.001	0	0.001	**0.970**	0.002
	May	7.1	27	0	0	**0.502**	0	0	0.002	0	**0.323**	**0.149**	0.025
	Aug	10.5	10	0	0.018	0	0.082	0	0	0.020	0.003	**0.842**	0.035
	Nov	9.8	23	0	0	0.052	0.076	0	**0.375**	0	0.043	**0.444**	0.009
551-850	Feb	5.5	13	0	0	0.003	**0.912**	0	0.008	0	0.003	0.068	0.007
	May	7.3	30	0	0	**0.811**	**0.135**	0	0	0	0.018	0.030	0.005
	Aug	9.8	6	0.084	0	0	0	**0.840**	0	0	0	0.075	0
	Nov	10.0	9	0	0	0	**0.133**	0.006	**0.224**	0	0.002	**0.634**	0

Table 3.3. Energy density estimates (J/g wet weight) of lake trout prey organisms.

Prey item	Surrogate	Energy density (J/g)	Reference
Burbot		5125	Johnson et al. (1999)
Chinook salmon[a]		5863	Stewart and Ibarra (1991)
Cyprinids	Peamouth	7093	Mazur (2004)
Kokanee[a]	Sockeye salmon	6008	Beauchamp et al. (1989)
Lake trout[a]		6009	Stewart et al. (1983)
Threespine stickleback		6949	Mazur (2004)
Unidentified salmonids[a]	Sockeye salmon	6008	Beauchamp et al. (1989)
Other fish	Sculpin	4178-4514[b]	Mazur (2004)
Mysis relicta		2976-3720[b]	Lasenby (1971), Adare and Lasenby (1994)
Other invertebrates	Crayfish	3318	Mazur (2004)

[a] Estimated for a prey weight of 100 g.

[b] Energy density varied seasonally within the specified range.

Table 3.4. Biomass of kokanee in three regions of Lake Chelan estimated with a hydroacoustics survey during August 2005.

Lake region	Surface area (ha)	*n* Transects	Biomass (kg)					
			Age 0		Age 1		Age 2-4	
			Mean	SE	Mean	SE	Mean	SE
Stehekin River area	704	2	332	234	2,002	1,215	20,086	14,837
Lucerne Basin	9,281	16	415	48	2,676	573	14,066	2,689
Wapato Basin	3,502	4	75	16	613	56	2,844	294
Total	13,486	22	823	67	5,291	562	36,996	4,043

FIGURES

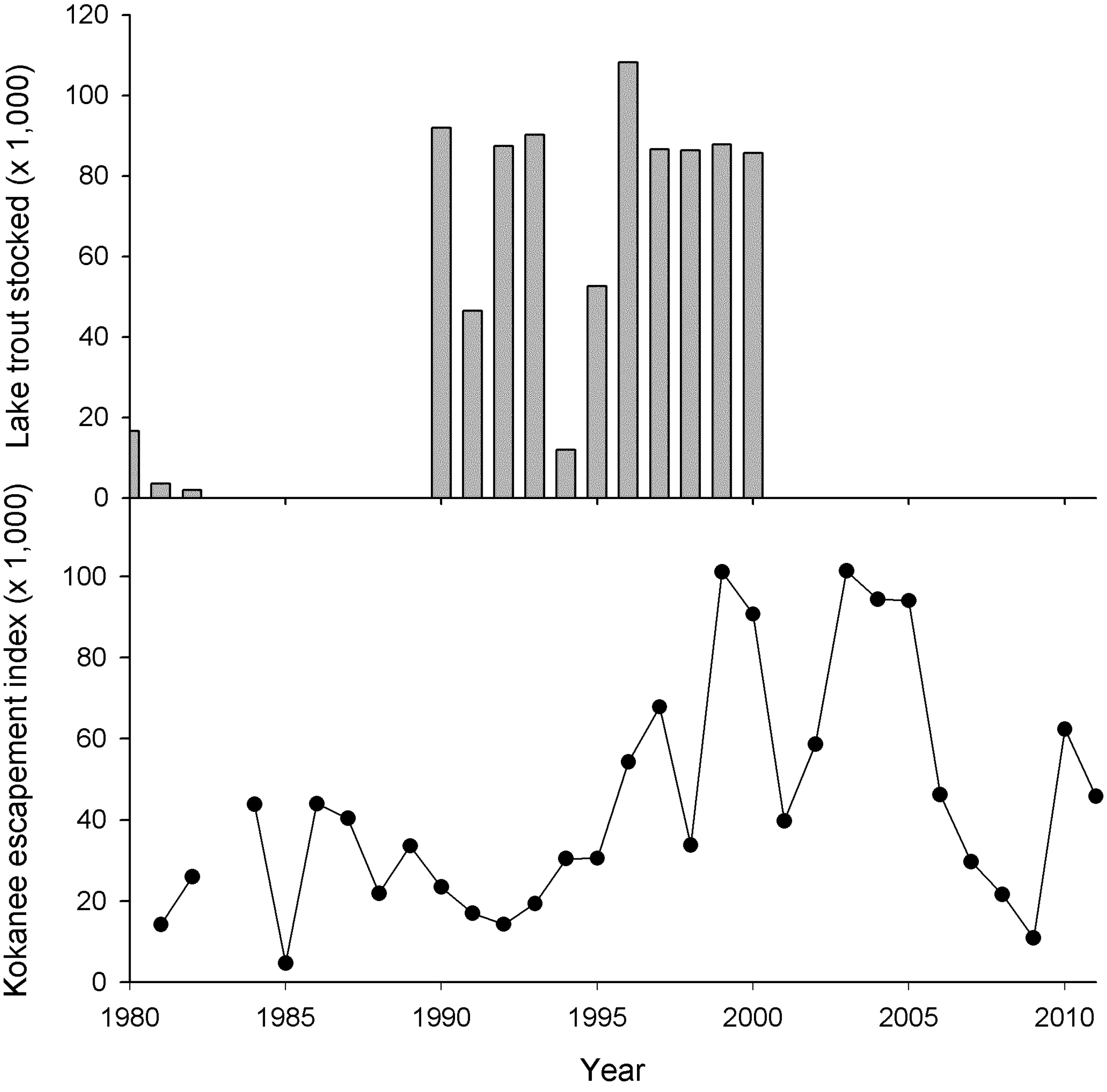

Figure 3.1. Numbers of lake trout stocked into Lake Chelan (top panel; Washington Department of Fish and Wildlife data). Index of kokanee escapement in the Lake Chelan drainage (bottom panel; data from Keesee and Keller 2012). Escapement is estimated from spawner surveys in five major tributaries conducted every 7-14 days, using the area-under-the-curve method (Neilson and Geen 1981).

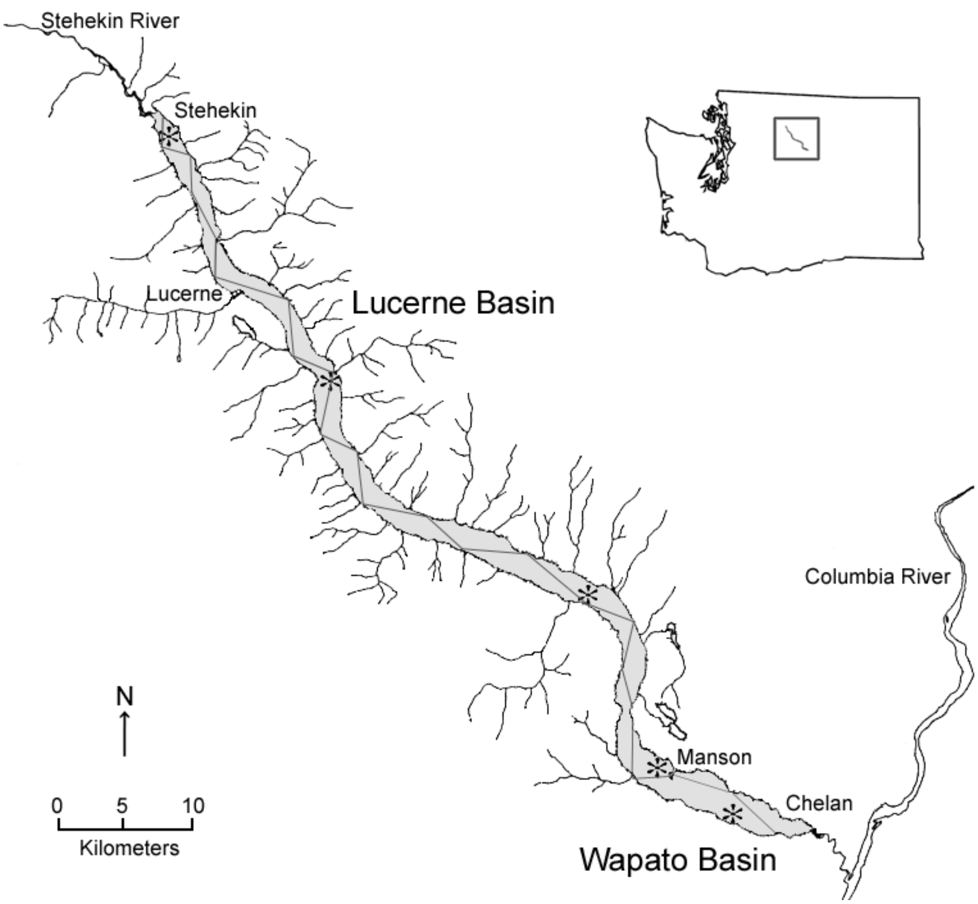

Figure 3.2. Map of Lake Chelan showing the two lake basins, principal sampling sites (asterisks), and hydroacoustic transects (lines). The inset shows the location of the lake in north-central Washington, USA.

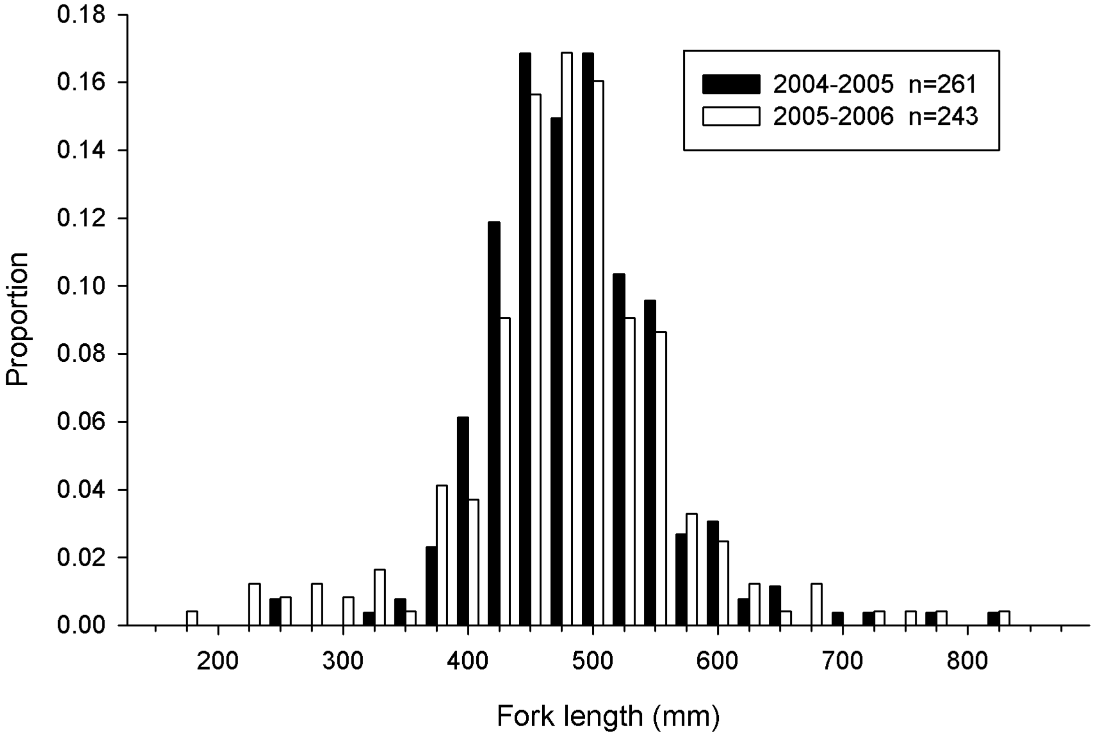

Figure 3.3. Length frequency distribution of lake trout captured in gill nets during August 2004-June 2005 and August 2005-June 2006.

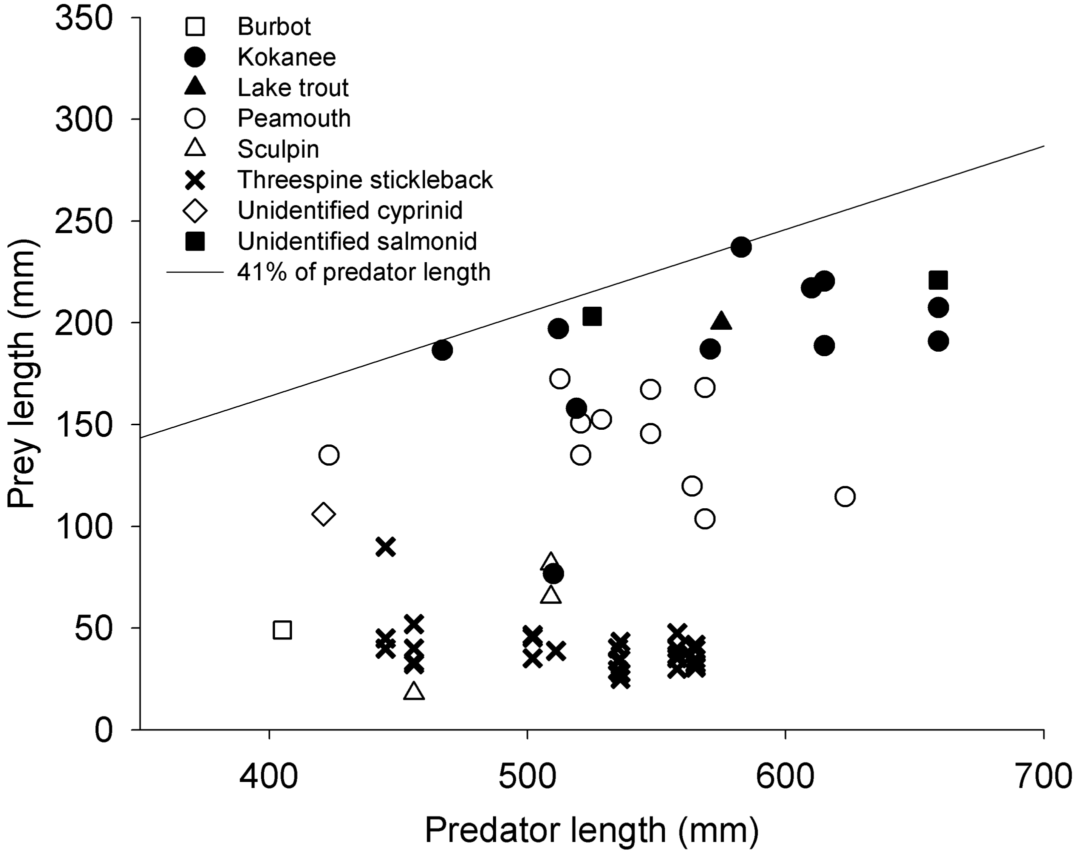

Figure 3.4. Relationship between lengths of piscivorous lake trout and lengths of ingested prey fishes. Symbols indicate prey species. Prey length indicates total length for burbot and threespine stickleback, and fork length for all other species. All prey were ≤ 41% of predator lengths (n = 62).

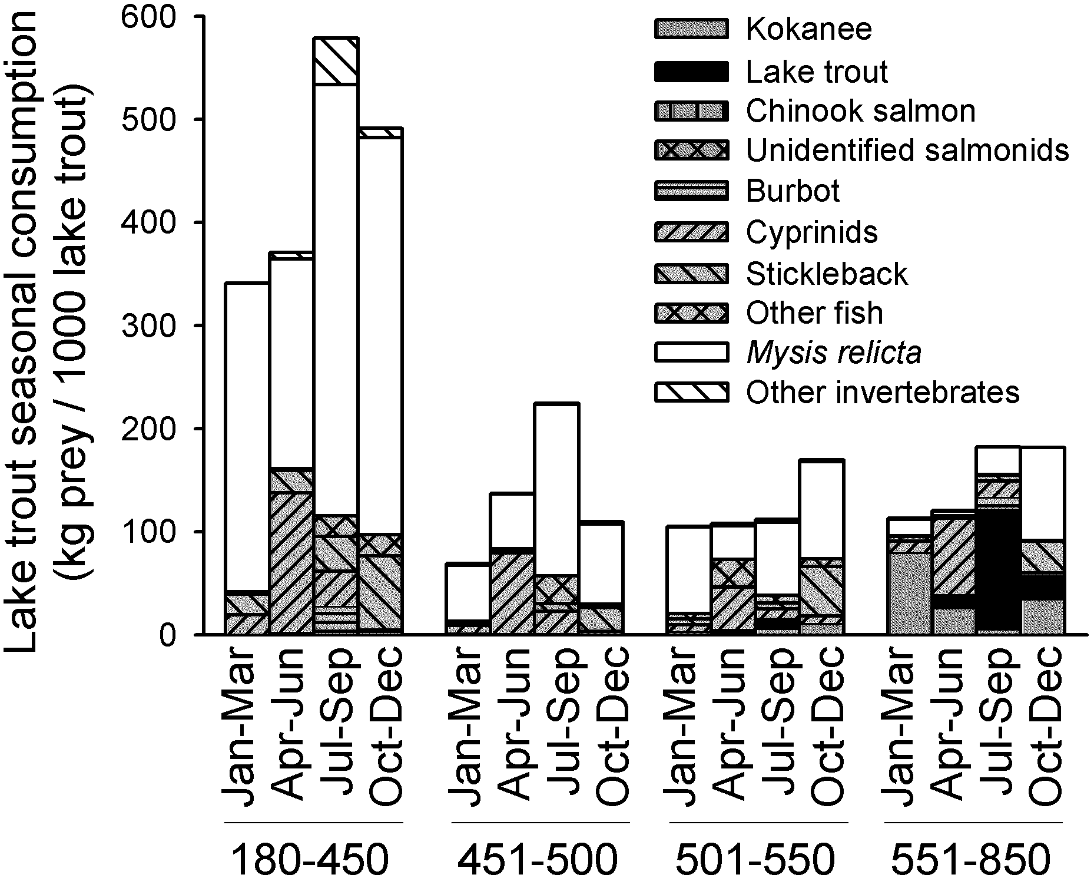

Figure 3.5. Seasonal prey consumption by a size-structured population unit of 1,000 lake trout. Consumption was estimated using a bioenergetics model and summarized for four size classes of lake trout (180-450, 451-500, 501-550, and 551-850 mm fork length).

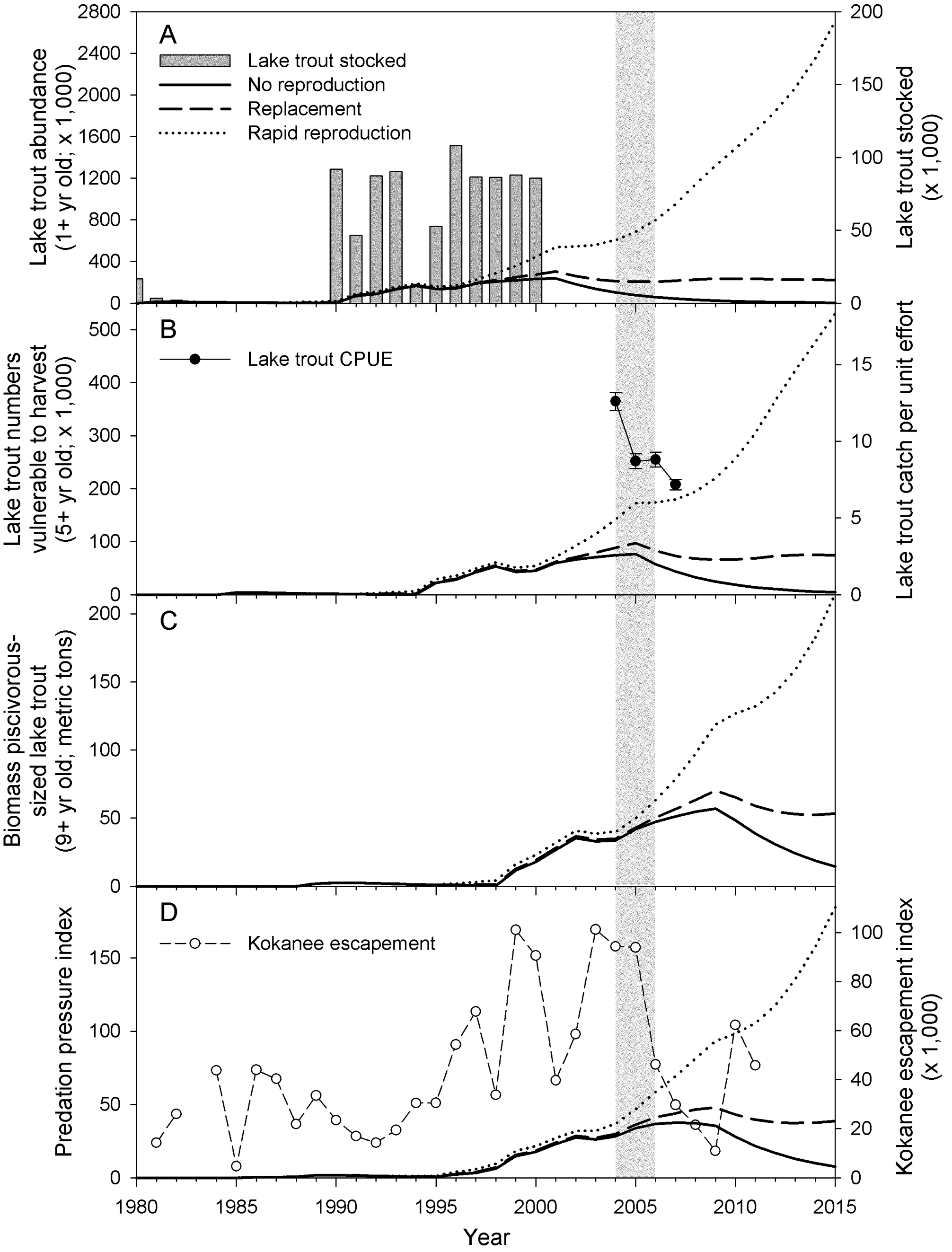

Figure 3.6. Simulated population dynamics of lake trout under three scenarios: no reproduction, replacement, and rapid reproduction. **(A)** Numbers of lake trout stocked (bars) and abundance of lake trout age ≥ 1 year (lines). **(B)** Numbers of lake trout vulnerable to harvest (age ≥ 5 years) and lake trout catch per unit effort by anglers (means ± 1 SE). **(C)** Biomass of the largest lake trout size class (> 550 mm FL; age ≥ 9 years), which preyed most heavily on kokanee. **(D)** Index of lake trout predation pressure on kokanee and index of kokanee escapement; (data from Keesee and Keller 2012). Shaded bar indicates years of field sampling, 2004-2006.

Chapter 4. Temperature and depth mediate resource competition and apparent competition between *Mysis diluviana* and kokanee

(Schoen, E.R., Beauchamp, D.A., Buettner, A.R., and Overman, N.C. *In press*. Temperature and depth mediate resource competition and apparent competition between *Mysis diluviana* and kokanee. Ecological Applications.)

ABSTRACT

In many food webs, species in similar trophic positions can interact either by competing for resources or boosting shared predators (apparent competition), but little is known about how the relative strengths of these interactions vary across environmental gradients. Introduced *Mysis diluviana* shrimp interact with planktivorous fishes such as kokanee salmon (lacustrine *Oncorhynchus nerka*) through both of these pathways, and effective management depends on understanding which interaction is more limiting under different conditions. An "environmental matching" hypothesis predicts the ecological impacts of *Mysis* are maximized under cool conditions near its thermal optimum. In addition, we hypothesized *Mysis* is more vulnerable to predation by lake trout in relatively shallow waters, and therefore *Mysis* enhances lake trout density and limits kokanee through apparent competition more strongly in shallower habitats. We tested whether these hypotheses could explain food web differences between two connected lake basins, one relatively shallow and the other extremely deep. The shallower basin warmed faster, thermally excluded *Mysis* from surface waters for 75% longer, and supported 2.5-18 times greater seasonal production of cladoceran zooplankton than the deeper basin, standardized by surface area. *Mysis* consumed 14-22% less zooplankton in the shallower basin, and lower ratios of total planktivore consumption to zooplankton production (C:P) indicated less potential for resource competition with kokanee, consistent with environmental matching. Lake trout diets contained more *Mysis* in the shallower basin and at shallower sampling sites within both basins. The catch rate of lake trout was seven times greater and the predation risk for kokanee was 4-5 times greater in the shallower basin than in the deeper basin, consistent with stronger apparent competition in shallower habitats. Understanding how the strengths of these interactions are mediated by temperature and depth would enable managers to select appropriate strategies to address the unique combinations of conditions in hundreds of affected systems.

INTRODUCTION

Indirect food web interactions are widespread, and determining how they influence community dynamics is an important goal for ecologists (Werner and Peacor 2003, Knight et al. 2005, Wootton and Emmerson 2005). This can be difficult when species interact through multiple pathways simultaneously. For instance, species in similar trophic positions can interact by competing for shared resources or by boosting shared natural enemies (termed “apparent competition” [Holt 1977] or “hyperpredation” [Smith and Quin 1996]). Distinguishing between these interactions is important when prioritizing conservation and management strategies (Noonburg and Byers 2005, White et al. 2006). The relatively few case studies examining both interactions suggest community dynamics are driven more strongly by resource competition in some systems (Petren and Case 1996, Hanley et al. 1998, Juliano 1998) and apparent competition in others (Smith and Quin 1996, Ellis et al. 2011). Practitioners would benefit from understanding how physical and biotic factors influence these interaction strengths.

Environmental gradients provide a useful framework for understanding the varying strengths of trophic interactions. For example, changes in temperature can alter trophic dynamics through asymmetric shifts in the production and consumption rates of ectothermic species (Taniguchi et al. 1998, Rahel and Olden 2008, Fey and Herren 2014). An *environmental matching hypothesis* predicts species will have greater impacts in habitats closely matching their thermal optima for growth and consumption (Ricciardi et al. 2013, Iacarella et al. 2015). Depth also structures aquatic food webs: smaller, shallower lakes and fjords tend to exhibit stronger top-down control than larger, deeper systems (Jeppesen et al. 1997, Tessier and Woodruff 2002, Aksnes et al. 2004). Stronger predation in shallower waters can be explained by a lack of refuge for pelagic prey (Tessier and Woodruff 2002, Aksnes et al. 2004) and by apparent competition caused by greater benthic resource subsidies to bentho-pelagic predators (Schindler et al. 1996, Vander Zanden et al. 2005). Thus, we expect the strengths of resource competition and apparent competition to change along gradients of temperature and depth.

Understanding how environmental drivers influence the strengths of these indirect interactions could help to resolve a longstanding fisheries management dilemma. The opossum shrimp *Mysis diluviana* was introduced into hundreds of North American and European lakes and reservoirs during the 20th century, primarily to feed planktivorous fishes (Lasenby et al. 1986). In reality, few of the planktivores in these systems fed on *Mysis*, but they often shared the same preferred prey, cladoceran zooplankton, and the same predators, including lake trout (*Salvelinus namaycush*; Figure 4.1). *Mysis* introductions reduced the density and seasonal availability of cladocerans (Morgan et al. 1978, Rieman and Falter 1981, Martinez and Bergersen 1991, Spencer et al. 1999) and enhanced the density but reduced the size of lake trout (Bowles et al. 1991, Martinez et al. 2009, Ellis et al. 2011). Planktivorous fishes such as kokanee (lacustrine sockeye salmon, *Oncorhynchus nerka*) then declined or disappeared altogether from many of these systems (Lasenby et al. 1986). Many studies attribute these impacts to resource competition (e.g., Nesler and Bergersen 1991, Spencer et al. 1991, Chipps and Bennett 2000, Whall and Lasenby 2009); however, apparent competition provides a better explanation for kokanee crashes in two lakes (Bowles et al. 1991, Ellis et al. 2011) and potentially many others (Martinez et al. 2009). This distinction is crucial in practice. If *Mysis* primarily limits planktivorous fishes through resource competition, then climate warming (Johnson and Martinez 2012) or bottom-up management strategies such as lake fertilization (Ashley et al. 1997) could mitigate these impacts. However, if apparent competition is stronger, then managers would instead focus on top-down strategies such as limiting predator densities (Martinez et al. 2009).

In this study, we asked whether temperature and depth mediate the strengths of interactions among mysids, kokanee, their primary predator (lake trout), and their cladoceran prey. First, temperatures above 14˚ C repel *Mysis* (Boscarino et al. 2007) and sharply curtail its feeding rate (Iacarella et al. 2015), while kokanee/sockeye salmon can effectively feed and grow at temperatures up to 20˚ C or higher with an adequate food supply (Beauchamp 2009). Accordingly, some lakes and reservoirs exhibit reduced *Mysis* density, prolonged availability of cladocerans such as *Daphnia*, and greater kokanee growth in warmer than in cooler summers (Rieman and Falter 1981, Martinez and Wiltzius 1995, Johnson and Martinez 2012). Therefore, the environmental matching hypothesis predicts warmer epilimnetic temperatures weaken the impacts of resource competition by *Mysis* on kokanee.

Next, we proposed two novel hypotheses linking basin morphometry to (1) the vulnerability of *Mysis* to lake trout predation and (2) the strength of apparent competition between *Mysis* and kokanee. *Mysis* migrate deeper before dawn, either reaching the lake bottom or suspending in diffuse layers deep in the water column (e.g., > 100 m; Beeton and Bowers 1982, Levy 1991). Lake trout feed easily on *Mysis* aggregated in the benthos (Holbrook et al.

2013), but probably feed less effectively when *Mysis* are dispersed in deep, unlit open water. Therefore, we proposed a *deep-water refuge* hypothesis that *Mysis* is more vulnerable to lake trout predation in shallower waters than in extremely deep waters. Finally, theory predicts that greater energetic subsidies to predators strengthen top-down control (Holt 1977, Courchamp et al. 2000). Thus, we proposed a corollary *depth-mediated apparent competition* hypothesis that introduced *Mysis* enhances lake trout populations more strongly and thereby limits kokanee through apparent competition more strongly in shallower lakes than in deeper lakes.

To test whether the strengths of resource competition and apparent competition could be explained by temperature and depth, we compared food web patterns between two connected lake basins exhibiting markedly different abiotic conditions. One basin was relatively shallow, while the other was deep and steep-sided. We expected the shallower basin to thermally stratify faster based on its smaller volume (Horne and Goldman 1994) and prior research. In regard to resource competition, we predicted *a*) the shallower basin would contain waters exceeding 14˚ C for longer periods than in the deeper basin; *b*) the density, standing-stock biomass, and production rate of cladocerans would be greater in the shallower basin; and *c*) the ratio of overall *Mysis* and kokanee consumption to zooplankton production (C:P ratio) would be lower, indicating less potential for resource competition in the shallower basin. In regard to apparent competition, we predicted *d*) *Mysis* would represent a greater proportion of the lake trout diet in the shallower basin than the deeper basin; *e*) lake trout density would be greater but maximum size would be smaller in the shallower basin, consistent with greater energetic support from *Mysis*; and *f*) kokanee would face a greater risk of lake trout predation, consistent with stronger apparent competition in the shallower basin.

STUDY AREA

Lake Chelan is a deep, glacially carved lake (maximum depth 453 m) located in the Cascade Range in north-central Washington (48° N, 120° W; Figure 4.2). The lake is composed of two basins joined by a narrow channel. Wapato Basin is moderately deep and bowl-shaped (mean depth 43 m and maximum depth 122 m), while Lucerne Basin is extremely deep and steep-sided (mean depth 180 m and maximum depth 453 m; Kendra and Singleton 1987). The lake is ultraoligotrophic and monomictic; Wapato Basin had a warmer epilimnion, a longer period of thermal stratification, and slightly greater productivity than Lucerne Basin during a previous study (Pelletier et al. 1989). The crustacean zooplankton community is composed predominantly of the copepods *Leptodiaptomus ashlandi* and *Diacyclops thomasi* and the cladocerans *Bosmina longirostris*, *Daphnia thorata, D. galeata,* and *D. longiremis*. Kokanee and *Mysis* are the dominant planktivorous species in the lake (Brown 1984). Kokanee were introduced in 1917 and established a naturally reproducing population, supplemented by stocking, that migrates seasonally between lake basins (Keesee and Keller 2013). *Mysis* were introduced in 1967 and became established by 1975 (Brown 1984). Lake trout were introduced beginning in 1980, were heavily stocked from 1990-2000, and are now a major predator of *Mysis*, kokanee, and other fishes (Martinez et al. 2009, Schoen et al. 2012).

METHODS

We collected field data to compare the interactions of zooplankton, *Mysis*, kokanee, and lake trout between two basins in Lake Chelan, Washington, USA. We sampled each basin in August, November, February, and late May through early June over a two-year period. We estimated the biomass and production rates of major zooplankton taxa and the consumption rates of the *Mysis* and kokanee populations to evaluate the potential for resource competition in each basin. We compared the diet composition, relative density, and growth patterns of lake trout between the two basins to evaluate effects of a potential *Mysis* subsidy to lake trout. Finally, we estimated the consumption rates of lake trout and the predation risk faced by kokanee in each basin to evaluate the potential for apparent competition.

Field sampling

We conducted standardized seasonal sampling from August 2004 through August 2006. We sampled water temperature, zooplankton, *Mysis*, and lake trout at five sites in the lake: two in Wapato Basin and three in Lucerne Basin (Figure 4.2). We recorded surface water temperatures six times daily with temperature loggers (iBCod type Z, Alpha-Mach Inc.) deployed at 1 m depth near the mid-point of each basin. We collected vertical temperature profiles seasonally with a Hydrolab Datasonde (Hach Environmental Inc.). We sampled zooplankton during daylight with vertical hauls from 80 m to the surface using a conical 35-cm-diameter, 153-µm-mesh ring net, and we collected supplemental shallow hauls in the metalimnion and epilimnion at selected sites. We sampled *Mysis* at night with vertical hauls from 80 m depth to the surface using a conical 1-m-diameter, 1-mm-mesh ring net. These hauls started below the scattering layer of *Mysis* as observed on an echosounder.

We collected kokanee by angling and with midwater gill nets. Kokanee densities were generally low, and we successfully collected samples only during May, June, and August. We captured lake trout and other fish species with sinking gill nets fished overnight at four depth strata ranging from 0-70 m (see Schoen et al. 2012). We recorded the length and mass and collected the stomach of each fish. To determine fish ages, we collected lake trout opercles

(Sharp and Bernard 1988) and kokanee scales from the area of earliest scale formation (DeVries and Frie 1996). Managers and anglers contributed additional scale and stomach samples. Two independent readers determined the ages of kokanee and lake trout. We identified stomach contents to the level of species for fish prey and zooplankton or order and life stage for macroinvertebrates. We recorded the blotted wet mass of each prey category and calculated diet proportions by mass (Chipps and Garvey 2007).

Zooplankton density, biomass, and production

We compared the density, standing stock biomass, and production rate of the dominant cladocerans (*Daphnia* spp. and *B. longirostris*) and copepods (*L. ashlandi* and *Diacyclops thomasi*) between lake basins in each season. We identified crustacean zooplankton to species, counted adults and eggs, and measured subsamples for body length. We calculated zooplankton density (individuals / L) and areal standing stock biomass (g wet mass / m^2) from counts, body sizes, and the diameter and efficiency of the net (see Appendix A).

We tested whether *Daphnia* and *Bosmina* densities, body lengths, and egg counts differed between basins by comparing hierarchical generalized linear models, including full models with effects of season, basin, and a season × basin interaction, and all possible reduced models. To test for differences in adult density and egg count, we evaluated negative binomial models with counts as the response variable, and we specified the effective sample volume (total sample volume multiplied by the proportion of the sample that was enumerated) as an offset (Gray 2005). For body length (log transformed), we compared Gaussian ANOVA models. We evaluated the models using AIC_c weights (Burnham and Anderson 2002). We estimated daily production rates (g wet mass $\cdot$ m^{-2} $\cdot$ d^{-1}) using the zooplankton production model of Shuter and Ing (1997) because of the long interval between sampling events. This model produces similar estimates as traditional egg-ratio models (Stockwell and Johannsson 1997). For the production calculations, we used the mean epilimnetic water temperature during stratified periods, which likely resulted in conservative estimates of productivity (Kuns and Sprules 2000), and the mean temperature of the upper 30 m of the water column during unstratified periods.

Density, distribution, and consumption rates of Mysis and kokanee

We enumerated each *Mysis* sample and calculated the areal density (mysids / m^2 of lake surface) by dividing the count by the area of the net opening, assuming 100% net efficiency (Nero and Davies 1982). We tested whether *Mysis* density (log transformed) varied between basins with a hierarchical set of ANOVA models identical in structure to the zooplankton models and evaluated using AIC$_c$ weights. We determined the vertical distribution of *Mysis* with short hydroacoustic transects in conjunction with each *Mysis* haul (Appendix B). We recorded the upper and lower depth limits of the continuous *Mysis* scattering layer in these echograms. We characterized the density and vertical distribution of kokanee with hydroacoustic surveys conducted at night during February, May, August, and November, 2005. Each survey consisted of 22 transects in a zig-zag pattern (our Figure 5.2; Simmonds and MacLennan 2005), and we estimated kokanee density by echo counting single targets with Echoview version 4.2 software (Myriax Pty). The hydroacoustic analysis followed the methods of Schoen et al. (2012) with modifications described in Appendix B.

We estimated the rates of zooplankton consumption by the *Mysis* and kokanee populations using bioenergetics models parameterized for *Mysis diluviana* (Rudstam 1989, Chipps 1998) and kokanee/sockeye salmon (Beauchamp et al. 1989). Both models have been corroborated using independent estimates of consumption (Beauchamp et al. 1989, Chipps and Bennett 2002). Model inputs for each consumer species included growth, the water temperatures experienced by the consumer, diet composition, and the energy densities of consumers and their prey (Appendix C). Juvenile *Mysis* (length < 8 mm) consumed phytoplankton, and adults consumed zooplankton and phytoplankton. Kokanee consumed cladocerans, copepods, and chironomid midge larvae. Both *Mysis* and kokanee prefer cladoceran prey, but consume copepods when cladoceran densities are low (Grossnickle 1982, Spencer et al. 1999, Beauchamp et al. 2004, Scheuerell et al. 2005). Therefore, we interpreted the overall zooplankton consumption rate as predatory demand primarily for cladocerans and secondarily for copepods.

We estimated the per-capita consumption of zooplankton prey (g wet mass / d) for each *Mysis* and kokanee age class during each seasonal period. We scaled these rates up to population-level consumption rates ($g \cdot m^{-2} \cdot d^{-1}$) by multiplying by the areal density of each cohort of consumer. We calculated ratios of the combined prey consumption rates for the *Mysis* and kokanee populations to the production rates of zooplankton (C:P) to indicate the relative potential for competition among planktivores among basins and seasons. We calculated C:P ratios two ways: including the production of cladocerans only or cladocerans plus copepods, to indicate the potential for competition for preferred prey or all zooplankton prey.

Lake trout diet, density, growth, and predation of kokanee

We tested whether the diet composition of lake trout differed with respect to bottom depth with analyses at two scales: lake basins and sampling sites within basins. First, we calculated diet proportions separately for the two lake basins, stratified into three size classes of lake trout to characterize the ontogenetic diet shift from *Mysis* to fish. Next, we calculated the proportion of *Mysis* in the diet at each of the five sampling sites, again stratified by size class. We graphically compared diet proportions among sites arranged along a gradient of lake morphometry, ranging from relatively shallow, bowl-shaped sites to extremely deep sites with steep shorelines. Due to the serpentine shape of the lake, we quantified this gradient by the maximum depth of the shortest cross-section of the lake through each site.

We compared the relative densities of lake trout in each lake basin based on the catch per unit of effort (CPUE) when sampling with the gill nets. We defined one unit of effort as one depth-stratified set of eight gill nets during each season (Schoen et al. 2012). The gill nets sampled lake trout only in the benthic zone, but their stomach contents contained a mixture of pelagic and benthic prey, indicating that pelagic-feeding lake trout were vulnerable to these nets. To evaluate the relative abundance of alternative prey for lake trout between basins, we also compared the CPUE of peamouth (*Mylocheilus caurinus*) and small northern pikeminnow (*Ptychocheilus oregonensis*; FL < 200 mm). We compared the growth of lake trout between basins by testing for differences in von Bertalanffy growth models and length-mass relationships (Appendix D).

To compare the relative risk of lake trout predation experienced by individual kokanee in each basin, we divided the number of kokanee consumed by lake trout by the abundance of kokanee. We reanalyzed a published bioenergetics estimate of population-level lake trout consumption in Lake Chelan (Schoen et al. 2012) to estimate the relative numbers of kokanee consumed annually in each lake basin (Appendix D). We interpreted the results as an index of the relative predation risk for kokanee in each basin due to uncertainty in the size structure of kokanee consumed by lake trout. We estimated the upper and lower bounds of relative predation risk in each basin based on the uncertainty in the lake trout consumption and kokanee abundance estimates. We assumed lake trout predation was a good indicator of overall predation risk, because other piscivores either had little or no kokanee in their diets (i.e., burbot *Lota lota*, northern pikeminnow, and smallmouth bass *Micropterus dolomieu*) or were very low in abundance (i.e., Chinook salmon *O. tshawytscha*) (Schoen and Beauchamp 2010).

We performed statistical analyses using R version 3.1.1 (R Core Team 2014).

RESULTS

Thermal regimes

The shallower Wapato Basin reached epilimnetic temperatures warm enough to exclude *Mysis* (≥ 14˚ C) at least 60 days earlier than the deeper Lucerne Basin during both years, and these warm epilimnetic temperatures persisted 75% longer and across a greater range of depths. Daily mean surface water temperatures first reached 14˚ C on 5/4/2005 and 5/15/2006 in Wapato Basin, but not until 7/9/2005 and 7/14/2006 in Lucerne Basin. During 2005, when temperatures were monitored for the entire growing season, the epilimnion remained above 14˚ C until six days later in Wapato Basin (10/31/2005) than in Lucerne Basin (10/25/2005) for a total of 175 days in Wapato Basin but only 101 days in Lucerne Basin. Vertical thermal profiles displayed the greatest differences between basins in May and June with epilimnetic temperatures and the depth of the thermocline increasing from northwest to southeast, in the direction of the prevailing winds. By August, all sites were fully stratified, and temperatures ≥ 14˚ C extended to 29 m at both sites in Wapato Basin and to 25-29 m at the three Lucerne Basin sites.

Zooplankton biomass and production

Overall, *Daphnia* and *Bosmina* in the shallower Wapato Basin were greater in density and produced more eggs than those in the deeper Lucerne Basin. These differences were most pronounced outside of the mid-summer peak in production. *Daphnia* densities ranged from

0.06-0.31 animals / L from November through June in Wapato Basin, while only reaching 0.002-0.07 / L in Lucerne Basin during the same period (Figure 4.3). *Bosmina* densities ranged from 0.35-0.45 animals / L from November through June in Wapato Basin, but only 0.03-0.12 / L in Lucerne Basin. Cladoceran densities in the epilimnion and metalimnion averaged 2-4 times higher than in integrated 80-m hauls. Cladocerans reproduced in all seasons in Wapato Basin, but in Lucerne Basin we counted no *Daphnia* eggs in February, May, or June samples and no *Bosmina* eggs in February or November samples. During the remaining seasons, *Daphnia* egg counts averaged 3.2 times greater and *Bosmina* egg counts averaged 2.4 times greater in Wapato Basin. *Daphnia* and *Bosmina* body lengths were similar (≤ 5% difference) between basins. All basin differences reported here were supported by model selection (Appendix: Table A1).

Integrating these values, the standing stock biomass and production rates of cladocerans were much greater overall in Wapato Basin than in Lucerne Basin. The mean areal biomass (g / m^2) of *Daphnia* was greater in Wapato Basin than in Lucerne Basin during February (9.9 times greater), May and June (130 times greater), and November (3.9 times greater), and was similar in both basins during August (Appendix A: Figure 4.A1). Mean biomass of *Bosmina* was 2.8-10 times greater in Wapato Basin than in Lucerne Basin during all seasons. Production of *Daphnia* was greater in Wapato Basin than in Lucerne Basin during all periods, due in part to warmer temperatures, with the greatest difference during May and June (200 times greater production) and the smallest difference in August (1.5 times greater production). Production of *Bosmina* was 2.9-11.0 times greater in Wapato Basin than in Lucerne Basin during all periods (Figure 4.4). The densities and biomasses of the copepod genera *Diacyclops* and *Leptodiaptomus* showed no consistent patterns between basins. However, the combined production rate of *Diacyclops* and *Leptodiaptomus* was 26-80% greater in Wapato Basin than in Lucerne Basin during February, May, and June, and similar (< 10% greater) between basins during August and November, due to differences in temperature and body size.

Mysis *and kokanee density, distribution, and consumption rates*

Mysis density was lower in Wapato Basin than in Lucerne Basin, but kokanee density was similar in both basins. Most of the variability in *Mysis* density could be explained by season alone (AIC_c weight = 0.62), but densities averaged 39% lower in Wapato Basin (Appendix C: Figure 4.C1; AIC_c weight, season + basin model = 0.26). The nighttime vertical distribution of *Mysis* was limited to depths with water temperatures < 14° C in and below the thermocline (Appendix B: Figure 4.B1). The annual mean density of kokanee was similar in both basins (0.1% less in Wapato Basin; 95% confidence interval: 43% less to 14% greater). Thus, kokanee abundance averaged 72% less (95% CI: 84-69% less) in the smaller Wapato Basin. Older kokanee migrated between basins seasonally, as indicated by reciprocal changes in abundance (Appendix B: Figure 4.B2). Many age-1 and older kokanee moved into Wapato Basin during May and June, and many age-2 and older fish also used Wapato Basin during November. Greater abundances in Lucerne Basin during August were largely driven by kokanee aggregated near the mouth of the Stehekin River as maturing adults staged to spawn. Kokanee were distributed above, within, and below the thermocline at night in both basins (Appendix B: Figure 4.B1).

Total consumption of zooplankton was lower in Wapato Basin than in Lucerne Basin. This pattern was driven by *Mysis*, which consumed 8-18 times more zooplankton lake-wide than did the kokanee population (Figure 4.4). *Mysis* consumption was still 2.6 times greater than kokanee consumption in Wapato Basin during May and June, when kokanee aggregated in large numbers. When standardized by basin surface area, *Mysis* consumed 14-22% less zooplankton ($g \cdot m^{-2} \cdot d^{-1}$) in Wapato Basin than in Lucerne Basin in all seasons. However, the supply of zooplankton was much greater in Wapato Basin, resulting in a lower ratio of planktivore consumption to zooplankton production (C:P) in Wapato Basin than in Lucerne Basin during all seasons (Appendix C: Table C1). C:P ratios were consistently lower in Wapato Basin whether considering the production of preferred cladoceran prey alone (72-94% lower) or including copepods as well (26-57% lower). In Wapato Basin, cladoceran production consistently exceeded zooplankton consumption rates (Figure 4.4). However, in Lucerne Basin, consumer demand surpassed cladoceran production during every period except August, forcing planktivores to rely on copepods or other prey for the balance of their energy budget.

Lake trout diet, density, and predation of kokanee

The diets of all size classes of lake trout included more *Mysis* in the shallower Wapato Basin than in the deeper Lucerne Basin. *Mysis* comprised a majority (93%) of the annual diet of small (≤ 420 mm fork length [FL]) lake trout in the shallower basin, but only 54% in the deeper basin (Figure 4.5). The diets of medium-sized (421-550 mm FL) lake trout contained 70% *Mysis* in Wapato Basin, but only 14% in Lucerne Basin. The diets of the largest lake trout (> 550 mm FL) contained 23% *Mysis* in Wapato Basin, but no *Mysis* in Lucerne Basin. Conversely, lake trout diets contained much smaller proportions of kokanee and cyprinid fishes in Wapato Basin than in Lucerne Basin (Figure 4.5). At the finer spatial scale of sampling sites within basins, lake trout relied more on *Mysis* prey at sites with shallower bathymetric cross-sections than at sites with deeper bathymetry. Within each size class of lake trout, the diet proportion of *Mysis* declined as sampling site depth and steepness increased (Figure 4.6).

Lake trout density and juvenile body condition were enhanced, while maximum body size was reduced in Wapato Basin compared to Lucerne Basin. In Wapato Basin, the catch per unit effort (CPUE) was 7.2 times greater for small (180-420 mm FL) lake trout, 7.8 times greater for medium-sized (421-550 mm) lake trout, and 6.2 times greater for large (551-850 mm) lake trout than in Lucerne Basin (Appendix D: Figure 4.D1). In contrast, lower CPUE of peamouth (58% lower) and small (< 200 mm FL) northern pikeminnow (24% lower) were recorded in Wapato than in Lucerne Basin. Lake trout grew in length at the same initial rate ω in both basins (125 mm / year), but achieved a smaller asymptotic maximum length L_∞ in Wapato Basin (657 mm FL) than in Lucerne Basin (707 mm FL; AIC_c weight = 0.99). Lake trout exhibited greater body condition at small lengths but gained mass more slowly with increasing length in Wapato Basin than in Lucerne Basin (AIC_c weight = 0.82).

The lake trout population in Wapato Basin consumed 5% more kokanee annually (nominal estimate; lower and upper bounds = 18% fewer to 17% more kokanee) than the lake trout population in Lucerne Basin (Appendix D). The annual mean abundance of kokanee was 72% less (95% CI: 84-69% less) in Wapato Basin than in Lucerne Basin (Appendix B). As a result, an individual kokanee faced a risk of predation 3.82 times greater in Wapato Basin than in Lucerne Basin (nominal estimate; lower and upper bounds = 3.74 and 5.24 times greater).

DISCUSSION

Our results suggest temperature mediates the strength of resource competition and depth mediates the strength of apparent competition in this system. As predicted by the environmental matching hypothesis, *Mysis* had greater consumptive effects in the habitat that most closely matched its optimal thermal regime, the cooler, deeper Lucerne Basin. However, *Mysis* was more vulnerable to lake trout predation in the shallower Wapato Basin, in support of the deep-water refuge hypothesis. Accordingly, lake trout densities were greater and lake trout imposed greater predation risk on kokanee in the shallower basin, as predicted by depth-mediated apparent competition hypothesis. We compared two non-independent food webs in connected lake basins, prompting several important considerations in interpreting our results. Fish could move throughout the lake, so differences in kokanee and lake trout density between basins were probably caused by a combination of demographic and behavioral effects, as we discuss below. Further, we could not measure interaction strengths directly (sensu Paine 1980), and other factors besides temperature and depth might have also contributed to the responses we observed. Given these limitations, the strengths of this study were that the comparison systems were very similar in climate, species composition, and management history, and were studied concurrently; yet, they contrasted sharply in the variables of interest. This comparison revealed associations between habitat and food web structure, unhindered by many of the complications common to cross-lake studies (Olden et al. 2006).

Thermal regimes, environmental matching, and resource competition

As predicted by the environmental matching hypothesis, cladocerans were more abundant and productive in the shallower basin, and kokanee faced less potential for resource competition from *Mysis*, as evidenced by lower C:P ratios. These patterns were explained by warmer temperatures that excluded *Mysis* from the epilimnion longer in the shallower basin than in the deeper basin. We noted three important methodological limitations of our approach, but found them unlikely to influence our conclusions. First, our quarterly sampling scheme could have missed short-term dynamics, such as mid-summer peaks in cladoceran densities. Nonetheless, the results showed kokanee had greater food availability in the shallower basin during most of the year, especially the critical spring and autumn periods when *Mysis* predation typically limits cladoceran densities most strongly (Spencer et al. 1999, Clarke and Bennett 2003). Second, our cladoceran production estimates were conservative during stratified periods, because they were based on integrated zooplankton hauls, which underestimate the high productivity of shallower, warmer strata (Kuns and Sprules 2000). Thus, the prolonged stratification in the shallower basin was likely even more beneficial to kokanee than we estimated (Johnson and Martinez 2012). Third, we estimated kokanee density with limited precision, especially during non-stratified periods, due to inherent limitations of the hydroacoustic approach (Beauchamp et al. 2009; see our Appendix B). However, this uncertainty had very little influence on the C:P ratios because mysids consumed an order of magnitude more zooplankton than did kokanee, in agreement with other studies (Chipps and Bennett 2000, Hyatt et al. 2005). Despite these limitations, we observed clear patterns supporting the environmental matching hypothesis.

Our findings were consistent with previous longitudinal studies suggesting kokanee faced weaker resource competition from *Mysis* in years when a fluctuating reservoir was shallow and warm than in years when it was deep and cool (Martinez and Wiltzius 1995, Johnson and Martinez 2012). Temperature was confounded with depth in these studies as well as ours, but we believe temperature was the driving factor due to its strong physiological and behavioral effects on *Mysis* (Boscarino et al. 2007, Iacarella et al. 2015). A useful counterexample is Lake Jonsvatn, Norway, where a shallower basin exhibits cooler waters and weaker thermal stratification than a deeper basin due to prevailing winds blowing from shallow to deep. In this lake, introduced *Mysis* had stronger impacts on cladocerans in the shallower, cooler basin than in the deeper, warmer basin (Koksvik et al. 2009). Together, these studies suggest that lake thermal regimes, rather than depth alone, mediate the strength of *Mysis* predation on cladocerans and resource competition with planktivorous fishes. Our results support the environmental matching hypothesis for identifying ecosystems most vulnerable to the consumptive and resource competitive impacts of *Mysis*, as well as systems where these impacts are likely to diminish with climate change (Ricciardi et al. 2013, Iacarella et al. 2015). However, these interactions do not necessarily reflect the *overall* impacts of a species, and they may be misleading when viewed in isolation. In our study, food provisioning of lake trout and apparent competition were actually stronger in the shallower, warmer basin where the environmental matching hypothesis predicted *Mysis* would have weaker impacts.

Depth gradients, predation refuge, and apparent competition

The diet composition of lake trout shifted markedly along a depth gradient, supporting the deep-water refuge hypothesis and revealing an important association between habitat and food web structure. Lake trout diets contained more *Mysis* in the shallower basin and at shallower sampling sites within basins. Since *Mysis* densities were actually lower in the shallower basin, this pattern suggested *Mysis* was more vulnerable to predation at shallower sites than at deeper sites (> 100-150 m). We interpreted the fine-scale diet data with caution because sample sizes were small at the three deepest sites, but sample sizes were robust at the basin scale.

We found additional support for the deep-water refuge hypothesis by comparing diet studies from other lakes: lake trout relied heavily on *Mysis* in relatively shallow lakes (mean depth < 100 m) (Beauchamp et al. 2007, Ellis et al. 2011, Guy et al. 2011), but consumed very little *Mysis* in an extremely deep, steep-sided lake (Clarke et al. 2005). Native lake trout in Lake Superior also consumed more *Mysis* at shallower sites than deeper sites (Dryer et al. 1965), even though *Mysis* biomass was lower at shallower sites (Sierszen et al. 2014). To our knowledge, our study is the first to associate lake morphometry with the strength of the food-provisioning interaction between *Mysis* and lake trout and to examine the ecological consequences. The daytime depth distribution of *Mysis* varies between lakes (e.g., Beeton and Bowers 1982, Levy 1991), and we propose that the vulnerability of *Mysis* to lake trout predation is related to the proportion of a lake that is sufficiently shallow and illuminated to cause *Mysis* to aggregate at the bottom during daylight. This threshold depth could be predicted with a model of the *Mysis* diel vertical migration (Boscarino et al. 2009) given the optical characteristics of the lake.

The *Mysis*-rich diet of lake trout in the shallower basin of Lake Chelan coincided with much greater lake trout density, supporting the depth-mediated apparent competition hypothesis. Lake trout catch rates were seven times greater in the shallower basin than in the deeper basin, and these differences could not be explained by the distribution of other prey resources, such as kokanee or cyprinids, which both had greater overall densities in the deeper basin. We considered whether the difference in lake trout CPUE could be an artifact of reduced gill net efficiency on the steeper slopes of the deep basin. However, this was unlikely because the catch rates of other littoral and profundal fishes were either greater in the deep basin or similar in both basins, suggesting net efficiency did not differ substantially (also see Schoen and Beauchamp 2010). Indeed, our comparison of gill net catch rates probably underestimated the positive effect of *Mysis* availability on lake trout density in the shallower basin, for two reasons. First the lake trout fishery operated predominantly in the shallower basin, presumably reducing densities there and masking the numerical response to *Mysis* prey. Second, lake trout could move between basins, and dispersal from the shallower basin would have spread the localized energetic benefits of *Mysis* availability across the overall lake trout population. Lake trout probably did not make frequent large-scale movements since they exhibited distinct growth patterns in the two basins. However, even limited dispersal of juveniles from shallower spawning and rearing habitats into the deeper basin would have reduced the difference in density we observed. Dispersal in the opposite direction was probably minimal because the deeper basin was too steep-sided to provide much suitable spawning and rearing habitat (Hansen et al. 2008).

Lake trout growth patterns also largely supported the depth-mediated apparent competition hypothesis. As expected, the body condition of small lake trout was greater and the asymptotic maximum size of adults was smaller in the shallower basin, but contrary to expectations, juvenile lake trout did not grow faster. These differences in growth between lake trout eating low-*Mysis* vs. high-*Mysis* diets were analogous to the changes in lake trout growth patterns documented in other lakes before versus after *Mysis* were introduced (Bowles et al. 1991, Stafford et al. 2002, Martinez et al. 2009).

The greater availability of *Mysis* to lake trout coincided with a 4- to 5-times greater predation risk for kokanee in the shallower basin than in the deeper basin, in support of the depth-mediated apparent competition hypothesis. Although it might appear kokanee benefited from predation buffering in the shallower basin, because lake trout consumed more *Mysis* and less kokanee per capita, this benefit was offset by the enhanced density of lake trout, resulting in a greater net risk of predation. These results were consistent with theory: when a food-limited predator gains access to alternative prey, other prey species may receive short-term benefits such as predation buffering, but the net effect is likely to be negative at the longer time-scale of the predator's numerical response (Holt 1977, Holt and Lawton 1994).

Overall, although we could not demonstrate causation, our results were consistent with the predictions that greater availability of *Mysis* prey in the shallower basin boosted the density of lake trout, influenced lake trout growth patterns, and enhanced the predation risk of kokanee relative to the deeper basin. Our study provides further evidence that shallower aquatic habitats tend to exhibit stronger top-down control than deeper ones (Jeppesen et al. 1997, Tessier and Woodruff 2002, Aksnes et al. 2004), but this was due to a slightly different mechanism than previously described. Previous studies have linked stronger predation in smaller, shallower systems to a lack of refuge for pelagic prey (Tessier and Woodruff 2002, Aksnes et al. 2004) or greater benthic prey subsidies to apex predators (Vander Zanden et al. 2005). In our study, these mechanisms were combined: *Mysis*, a pelagic/demersal prey, lacked refuge in shallower habitats and thus provided an enhanced energetic "subsidy" to an apex predator, which increased the predation risk of other pelagic prey.

Implications for fisheries management and invasion ecology in other systems

Disentangling resource competition and apparent competition has high applied value, because the most effective strategy for conserving kokanee and other planktivorous fishes in any given lake will depend on which interaction is more limiting. If *Mysis* primarily competes with kokanee for food, then enhancing cladoceran production may lessen these impacts. Warmer water temperatures driven either by climate change or reservoir management are likely to weaken resource competition (Johnson and Martinez 2012, Iacarella et al. 2015). Some nutrient enrichment programs have also successfully enhanced zooplankton production and planktivorous fish growth in lakes and reservoirs containing mysids (Hyatt et al. 2004, Schindler et al. 2010, but see Hyatt et al. 2005). However, stocking more kokanee would be counterproductive in food-limited systems, further exacerbating the competition for zooplankton. In contrast, if *Mysis* limits kokanee mainly by enhancing predators, then liberalized harvest of lake trout (Martinez et al. 2009) or more aggressive lake trout suppression efforts (Hansen et al. 2010, Pate et al. 2014) would be more effective. In predator-limited systems, kokanee populations might be sustained with enhanced stocking, but stocking levels sufficient to swamp predators can be cost-prohibitive (Johnson and Martinez 2000, Beauchamp et al. 2007). A directed *Mysis* harvest could potentially benefit kokanee via both interactions, but the only documented example of this approach, a subsidized commercial *Mysis* harvest in Lake Okanagan, BC, did not appear to benefit *Daphnia* or kokanee at recent levels of effort (Schindler et al. 2012). Each of these strategies involves considerable tradeoffs, such as direct financial costs, reduced water clarity, impacts on lucrative sport fisheries and tourism, and the potential for unintended ecological consequences.

Conducting a detailed food-web study in every lake is not practical, so general guidelines based on lake characteristics could allow for improved management of many ecosystems. Our study suggests *Mysis* competes for food most strongly in lakes with a short period of thermal stratification, and *Mysis* boosts lake trout most strongly in lakes with ample relatively shallow habitat (< 100-150 m depth). Lake trout populations appear to expand more slowly after *Mysis* introductions in deep, steep-sided lakes than in shallower ones (Bowles et al. 1991, Hansen et al. 2008, Ellis et al. 2011), but predation can still become limiting in deep systems over the long term (Martinez et al. 2009, Hansen et al. 2010). Thus, we recommend that managers consider the consequences of apparent competition in all systems with piscivores that consume *Mysis*. A near-exclusive focus on the consumptive and resource-competitive impacts of *Mysis* may have hindered understanding and effective management of a large number of lake and reservoir food webs in the past, and a broader emerging view may offer a more effective path forward.

Our findings also have broader implications for understanding how vulnerability to predation influences the impacts of nonnative species. The “enemy release” hypothesis predicts nonnative species have greater ecological impacts when they are less vulnerable to natural enemies, allowing them to become uncontrolled consumers (Pimm 1991, Colautti et al. 2004, Ricciardi et al. 2013). This hypothesis is intuitive, and it has become an important concept in invasion ecology (Keane and Crawley 2002, Fey and Herren 2014), although it has mixed empirical support for predicting the impacts of nonnative consumers (Ricciardi et al. 2013). Conversely, an alternative “enemy of my enemy” hypothesis predicts nonnative species will have greater impacts when they are *more* vulnerable to predators, due to stronger apparent competition (Colautti et al. 2004, Noonburg and Byers 2005). If depth mediates the vulnerability of *Mysis* to lake trout predation, as our results suggest, then the enemy release hypothesis would predict stronger *Mysis* impacts on planktivorous fishes in deeper lakes, while the enemy of my enemy hypothesis would predict the opposite pattern. *Mysis* has been introduced to hundreds of lakes with a wide range of depths, in the presence and absence of lake trout, and these systems could represent a large-scale unintentional experiment well suited for testing these hypotheses.

In conclusion, our study suggests the strengths of resource competition and apparent competition between planktivores in this study system are mediated by temperature and depth, respectively. Whereas climate change is expected to intensify the ecological impacts of many nonnative species (Rahel and Olden 2008, Fey and Herren 2014, Lawrence et al. 2014), we expect warming trends to diminish the resource competitive impacts of *Mysis* in many lakes due to its relatively low thermal optimum. Our results support the utility of the environmental matching hypothesis to predict consumptive and resource-competitive food web impacts. However, our study also highlights the importance of considering other interactions, such as food provisioning and apparent competition, among the overall ecological effects of a species. Temperature and depth gradients can provide a useful framework for predicting the strengths of indirect trophic interactions. Further research should investigate whether other environmental factors that influence predation rates, such as light (Hansen et al. 2013b, Davies et al. 2014), turbidity (Abrahams and Kattenfeld 1997, De Robertis et al. 2003), habitat complexity (Crowder and Cooper 1982, Jeppesen et al. 1997, Barrios-O'Neill et al. 2014), or anoxic zones (Altieri 2008, Hansen et al. 2013a) also mediate the strengths of indirect interactions.

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REFERENCES

Abrahams, M. and M. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology **40**:169-174.

Aksnes, D. L., J. Nejstgaard, E. Soedberg, and T. Sornes. 2004. Optical control of fish and zooplankton populations. Limnology and Oceanography **49**:233-238.

Altieri, A. H. 2008. Dead zones enhance key fisheries species by providing predation refuge. Ecology **89**:2808-2818.

Ashley, K., L. C. Thompson, D. C. Lasenby, L. McEachern, K. E. Smokorowski, and D. Sebastian. 1997. Restoration of an interior lake ecosystem: The Kootenay Lake fertilization experiment. Water Quality Research Journal of Canada **32**:295-323.

Barrios-O'Neill, D., J. T. A. Dick, M. C. Emmerson, A. Ricciardi, and H. J. MacIsaac. 2014. Predator-free space, functional responses and biological invasions. Functional Ecology doi: 10.1111/1365-2435.12347.

Beauchamp, D. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. American Fisheries Society Symposium **70**:53–72.

Beauchamp, D. A., D. Parrish, and R. A. Whaley. 2009. Salmonids/coldwater species in large standing waters. Pages 97-117 *in* S. Bonar, D. W. Willis, and W. A. Hubert, editors. Standard Sampling Methods for North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Beauchamp, D. A., C. J. Sergeant, M. M. Mazur, J. M. Scheuerell, D. E. Schindler, M. D. Scheuerell, K. L. Fresh, D. E. Seiler, and T. P. Quinn. 2004. Spatial-temporal dynamics of early feeding demand and food supply for sockeye salmon fry in Lake Washington. Transactions of the American Fisheries Society **133**:1014-1032.

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.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Beeton, A. and J. Bowers. 1982. Vertical migration of *Mysis relicta* Loven. Pages 53-61 *in* M. D. Morgan, editor. Ecology of Mysidacea. Springer, Netherlands.

Boscarino, B. T., L. G. Rudstam, E. R. Loew, and E. L. Mills. 2009. Predicting the vertical distribution of the opossum shrimp, *Mysis relicta*, in Lake Ontario: a test of laboratory-based light preferences. Canadian Journal of Fisheries and Aquatic Sciences **66**:101-113.

Boscarino, B. T., L. G. Rudstam, S. Mata, G. Gal, O. E. Johannsson, and E. L. Mills. 2007. The effects of temperature and predator-prey interactions on the migration behavior and vertical distribution of *Mysis relicta*. Limnology and Oceanography **52**:1599-1613.

Bowles, E. C., B. E. Rieman, G. R. Mauser, and D. H. Bennett. 1991. Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. American Fisheries Society Symposium **9**:65-74.

Brown, L. G. 1984. Lake Chelan fishery investigations. Chelan County Public Utility District No. 1 and Washington Department of Game, Olympia.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Chipps, S. R. 1998. Temperature-dependent consumption and gut-residence time in the opossum shrimp *Mysis relicta*. Journal of Plankton Research **20**:2401-2411.

Chipps, S. R. and D. H. Bennett. 2000. Zooplanktivory and nutrient regeneration by invertebrate (*Mysis relicta*) and vertebrate (*Oncorhynchus nerka*) planktivores: Implications for trophic interactions in oligotrophic lakes. Transactions of the American Fisheries Society **129**:569-583.

Chipps, S. R. and D. H. Bennett. 2002. Evaluation of a *Mysis* bioenergetics model. Journal of Plankton Research **24**:77-82.

Chipps, S. R. and J. E. Garvey. 2007. Quantitative assessment of food habits and feeding patterns. Pages 473-514 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Clarke, L. R. and D. H. Bennett. 2003. Seasonal zooplankton abundance and size fluctuations across spatial scales in Lake Pend Oreille, Idaho. Journal of Freshwater Ecology **18**:277-290.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish **14**:267-277.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters **7**:721-733.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. Journal of Animal Ecology **69**:154-164.

Crowder, L. B. and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63**:1802-1813.

Davies, T. W., J. P. Duffy, J. Bennie, and K. J. Gaston. 2014. The nature, extent, and ecological implications of marine light pollution. Frontiers in Ecology and the Environment **12**:347-355.

De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences **60**:1517-1526.

DeVries, D. R. and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 *in* B. R. Murphy and D. W. Willis, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Dryer, W. R., L. F. Erkkila, and C. L. Tetzloff. 1965. Food of lake trout in Lake Superior. Transactions of the American Fisheries Society **94**:169-176.

Ellis, B., J. Stanford, D. Goodman, C. Stafford, D. Gustafson, D. Beauchamp, D. Chess, J. Craft, M. Deleray, and B. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences **108**:1070-1075.

Fey, S. B. and C. M. Herren. 2014. Temperature-mediated biotic interactions influence enemy release of nonnative species in warming environments. Ecology **95**:2246-2256.

Gray, B. R. 2005. Selecting a distributional assumption for modelling relative densities of benthic macroinvertebrates. Ecological Modelling **185**:1-12.

Grossnickle, N. E. 1982. Feeding habits of *Mysis relicta*: an overview. Hydrobiologia **93**:101-107.

Guy, C. S., T. E. McMahon, W. A. Fredenberg, C. J. Smith, D. W. Garfield, and B. S. Cox. 2011. Diet overlap of top-level predators in recent sympatry: bull trout and nonnative lake trout. Journal of Fish and Wildlife Management **2**:183-189.

Hanley, K. A., K. Petren, and T. J. Case. 1998. An experimental investigation of the competitive displacement of a native gecko by an invading gecko: no role for parasites. Oecologia **115**:196-205.

Hansen, A. G., D. A. Beauchamp, and C. M. Baldwin. 2013a. Environmental constraints on piscivory: Insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout. Transactions of the American Fisheries Society **142**:300-316.

Hansen, A. G., D. A. Beauchamp, and E. R. Schoen. 2013b. Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. Transactions of the American Fisheries Society **142**:854-867.

Hansen, M., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator–prey dynamics in Lake Pend Oreille, Idaho, USA. Hydrobiologia **650**:85-100.

Hansen, M. J., N. J. Horner, M. Liter, M. P. Peterson, and M. A. Maiolic. 2008. Dynamics of an increasing lake trout population in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management **28**:1160-1171.

Holbrook, B. V., T. R. Hrabik, D. K. Branstrator, and A. F. Mensinger. 2013. Foraging mechanisms of age-0 lake trout (*Salvelinus namaycush*). Journal of Great Lakes Research **39**:128-137.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology **12**:197-229.

Holt, R. D. and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics **25**:495-520.

Horne, A. J. and C. R. Goldman. 1994. Limnology. McGraw-Hill, New York.

Hyatt, K. D., D. J. McQueen, K. S. Shortreed, and D. P. Rankin. 2004. Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization: Review and summary of results. Environmental Reviews **12**:133-162.

Hyatt, K. D., C. R. Ramcharan, D. J. McQueen, and K. L. Cooper. 2005. Trophic triangles and competition among vertebrate (*Oncorhynchus nerka*, *Gasterosteus aculeatus*) and macroinvertebrate (*Neomysis mercedis*) planktivores in Muriel Lake, British Columbia, Canada. Ecoscience **12**:11-26.

Iacarella, J. C., J. T. A. Dick, M. E. Alexander, and A. Ricciardi. 2015. Ecological impacts of invasive alien species along temperature gradients: testing the role of environmental matching. Ecological Applications doi: 10.1890/14-0545.1.

Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. Hydrobiologia **342**:151-164.

Johnson, B. M. and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management **20**:127-143.

Johnson, B. M. and P. J. Martinez. 2012. Hydroclimate mediates effects of a keystone species in a coldwater reservoir. Lake and Reservoir Management **28**:70-83.

Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: Interspecific resource competition or apparent competition? Ecology **79**:255-268.

Keane, R. M. and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution **17**:164-170.

Keesee, B. G. and L. M. Keller. 2013. Lake Chelan kokanee spawning ground surveys 2012. Final report. Chelan County Public Utility District, Wenatchee, Washington.

Kendra, W. and L. R. Singleton. 1987. Morphometry of Lake Chelan. Water Quality Investigations Section, Washington State Dept. of Ecology, Olympia.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature **437**:880-883.

Koksvik, J. I., H. Reinertsen, and J. Koksvik. 2009. Plankton development in Lake Jonsvatn, Norway, after introduction of *Mysis relicta*: a long-term study. Aquatic Biology **5**:293-304.

Kuns, M. M. and W. G. Sprules. 2000. Zooplankton production in Lake Ontario: a multistrata approach. Canadian Journal of Fisheries and Aquatic Sciences **57**:2240-2247.

Lasenby, D. C., T. G. Northcote, and M. Furst. 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Canadian Journal of Fisheries and Aquatic Sciences **43**:1277-1284.

Lawrence, D. J., B. Stewart-Koster, J. D. Olden, A. S. Ruesch, C. E. Torgersen, J. J. Lawler, D. P. Butcher, and J. K. Crown. 2014. The interactive effects of climate change, riparian management, and a nonnative predator on stream-rearing salmon. Ecological Applications **24**:895-912.

Levy, D. A. 1991. Acoustic analysis of diel vertical migration behavior of *Mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **48**:67-72.

Martinez, P., P. Bigelow, M. Deleray, W. Fredenberg, B. Hansen, N. Horner, S. Lehr, R. Schneidervin, S. Tolentino, and A. Viola. 2009. Western lake trout woes. Fisheries **34**:424-442.

Martinez, P. J. and E. P. Bergersen. 1991. Interactions of zooplankton, *Mysis relicta*, and kokanees in Lake Granby, Colorado. American Fisheries Society Symposium **9**:49–64.

Martinez, P. J. and W. J. Wiltzius. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management **15**:220-228.

Morgan, M. D., S. T. Threlkeld, and C. R. Goldman. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. Journal of the Fisheries Research Board of Canada **35**:1572-1579.

Nero, R. W. and I. J. Davies. 1982. Comparison of two sampling methods for estimating the abundance and distribution of *Mysis relicta*. Canadian Journal of Fisheries and Aquatic Sciences **39**:349-355.

Nesler, T. P. and E. P. Bergersen, editors. 1991. Mysids in fisheries: hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, Maryland.

Noonburg, E. G. and J. E. Byers. 2005. More harm than good: When invader vulnerability to predators enhances impact on native species. Ecology **86**:2555-2560.

Olden, J. D., O. P. Jensen, and M. J. Vander Zanden. 2006. Implications of long-term dynamics of fish and zooplankton communities for among-lake comparisons. Canadian Journal of Fisheries and Aquatic Sciences **63**:1812-1821.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure - the 3rd Tansley lecture. Journal of Animal Ecology **49**:667-685.

Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2014. Managing for coexistence of kokanee and trophy lake trout in a montane reservoir. North American Journal of Fisheries Management **34**:908-922.

Pelletier, G., C. R. Patmont, E. B. Welch, D. Bandon, and C. C. Ebbesmeyer. 1989. Lake Chelan Water Quality Assessment. Washington Department of Ecology, Olympia.

Petren, K. and T. J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology **77**:118-132.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahel, F. J. and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology **22**:521-533.

Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs **83**:263-282.

Rieman, B. E. and C. M. Falter. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Transactions of the American Fisheries Society **110**:613-620.

Rudstam, L. G. 1989. A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. Journal of Plankton Research **11**:971-983.

Scheuerell, J. M., D. E. Schindler, M. D. Scheuerell, K. L. Fresh, T. H. Sibley, A. H. Litt, and J. H. Shepherd. 2005. Temporal dynamics in foraging behavior of a pelagic predator. Canadian Journal of Fisheries and Aquatic Sciences **62**:2494-2501.

Schindler, D., J. Carter, T. Francis, P. Lisi, P. Askey, and D. Sebastian. 2012. *Mysis* in the Okanagan Lake food web: a time-series analysis of interaction strengths in an invaded plankton community. Aquatic Ecology **46**:215-227.

Schindler, D. E., S. R. Carpenter, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, and P. A. Soranno. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. Pages 96–105 *in* G. A. Polis and K. O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, New York.

Schindler, E., D. Sebastian, H. Andrusak, L. Vidmanic, S. Harris, G. Andrusak, F. Pick, L. Ley, P. Hamilton, and D. Johner. 2010. Kootenay Lake nutrient restoration program year 16

(North Arm) and year 4 (South Arm) (2007) report. Ministry of Environment, Victoria, British Columbia.

Schoen, E. R. and D. A. Beauchamp. 2010. Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management. Washington Cooperative Fish and Wildlife Research Unit, US Geological Survey, University of Washington, Seattle.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society **141**:1191-1206.

Sharp, D. and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management **8**:367-372.

Shuter, B. J. and K. K. Ing. 1997. Factors affecting the production of zooplankton in lakes. Canadian Journal of Fisheries and Aquatic Sciences **54**:359-377.

Sierszen, M. E., T. R. Hrabik, J. D. Stockwell, A. M. Cotter, J. C. Hoffman, and D. L. Yule. 2014. Depth gradients in food−web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshwater Biology **59**:1197-1212.

Simmonds, J. and D. MacLennan. 2005. Fisheries Acoustics: Theory and Practice. 2nd edition. Blackwell Science, Oxford, UK.

Smith, A. P. and D. G. Quin. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. Biological Conservation **77**:243-267.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. Bioscience **41**:14-21.

Spencer, C. N., D. S. Potter, R. T. Bukantis, and J. A. Stanford. 1999. Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. Journal of Plankton Research **21**:51-64.

Stafford, C. P., J. A. Stanford, F. R. Hauer, and E. B. Brothers. 2002. Changes in lake trout growth associated with *Mysis relicta* establishment: A retrospective analysis using otoliths. Transactions of the American Fisheries Society **131**:994-1003.

Stockwell, J. D. and O. E. Johannsson. 1997. Temperature-dependent allometric models to estimate zooplankton production in temperate freshwater lakes. Canadian Journal of Fisheries and Aquatic Sciences **54**:2350-2360.

Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences **55**:1894-1901.

Tessier, A. J. and P. Woodruff. 2002. Cryptic trophic cascade along a gradient of lake size. Ecology **83**:1263-1270.

Vander Zanden, M. J., T. E. Essington, and Y. Vadeboncoeur. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? Canadian Journal of Fisheries and Aquatic Sciences **62**:1422-1431.

Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology **84**:1083-1100.

Whall, J. D. and D. C. Lasenby. 2009. Differences in the trophic role of *Mysis diluviana* in two intermontane lakes. Aquatic Biology **5**:281-292.

White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. Diversity and Distributions **12**:443-455.

Wootton, J. T. and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology, Evolution, and Systematics **36**:419-444.

FIGURES

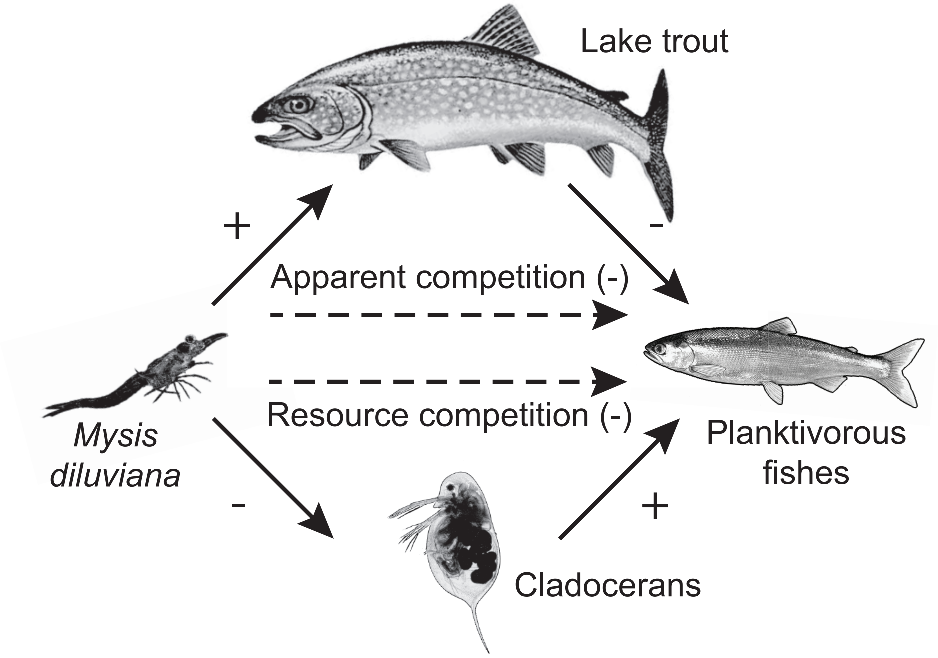

Figure 4.1. *Mysis diluviana* and planktivorous fish share preferred prey resources (cladoceran zooplankton) and predators (lake trout). Solid arrows indicate positive (+) and negative (-) direct interactions linking *Mysis* to planktivorous fish, and dashed arrows represent negative indirect interactions. Similar interactions from planktivorous fishes to *Mysis* are omitted for clarity. Illustration credits: National Oceanic and Atmospheric Administration, P. Olsen, K. Hambright.

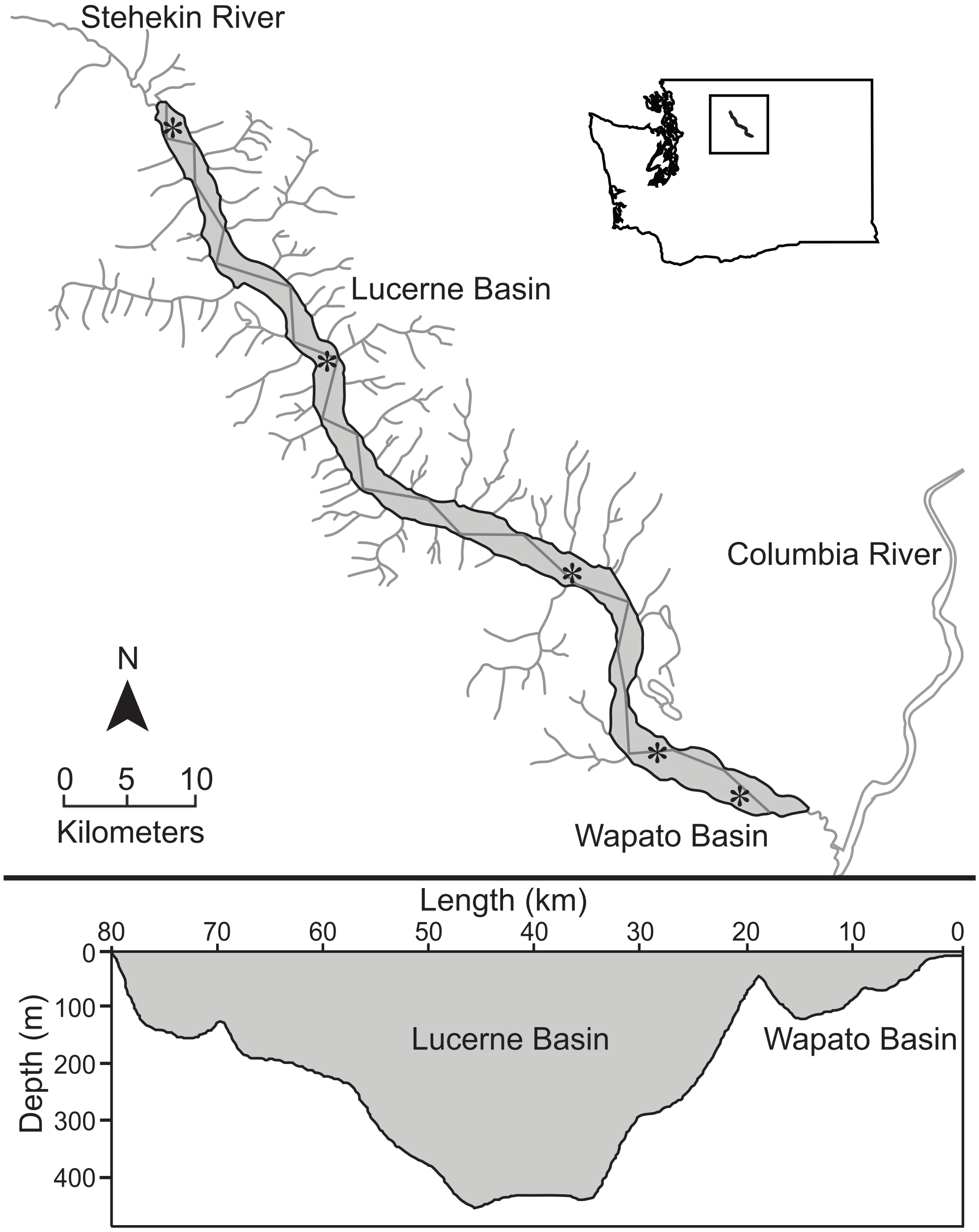

Figure 4.2. Map of Lake Chelan, Washington, USA (top panel) showing principal sampling sites (asterisks), and hydroacoustic transects (lines). Longitudinal depth profile of Lake Chelan (bottom panel) showing depth difference between lake basins. Horizontal axis represents distance from lake outlet along the primary axis of the lake.

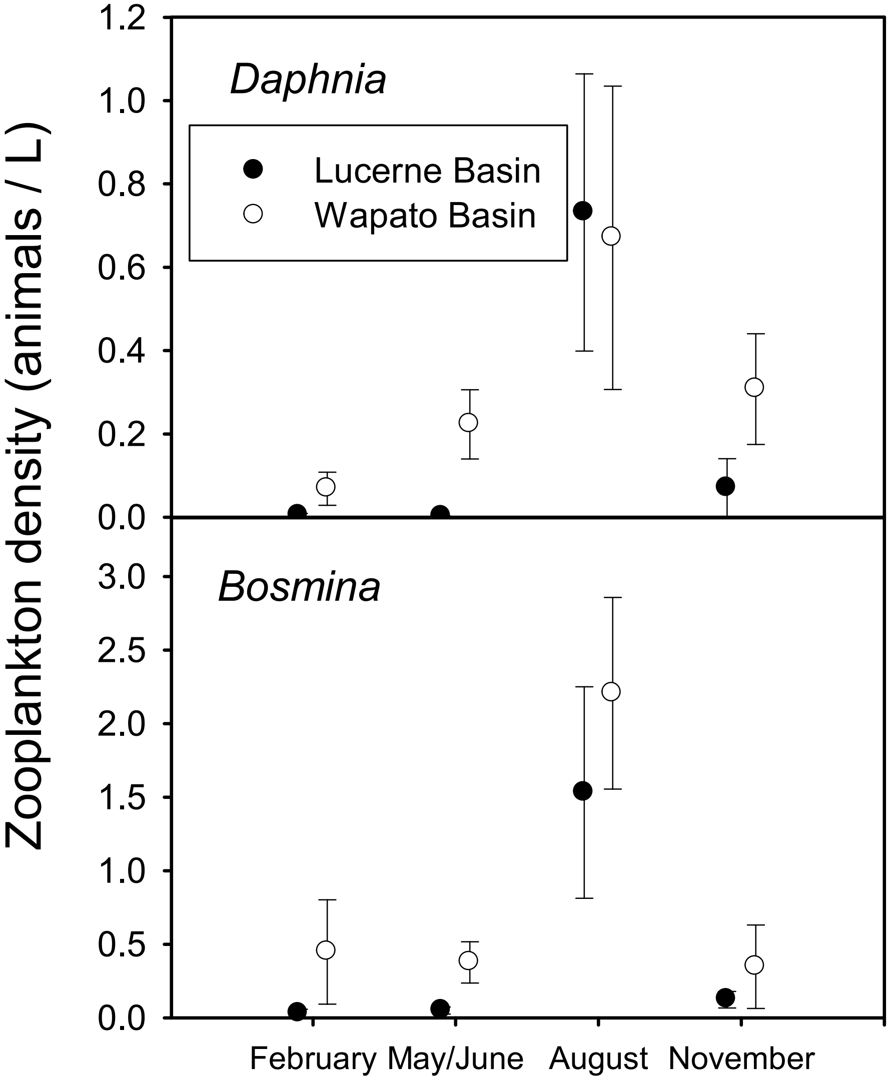

Figure 4.3. Density of primary cladoceran taxa (*Daphnia* spp. and *Bosmina longirostris*) in each lake basin. Cladoceran density was greater in the shallower Wapato Basin than in the deeper Lucerne Basin except during August. Symbols represent means ±1 standard error.

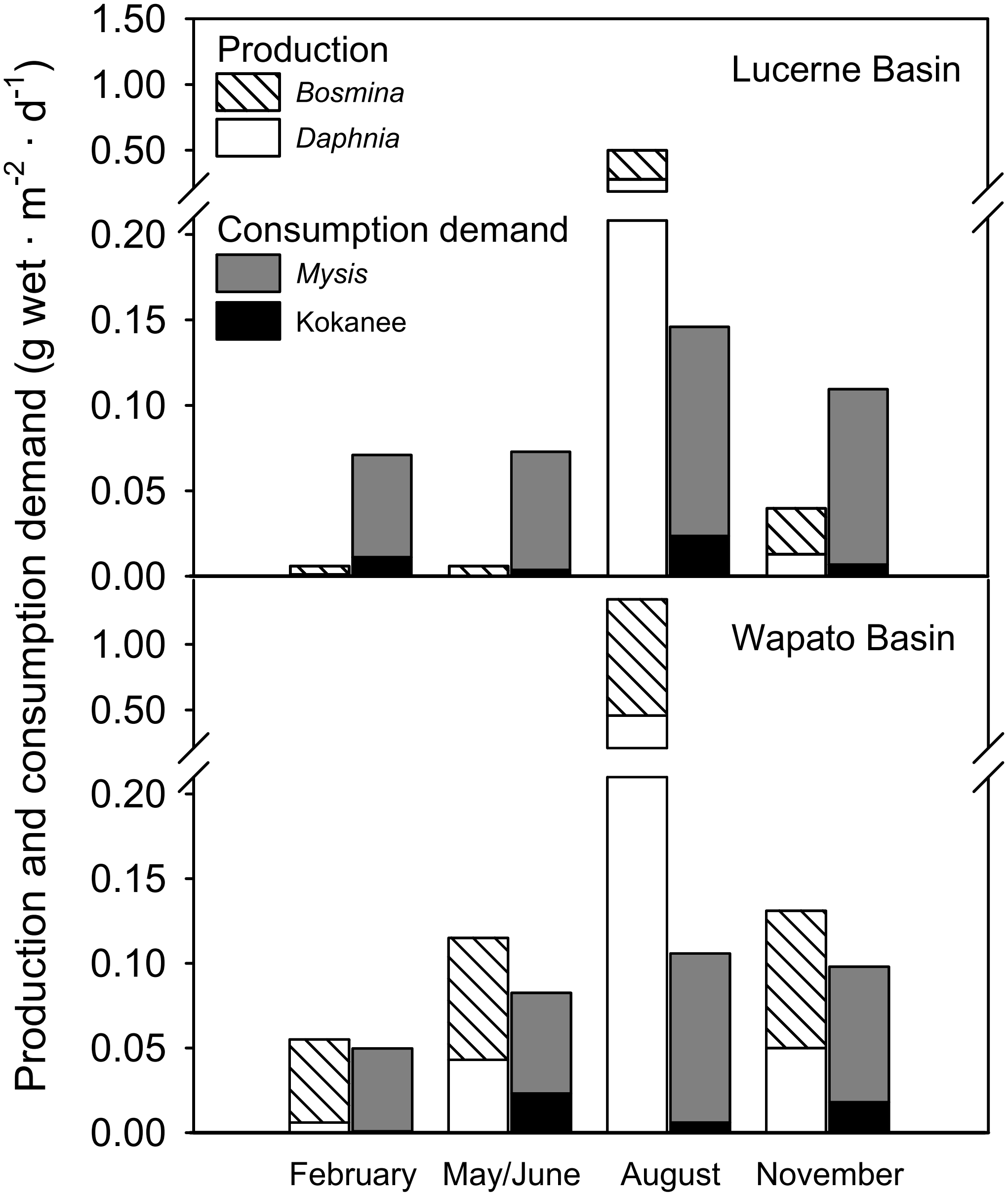

Figure 4.4. Production rates of major zooplankton taxa and consumption rates of zooplankton by *Mysis* and kokanee populations in each lake basin. Production of preferred cladoceran prey (*Daphnia* and *Bosmina*) was greater in the shallower Wapato Basin than in the deeper Lucerne Basin in all periods. Consumption by the *Mysis* population far exceeded consumption by kokanee. Cladoceran production consistently met or exceeded planktivore consumption demand in Wapato Basin but not in Lucerne Basin.

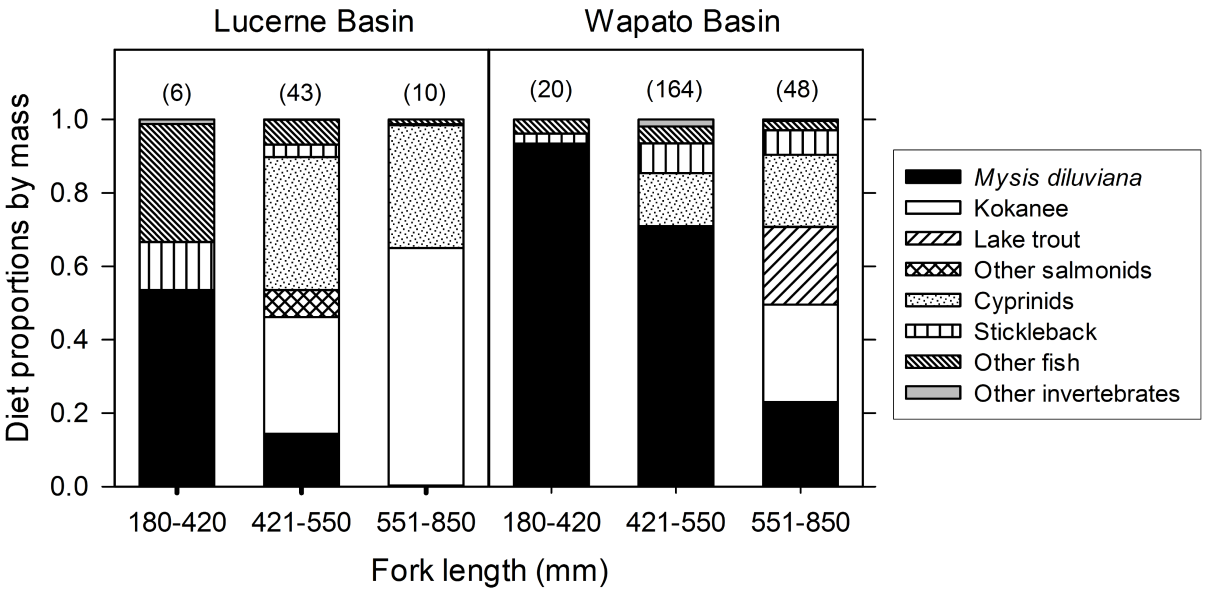

Figure 4.5. Diet composition of three size classes of lake trout in the two lake basins (proportions of diet by mass). Within each size class, *Mysis* represented a smaller fraction of the lake trout diet in the shallower Wapato Basin than in the deeper Lucerne Basin. Sample sizes of non-empty stomachs are shown in parentheses.

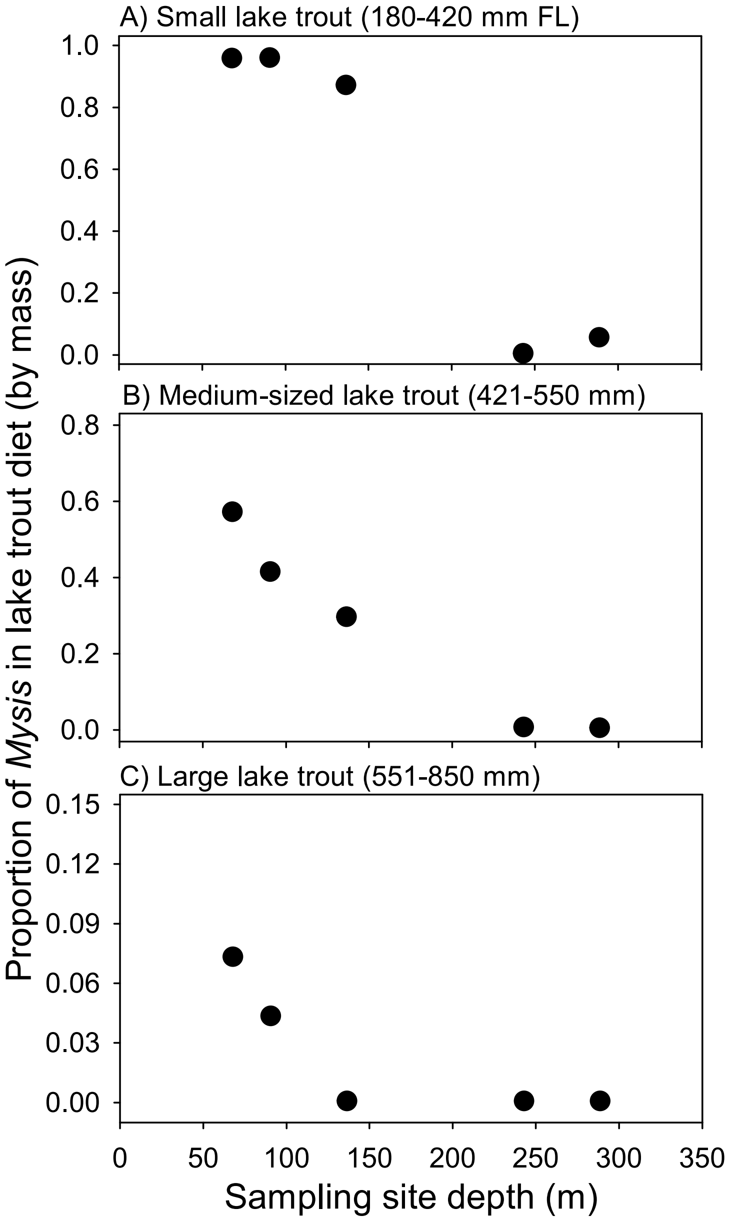

Figure 4.6. Diet proportion of *Mysis* (by mass) with respect to sampling site depth (m) for three size classes of lake trout: (A) 180-420 mm fork length (FL), (B) 421-550 mm, and (C) 551-850 mm. *Y*-axes differ among panels. Within each size class, *Mysis* represented a smaller fraction of the diet at deeper sites. The shallowest two sites were within Wapato Basin, and the deepest three sites were within Lucerne Basin.

APPENDIX A. ZOOPLANKTON ANALYSIS: DETAILED METHODS, MODEL SELECTION RESULTS, AND STANDING STOCK BIOMASS FIGURE.

We identified, enumerated, and measured subsamples of each zooplankton sample. We counted eggs attached to or contained within individual zooplankton of each taxon. Loose eggs were identified as cladoceran or copepod based on size and assigned to taxa within those groups based on the proportion of adults in the sample. We measured a subsample of zooplankton of each taxon from the base of the helmet to the base of the tail spine or setae using an ocular micrometer. We estimated the wet mass of each taxon from length data using taxa-specific length-mass relationships and a wet : dry mass ratio of 10:1 (Dumont et al. 1975, Rieman and Falter 1981). We estimated the efficiency of the zooplankton net as 33.8% ± 2.0% (mean ± SE) by comparison with a metered Clarke-Bumpus sampler (Clarke and Bumpus 1950). For this comparison, we sampled zooplankton from 10 m to the surface with seven replicate vertical hauls using the ring net and one oblique tow with the Clarke-Bumpus sampler conducted at the same time and location. The Clarke-Bumpus tow followed a widely curved path to ensure that it cut across Langmuir cells, reducing fine-scale patchiness (Edmondson and Litt 1982).

References

Clarke, G. and D. Bumpus. 1950. The plankton sampler—an instrument for quantitative plankton investigation. Limnological Society of America Special Publication **5**:8.

Dumont, H. J., I. Vandevelde, and S. Dumont. 1975. Dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from plankton, periphyton and benthos of continental waters. Oecologia **19**:75-97.

Edmondson, W. and A. H. Litt. 1982. *Daphnia* in Lake Washington. Limnology and Oceanography **27**:272-293.

Rieman, B. E. and C. M. Falter. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Transactions of the American Fisheries Society **110**:613-620.

Table 4.A1. Model selection results evaluating the effects of season, lake basin, or a combination of these factors on the adult density, egg density, and body length of *Daphnia* and *Bosmina*.

Model	k	$-2l$	AIC$_c$	ΔAIC$_c$	w_i
Daphnia adult density					
Season	5	178.6	191.0	7.43	0.015
Basin	3	188.3	195.2	11.68	0.002
Season + Basin	6	168.1	183.6	***0***	***0.603***
Season + Basin + Season×Basin	9	157.9	184.5	***0.92***	***0.381***
Bosmina adult density					
Season	5	232.3	244.7	4.23	0.105
Basin	3	242.1	249.0	8.50	0.012
Season + Basin	6	225.0	240.5	***0***	***0.868***
Season + Basin + Season×Basin	9	222.0	248.6	8.14	0.015
Daphnia egg density					
Season	5	108.2	120.7	5.64	0.040
Basin	3	118.1	125.0	9.93	0.005
Season + Basin	6	99.4	115.1	***0***	***0.671***
Season + Basin + Season×Basin	9	89.8	116.8	***1.75***	***0.280***
Bosmina egg density					
Season	5	138.6	151.1	3.01	0.104
Basin	3	141.5	148.4	***0.34***	***0.396***
Season + Basin	6	132.4	148.1	***0***	***0.469***
Season + Basin + Season×Basin	9	126.5	153.5	5.42	0.031
Daphnia body length					
Season	5	-133.76	-123.58	***0***	***0.63***
Basin	3	-95.14	-89.08	34.5	0
Season + Basin	6	-133.88	-121.65	***1.93***	***0.24***
Season + Basin + Season×Basin	9	-138.86	-120.34	3.24	0.13
Bosmina body length					
Season	5	45.2	55.45	6.62	0.03
Basin	3	64.86	70.97	22.13	0
Season + Basin	6	39.48	51.82	2.99	0.18
Season + Basin + Season×Basin	9	30.08	48.83	***0***	***0.79***

Notes: Values shown for each model include the number of parameters k, the log likelihood l, the differences of the corrected Akaike's information criterion among models (ΔAIC$_c$), and Akaike weights (w_i). Values in bold italics correspond to the best-fitting models (i.e., ΔAIC$_c \leq 2$).

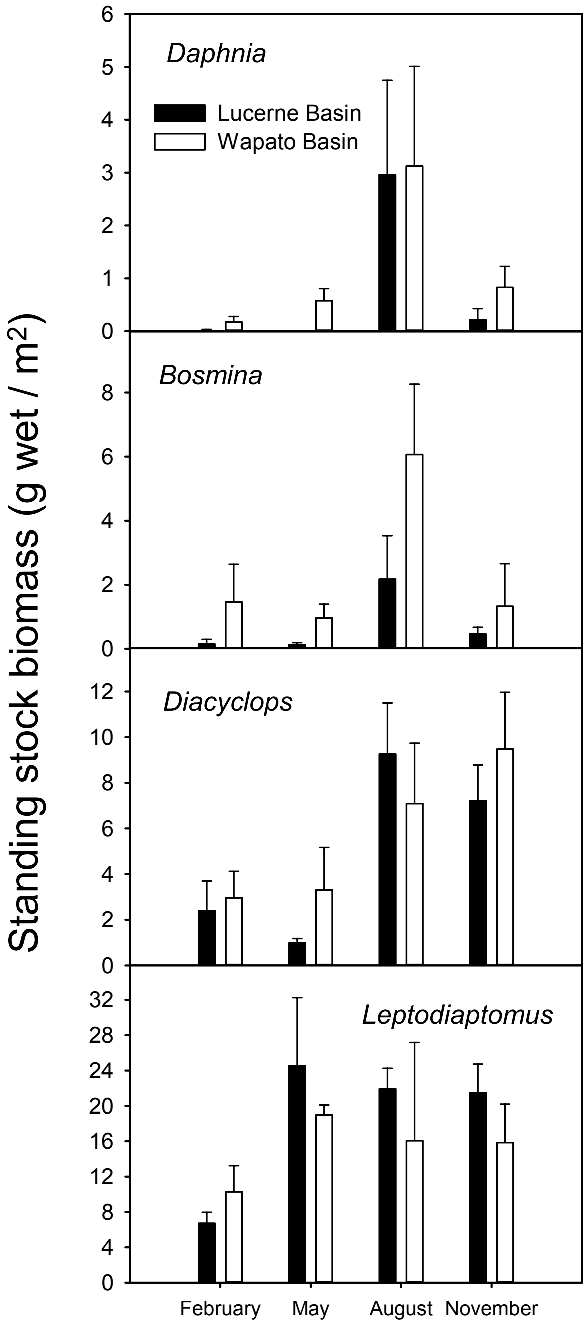

Figure 4.A1. Seasonal standing stock biomass of primary cladoceran (*Daphnia* and *Bosmina*) and copepod (*Diacyclops* and *Leptodiaptomus*) taxa in Lucerne and Wapato Basins. Bars represent means plus one standard error.

APPENDIX B. HYDROACOUSTICS ANALYSIS: DETAILED METHODS, KOKANEE DENSITY AND ABUNDANCE, AND VERTICAL DISTRIBUTION OF KOKANEE AND *MYSIS*.

We conducted hydroacoustic surveys at night during February, May, August, and November, 2005. Each survey consisted of 22 transects in a zig-zag pattern (Simmonds and MacLennan 2005). We used a Biosonics DE 6000 echosounder and a 200-kHz split-beam transducer with a 6.7° beam width. We used a target-strength threshold of -55 dB, allowing detection of fish as small as 30 mm total length (Love 1971). We conducted supplemental short transects in conjunction with each *Mysis* haul to determine the vertical distribution of *Mysis*. We used a target-strength threshold of -70 dB for *Mysis* transects, a compromise level that allowed us to detect the *Mysis* scattering layer as deep at 100 m, although it was not sensitive enough to detect individual mysids (Rudstam et al. 2008). We recorded the upper and lower limits of the continuous *Mysis* scattering layer in these echograms. We followed the hydroacoustic data acquisition methods and stratified statistical design of Schoen et al. (2012) for the kokanee surveys. We estimated kokanee density by echo counting single acoustic targets with Echoview version 4.2 software (Myriax Pty). Kokanee were dispersed from schools during the night-time surveys and relatively low in density (August mean density = 46.6 kokanee / ha), justifying this approach (Rudstam et al. 2012). We excluded data collected within 4 m of the transducer face from the analysis due to near-field distortion and the potential for boat avoidance (Rudstam et al. 2012). We assumed that all small (< 330 mm FL), pelagic targets (> 5 m above the lake bottom) were kokanee because kokanee comprised 95% of the mid-water gill net catch and modal sizes of acoustic targets corresponded with the size distribution of kokanee. We used size modes of hydroacoustic targets to assign targets to kokanee age classes.

We estimated the areal density of kokanee in each lake basin, partitioned by age class and season. We converted density to abundance by multiplying by the surface area of the pelagic zone (defined here as bottom depth > 15 m) of each basin (Kendra and Singleton 1987). The August survey was conducted under optimal conditions for determining kokanee abundance, on moonless nights during peak thermal stratification (Beauchamp et al. 2009). During the other months, kokanee were only partially detectable due to a shallower distribution and greater potential for boat avoidance. Thus, we used the August survey to determine the absolute abundance of kokanee, and we used the February, May, and November surveys to quantify seasonal changes in relative abundance between lake basins. We then estimated the absolute abundance of kokanee during February, May, and November by adjusting the August abundance to account for mortality (see below) and partitioning the lake-wide population between basins using the relative abundances determined in the seasonal surveys. We quantified the uncertainty in the density, abundance, and survival estimates with 95% BCa bootstrapped confidence intervals calculated in R with the 'boot' package (Canty and Ripley 2014).

We estimated age-specific kokanee survival rates from our hydroacoustic data and the literature. We estimated the annual survival rate of age-0 and age-1 kokanee based on the ratio of these age classes detected in the August 2005 hydroacoustic survey. We assumed recruitment of these cohorts was nearly equal (Miranda and Bettoli 2007), which was reasonable because similar numbers of kokanee spawned in the 2003 and 2004 brood years (5% difference; Schoen and Beauchamp 2010) and similar numbers of age-0 kokanee were stocked in 2004 and 2005 (7% difference; Keesee and Keller 2013). We estimated an annual survival rate $S = 49.5\%$ (95% CI: 43.8-60.4%; instantaneous annual mortality rate $Z = 0.703$, 95% CI: 0.505-0.826) for age-0 and age-1 kokanee. This was similar to survival rates reported for juvenile kokanee in other lakes (reviewed by McGurk 1999). We used literature data to estimate the survival of older kokanee age classes. The hydroacoustics data were not suitable for estimating survival of the age-2 and older cohorts because their size modes overlapped and spawner numbers varied substantially between their respective brood years, violating the assumption of equal recruitment. Instead, we estimated the survival rate of kokanee 2 years and older as 33% ($Z = 1.11 \pm 0.133$ / yr; mean ± SE), the survival rate reported for 48 brood years of age 2-3 kokanee across eight other lakes (McGurk 1999). To incorporate uncertainty in this literature-based survival rate into our abundance calculations, we randomly drew a value of Z from a normal distribution with the above parameters for each bootstrapped simulation.

References

Beauchamp, D. A., D. Parrish, and R. A. Whaley. 2009. Salmonids/coldwater species in large standing waters. Pages 97-117 *in* S. Bonar, D. W. Willis, and W. A. Hubert, editors. Standard Sampling Methods for North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Canty, A. and B. Ripley. 2014. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-11.

Keesee, B. G. and L. M. Keller. 2013. Lake Chelan kokanee spawning ground surveys 2012. Final report. Chelan County Public Utility District, Wenatchee, Washington.

Kendra, W. and L. R. Singleton. 1987. Morphometry of Lake Chelan. Water Quality Investigations Section, Washington State Dept. of Ecology, Olympia.

Love, R. 1971. Dorsal aspect target strength of an individual fish. The Journal of the Acoustical Society of America **49**:816.

McGurk, M. D. 1999. Size dependence of natural mortality rate of sockeye salmon and kokanee in freshwater. North American Journal of Fisheries Management **19**:376-396.

Miranda, L. E. and P. W. Bettoli. 2007. Mortality. Pages 229-277 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Rudstam, L. G., J. M. Jech, S. L. Parker-Stetter, J. K. Horne, P. J. Sullivan, and D. M. Mason. 2012. Fisheries acoustics. Pages 597-636 *in* A. V. Zale, D. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Rudstam, L. G., F. R. Knudsen, H. Balk, G. Gal, B. T. Boscarino, and T. Axenrot. 2008. Acoustic characterization of *Mysis relicta* at multiple frequencies. Canadian Journal of Fisheries and Aquatic Sciences **65**:2769-2779.

Schoen, E. R. and D. A. Beauchamp. 2010. Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management. Washington Cooperative Fish and Wildlife Research Unit, US Geological Survey, University of Washington, Seattle.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society **141**:1191-1206.

Simmonds, J. and D. MacLennan. 2005. Fisheries Acoustics: Theory and Practice. 2nd edition. Blackwell Science, Oxford, UK.

Beauchamp, D. A., D. Parrish, and R. A. Whaley. 2009. Salmonids/coldwater species in large standing waters. Pages 97-117 *in* S. Bonar, D. W. Willis, and W. A. Hubert, editors. Standard Sampling Methods for North American Freshwater Fishes. American Fisheries Society, Bethesda, Maryland.

Canty, A. and B. Ripley. 2014. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-11.

Keesee, B. G. and L. M. Keller. 2013. Lake Chelan kokanee spawning ground surveys 2012. Final report. Chelan County Public Utility District, Wenatchee, Washington.

Kendra, W. and L. R. Singleton. 1987. Morphometry of Lake Chelan. Water Quality Investigations Section, Washington State Dept. of Ecology, Olympia.

Love, R. 1971. Dorsal aspect target strength of an individual fish. The Journal of the Acoustical Society of America **49**:816.

McGurk, M. D. 1999. Size dependence of natural mortality rate of sockeye salmon and kokanee in freshwater. North American Journal of Fisheries Management **19**:376-396.

Miranda, L. E. and P. W. Bettoli. 2007. Mortality. Pages 229-277 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Rudstam, L. G., J. M. Jech, S. L. Parker-Stetter, J. K. Horne, P. J. Sullivan, and D. M. Mason. 2012. Fisheries acoustics. Pages 597-636 *in* A. V. Zale, D. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Rudstam, L. G., F. R. Knudsen, H. Balk, G. Gal, B. T. Boscarino, and T. Axenrot. 2008. Acoustic characterization of *Mysis relicta* at multiple frequencies. Canadian Journal of Fisheries and Aquatic Sciences **65**:2769-2779.

Schoen, E. R. and D. A. Beauchamp. 2010. Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management. Washington Cooperative Fish and Wildlife Research Unit, US Geological Survey, University of Washington, Seattle.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society **141**:1191-1206.

Simmonds, J. and D. MacLennan. 2005. Fisheries Acoustics: Theory and Practice. 2nd edition. Blackwell Science, Oxford, UK.

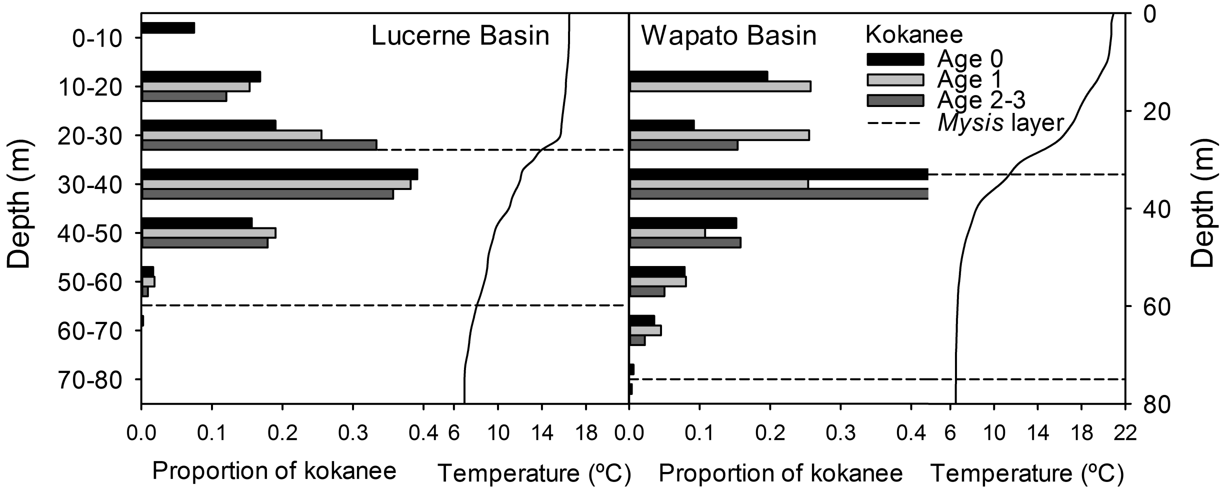

Figure 4.B1. Typical vertical distributions of kokanee and *Mysis* at night in Lucerne and Wapato Basins (August 2005 distributions depicted here). Kokanee and *Mysis* distributions were determined from hydroacoustic surveys. Dashed lines represent the vertical extent of the *Mysis* scattering layer viewed on hydroacoustic echograms. Solid curves represent thermal profiles. In both basins, kokanee were distributed both above and below the thermocline, while *Mysis* were restricted to deeper waters cooler than 14° C.

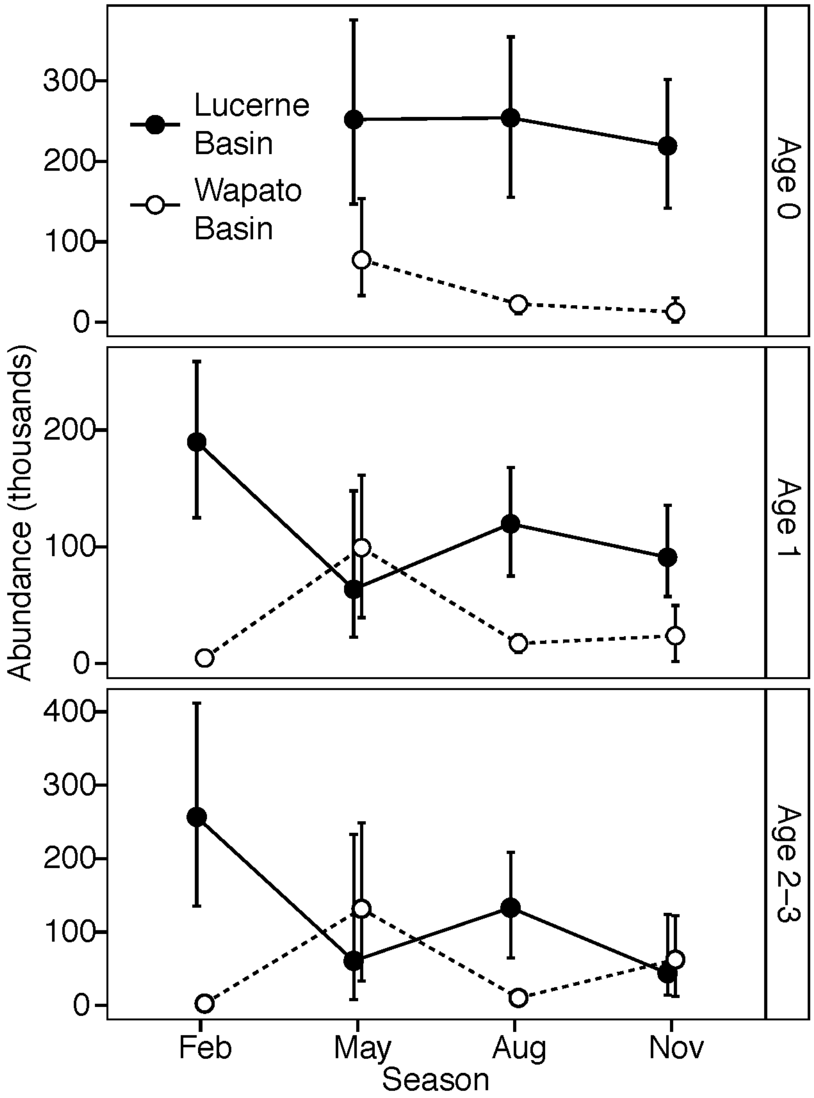

Figure 4.B2. Seasonal kokanee abundance in Lucerne and Wapato Basins as estimated from hydroacoustic surveys. Error bars represent 95% bootstrapped confidence intervals. Values are slightly shifted horizontally to show overlapping points.

Appendix C. Bioenergetics models for *Mysis* and kokanee: detailed methods and consumption : production ratios.

We quantified growth of *Mysis* by tracking the mean wet mass of each age class (Figure 4.C1). We measured *Mysis* individuals for body length, from the tip of the rostrum to the tip of the telson, and for blotted wet mass. We identified *Mysis* age classes from modes in length-frequency histograms. *Mysis* exhibited a 1.5-year life span, with juveniles released by females between February and May and the parental generation senescing by the following November. Total *Mysis* growth from juvenile to adult was similar among lake basins, but seasonal growth patterns differed slightly (Figure 4.C1). *Mysis* in Wapato Basin grew rapidly between May and August but grew more slowly during the rest of the year, while *Mysis* grew at a relatively consistent rate year round in Lucerne Basin. To determine whether size-selective predation negatively biased estimates of *Mysis* growth in the Wapato Basin during August, when growth appeared to be slow or slightly negative, we compared the length distribution of mysids collected in net tows to the length distribution of *Mysis* found in lake trout and burbot *Lota lota* stomachs collected during that period. We reconstructed the body lengths of partially digested *Mysis* based on lengths of eye stalks, which were usually intact in stomach samples (Gal et al. 2006). We derived a linear regression relating body length (BL) to eye-stalk length (EL), both measured in mm, using intact mysids collected by net ($n = 90$, $r^2 = 0.87$, $p < 0.001$):

$$BL = 144.7\ EL - 1.70. \qquad (4C.1)$$

Mysis in stomachs were slightly larger than *Mysis* collected in nets, suggesting that predation was weakly size selective, although this difference was not significant ($t = 1.471$, df = 225, $p = 0.14$).

We characterized kokanee growth with a mass-at-age relationship. We calculated mean wet mass for age 1, 2, and 3 kokanee captured during May and for maturing kokanee captured in August, which were preparing to spawn at age 4 (Table 4.C2). Kokanee grew to a mean body mass of 262.1 ± 8.6 g at age 3 in August (mean ± SE). We estimated the mass of age-0 kokanee in May from the mean acoustic target strength of age-0 kokanee detected during the May survey, using Love's (1971) target strength-total length relationship, a total length to fork length relationship for kokanee (Hyatt and Hubert 2000), and a length-mass relationship for Lake Chelan kokanee (Schoen et al. 2012). We treated kokanee as a single population moving between Wapato and Lucerne Basins, with identical growth inputs in each basin.

We estimated the thermal experience of *Mysis* as the mean temperature of the hypolimnion, metalimnion, and the depth reached at the apex of the vertical migration, weighted by time spent in each depth zone (Table 4.C3). We assumed mysids spent the daylight and civil twilight period in the hypolimnion, one hour in the metalimnion during each of the upward and downward migrations, and the remainder of the diel period at the apex depth (seasonal daylight data for Chelan, WA from US Naval Observatory, Astronomical Applications Department: <http://aa.usno.navy.mil>). We estimated the thermal experience of kokanee as the mean temperature of the metalimnion or the mean temperature of the upper 50 m of the water column during non-stratified periods (Table 4.C4).

We estimated the diet compositions of *Mysis* and kokanee from field and literature data. We estimated the proportions of phytoplankton and zooplankton in the diets of juvenile *Mysis* (length < 8 mm) and adult *Mysis* with a simple two-source linear mixing model (Phillips and Gregg 2001) using stable isotope signatures from Lake Chelan (Schoen and Beauchamp 2010). We used filter-feeding clams (*Corbicula* spp.) as a surrogate for zooplankton to reduce isotopic variability, and we assumed that clams and zooplankton were herbivorous, with a trophic fractionation rate of 3.4‰ $\delta^{15}N$ (Post 2002). This model assigned juvenile *Mysis* a fully herbivorous diet, in agreement with literature data (Rybock 1978, Chipps 1997, Johannsson et al. 2001). The model assigned adult *Mysis* a diet of 70% zooplankton and 30% phytoplankton that was similar to the omnivorous diets reported in other oligotrophic lakes (Grossnickle 1982, Johannsson et al. 2001, Nordin et al. 2007). We determined the basin-specific, seasonal diet composition of kokanee from stomach samples collected between May and August (our table 4.C4; Brown 1984). Kokanee diets collected in Wapato Basin during May and June consisted predominantly of *Diacyclops* (age 1 kokanee) or chironomids, *Daphnia*, and *Bosmina* (ages 2 and 3 kokanee). In the Lucerne Basin during August, kokanee ate *Daphnia* and *Bosmina* almost exclusively. When field data were not available, we assumed the proportions of cladocerans and copepods in the kokanee diet were equal to their relative abundance in net samples, except we assumed kokanee consumed exclusively cladocerans when the cladoceran density exceeded 0.4 animals / L, a prey-switching threshold for juvenile sockeye salmon (*O. nerka*) (Scheuerell et al. 2005).

We compiled energy densities of *Mysis*, kokanee, and their prey from literature values (Tables 4.C3 and 4.C4). We used reported energy densities of adult and juvenile *Mysis* (Lasenby 1971) for May and August, and the adult value was reduced by 20% during November and February to account for diminished *Mysis* lipid reserves during winter (Adare and Lasenby 1994, Chipps and Bennett 2000). The energy density of kokanee varied with body size following Beauchamp et al. (1989). We adjusted the energy density of zooplankton prey seasonally for *Mysis*. We used the energy density of cladocerans (1620 J / g) during August, when *Daphnia* and *Bosmina* were abundant, and we used the energy density of copepods (2260 J / g; Luecke and Brandt 1993) during all other months. We used a higher energy density of 3800 J / g for cladocerans consumed by kokanee to account for water squeezed out of the carapace during ingestion, and we corrected the model outputs to indicate the biomass of live cladocerans removed from the lake (Luecke and Brandt 1993, Stockwell et al. 1999).

References

Adare, K. I. and D. C. Lasenby. 1994. Seasonal changes in the total lipid content of the opossum shrimp, *Mysis relicta* (Malacostraca, Mysidacea). Canadian Journal of Fisheries and Aquatic Sciences **51**:1935-1941.

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.

Brown, L. G. 1984. Lake Chelan fishery investigations. Chelan County Public Utility District No. 1 and Washington Department of Game, Olympia.

Chipps, S. R. 1997. *Mysis relicta* in Lake Pend Oreille: seasonal energy requirements and implications for mysid-cladoceran interactions. Doctoral dissertation. University of Idaho.

Chipps, S. R. and D. H. Bennett. 2000. Zooplanktivory and nutrient regeneration by invertebrate (*Mysis relicta*) and vertebrate (*Oncorhynchus nerka*) planktivores: Implications for trophic interactions in oligotrophic lakes. Transactions of the American Fisheries Society **129**:569-583.

Gal, G., L. G. Rudstam, E. L. Mills, J. R. Lantry, O. E. Johannsson, and C. H. Greene. 2006. Mysid and fish zooplanktivory in Lake Ontario: quantification of direct and indirect effects. Canadian Journal of Fisheries and Aquatic Sciences **63**:2734-2747.

Grossnickle, N. E. 1982. Feeding habits of *Mysis relicta*: an overview. Hydrobiologia **93**:101-107.

Hyatt, M. H. and W. A. Hubert. 2000. Proposed standard-weight (W_s) equations for kokanee, golden trout and bull trout. Journal of Freshwater Ecology **15**:559-563.

Johannsson, O. E., M. F. Leggett, L. G. Rudstam, M. R. Servos, M. A. Mohammadian, G. Gal, R. M. Dermott, and R. H. Hesslein. 2001. Diet of *Mysis relicta* in Lake Ontario as revealed by stable isotope and gut content analysis. Canadian Journal of Fisheries and Aquatic Sciences **58**:1975-1986.

Lasenby, D. C. 1971. The ecology of *Mysis relicta* in an arctic and a temperate lake. Doctoral dissertation. University of Toronto, Toronto.

Love, R. 1971. Dorsal aspect target strength of an individual fish. The Journal of the Acoustical Society of America **49**:816.

Luecke, C. and D. Brandt. 1993. Estimating the energy density of daphnid prey for use with rainbow trout bioenergetics models. Transactions of the American Fisheries Society **122**:386-389.

Nordin, L. J., M. T. Arts, O. E. Johannsson, and W. D. Taylor. 2007. An evaluation of the diet of *Mysis relict*a using gut contents and fatty acid profiles in lakes with and without the invader *Bythotrephes longimanus* (Onychopoda, Cercopagidae). Aquatic Ecology **42**:421-436.

Phillips, D. L. and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia **127**:171-179.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology **83**:703-718.

Rybock, J. T. 1978. *Mysis relicta* Loven in Lake Tahoe: Vertical distribution and nocturnal predation. Doctoral dissertation. University of California-Davis.

Scheuerell, J. M., D. E. Schindler, M. D. Scheuerell, K. L. Fresh, T. H. Sibley, A. H. Litt, and J. H. Shepherd. 2005. Temporal dynamics in foraging behavior of a pelagic predator. Canadian Journal of Fisheries and Aquatic Sciences **62**:2494-2501.

Schoen, E. R. and D. A. Beauchamp. 2010. Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management. Washington Cooperative Fish and Wildlife Research Unit, US Geological Survey, University of Washington, Seattle.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society **141**:1191-1206.

Stockwell, J. D., K. L. Bonfantine, and B. M. Johnson. 1999. Kokanee foraging: A *Daphnia* in the stomach is worth two in the lake. Transactions of the American Fisheries Society **128**:169-174.

Table 4.C1. Ratios of the combined zooplankton consumption rate of the *Mysis diluviana* and kokanee populations to the production rates of cladocerans only, or cladocerans and copepods (C:P ratios) in Lucerne and Wapato Basins.

	Cladocerans only		Cladocerans + Copepods	
Month	Lucerne	Wapato	Lucerne	Wapato
February	12.04	0.91	0.56	0.24
May/June	11.29	0.72	0.25	0.13
August	0.28	0.08	0.08	0.04
November	2.72	0.75	0.16	0.12

Table 4.C2. Growth inputs used in bioenergetics simulations for kokanee.

Age	Month	Body mass (g wet)
0	May	1.25
1	May	37.5
2	May	165.8
3	May	225.2
3	August	262.1

Note: Age 3 kokanee captured during August were maturing adults preparing to spawn 1-2 months later at age 4.

Table 4.C3. Thermal experience, diet composition (by mass), and energy density inputs used in bioenergetics simulations for *Mysis diluviana*.

		Thermal experience (ºC)		*Mysis* energy density (J / g wet)	Diet composition	
Age	Month	Lucerne	Wapato		Algae (2558)[†]	Zooplankton (1,620-2,260)[‡]
0	May	7.0	5.9	3135	1	0
0	August	8.4	6.8	3720	0.3	0.7
0	November	8.8	9.4	2976	0.3	0.7
1	February	6.3	5.4	2976	0.3	0.7
1	May	7.0	5.9	3720	0.3	0.7
1	August	8.4	6.8	3720	0.3	0.7

Notes: Thermal experience is reported separately for Lucerne and Wapato Basins. The energy density (J / g wet mass) of each prey type is indicated in parentheses.

[†] Cummins and Wuycheck (1971).

[‡] The energy density of zooplankton varied seasonally (see text).

Table 4.C4. Thermal experience, diet composition (by mass), and prey energy density inputs used in bioenergetics simulations for kokanee in Lucerne and Wapato Basins.

	Thermal experience (ºC)		Diet composition: Lucerne			Diet composition: Wapato		
Month	Lucerne	Wapato	Chironomids (3400)	Cladocerans (3800)	Copepods (2260)	Chironomids (3400)	Cladocerans (3800)	Copepods (2260)
Feb	6.3	5.4	0.00	0.00	1.00	0.00	1.00	0.00
May	8.0	9.4	0.00	0.00	1.00	0.49	0.48	0.03
Aug	12.1	13.8	0.00	1.00	0.00	0.00	1.00	0.00
Nov	9.1	8.5	0.00	0.01	0.99	0.00	1.00	0.00

Note: The energy density (J / g wet mass) of each prey type is indicated in parentheses.

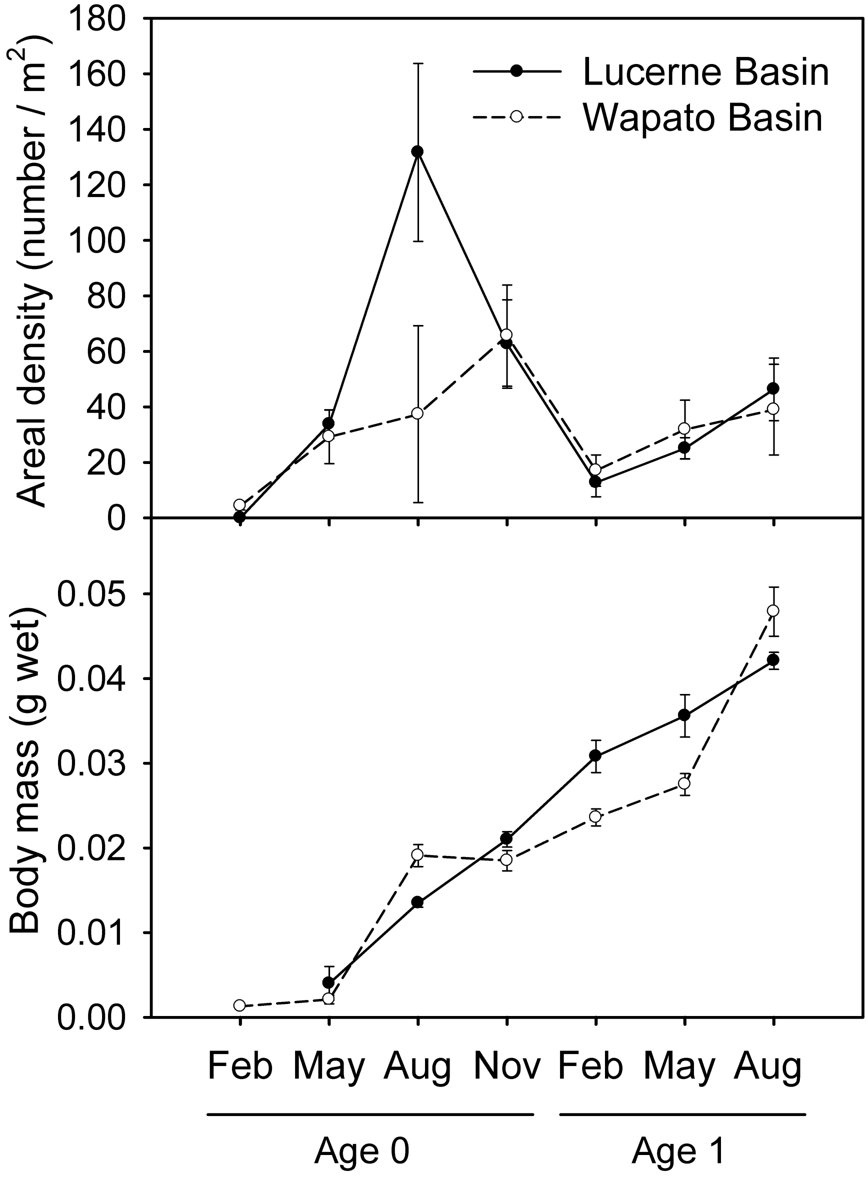

Figure 4.C1. Density of *Mysis diluviana* in the upper 80 m of the water column at night (top panel). *Mysis* densities varied seasonally due to mortality and changes in the proportion of the population that ascended into the water column. Growth of *Mysis* (bottom panel). *Mysis* exhibited a 1.5 year life cycle with two overlapping generations present during February through August. Symbols represent means ± 1 standard error.

APPENDIX D. LAKE TROUT GROWTH MODELS, LAKE TROUT CATCH RATES, AND PREDATION RISK FOR KOKANEE

Lake trout growth models

We compared the growth patterns of lake trout between basins using a von Bertalanffy growth model:

$$L_t = L_\infty \cdot (1 - e^{-(\omega/L_\infty)\cdot t}) \qquad (4D.1)$$

where L_t is fork length (mm) at age t (years), L_∞ is the asymptotic maximum length (mm), and ω is the growth rate in length of young fish (mm/year) (Gallucci and Quinn 1979). We tested whether growth patterns differed between lake basins by fitting a full model with separate L_∞ and ω values for each basin and three reduced models with basin-specific values for L_∞ only, ω only, and identical parameters for both basins, assuming lognormal process error. We evaluated models using AIC_c weights (Burnham and Anderson 2002).

Next, we compared the length-mass relationship of lake trout between basins using the following model:

$$M = a \cdot \text{FL}^b \qquad (4D.2)$$

where M is wet mass (g), FL is fork length (mm), and a and b are fitted parameters. We $\log_{10}$-transformed both sides of this relationship and tested whether the length-mass relationship differed between lake basins by a set of candidate models as above. The full model predicted *log*(M) and included basin as a factor, *log*(FL) as a covariate, and an interaction between basin and *log*(FL). We selected the most parsimonious model using AIC_c and back-transformed it into the form of equation 4D.2. We reported model selection results in the main text. The relationship of fork length FL (mm) to wet mass M (g) for Wapato Basin ($r^2 = 0.93$, $n = 390$, $P < 0.0001$) was:

$$M = 0.0000141 \bullet \mathrm{FL}^{2.98}, \tag{4D.3}$$

and for Lucerne Basin ($r^2 = 0.93$, $n = 105$, $P < 0.0001$) was:

$$M = 0.00000360 \bullet \mathrm{FL}^{3.18}. \tag{4D.4}$$

Predation risk for kokanee

We reanalyzed a published estimate of population-level lake trout consumption in Lake Chelan (Schoen et al. 2012) to estimate the biomass of kokanee consumed in each lake basin. The published analysis used a bioenergetics model with field input data pooled from both lake basins coupled with an age-structured population model. During the years of field sampling for the current study (2004-2006), most predatory-sized lake trout in the system were stocked, and the model estimated their numbers from agency stocking records and a mortality rate determined using catch curve analysis. Naturally spawned offspring of stocked lake trout made up a smaller, unquantified fraction of the population. The population model estimated the abundance of naturally spawned lake trout with three scenarios encompassing the possible range of reproductive rates (Schoen et al. 2012). These scenarios produced nominal, upper, and lower estimates of kokanee consumption by lake trout.

We reran this analysis using basin-specific field data for growth using the models specified above, diet composition (Figure 4.5), and thermal experience (Table 4.D1) and left all other model inputs unchanged. We estimated thermal experience from seasonal thermal profiles and depth distribution patterns (Beauchamp et al. 2007). To maintain adequate sample sizes for diet composition (Beauchamp et al. 2007, Vinson and Budy 2011) while splitting the original dataset by basin, we pooled the diet data across seasons. The model estimated the annual biomass of kokanee consumed by the lake trout population in each basin. We estimated the relative numbers of kokanee consumed annually in each basin by dividing the biomass of kokanee consumed by the mean reconstructed body weight of kokanee prey found in lake trout stomachs (71.8 g, SD = 38.5; Schoen and Beauchamp 2010). We considered this a relative result because the size structure of kokanee consumed by lake trout was not known precisely. We estimated the relative risk of lake trout predation faced by individual kokanee in each basin by dividing the relative numbers of kokanee consumed by lake trout in the basin (nominal estimate) by the mean annual kokanee abundance in the basin. To determine how uncertainty in lake trout predation and kokanee abundance influenced these nominal predation rate estimates, we also estimated the upper and lower bounds of predation risk for kokanee in each basin. We estimated the upper bound of predation risk as the upper estimate of kokanee consumed divided by the lower 95% confidence limit of annual mean kokanee abundance. We estimated the lower bound of predation risk as the lower estimate of kokanee consumed divided by the upper 95% confidence limit of annual mean kokanee abundance.

The lake trout population consumed similar numbers of kokanee in each basin, but fewer kokanee were present in Wapato Basin, so kokanee experienced greater predation risk in Wapato Basin. The lake trout population in Wapato Basin consumed 20.2 metric tons of kokanee annually (nominal estimate; lower and upper bounds = 19.3 and 24.4 tons), as estimated by the bioenergetics model. In comparison, the lake trout population in Lucerne Basin consumed an estimated 19.2 tons of kokanee annually (nominal estimate; lower and upper bounds = 16.4 and 29.6 tons). This represented an index value of 282,000 kokanee consumed annually in Wapato Basin (nominal estimate; lower and upper bounds = 269,000 and 339,000 kokanee), versus 267,000 kokanee in Lucerne Basin (nominal estimate; lower and upper bounds = 229,000 and 413,000 kokanee). Due to uncertainty in the size structure of kokanee consumed by lake trout, we focused our interpretation on the relative differences in predation risk between basins. The lake trout population in Wapato Basin consumed 5% more kokanee annually (nominal estimate; lower and upper bounds = 18% fewer to 17% more kokanee) than the lake trout population in Lucerne Basin. The annual mean abundance of kokanee was 72% less (95% CI: 84-69% less) in Wapato Basin than in Lucerne Basin (Appendix B). Kokanee faced a resulting annual risk of predation 3.82 times greater in Wapato Basin than in Lucerne Basin (nominal estimate; lower and upper bounds = 3.74 and 5.24 times greater).

References

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Gallucci, V. F. and T. J. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. Transactions of the American Fisheries Society **108**:14-25.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society **141**:1191-1206.

Vinson, M. R. and P. Budy. 2011. Sources of variability and comparability between salmonid stomach contents and isotopic analyses: study design lessons and recommendations. Canadian Journal of Fisheries and Aquatic Sciences **68**:137-151.

Table 4.D1. Thermal experience inputs used in bioenergetics simulations for lake trout in Lucerne and Wapato Basins.

Month	Size class (FL, mm)	Thermal experience (°C)	
		Lucerne	Wapato
February	180-420	6.3	5.2
	421-550	6.3	5.2
	551-850	6.3	5.3
May	180-420	8.2	5.8
	421-550	8.3	6.9
	551-850	9.0	7.0
August	180-420	8.2	11.0
	421-550	11.5	10.8
	551-850	11.5	9.8
November	180-420	10.7	8.2
	421-550	10.6	9.2
	551-850	10.7	9.9

Note: No field data were available for the 551-850 mm size class in the Lucerne Basin during August, so we substituted the thermal experience of the 421-550 mm size class.

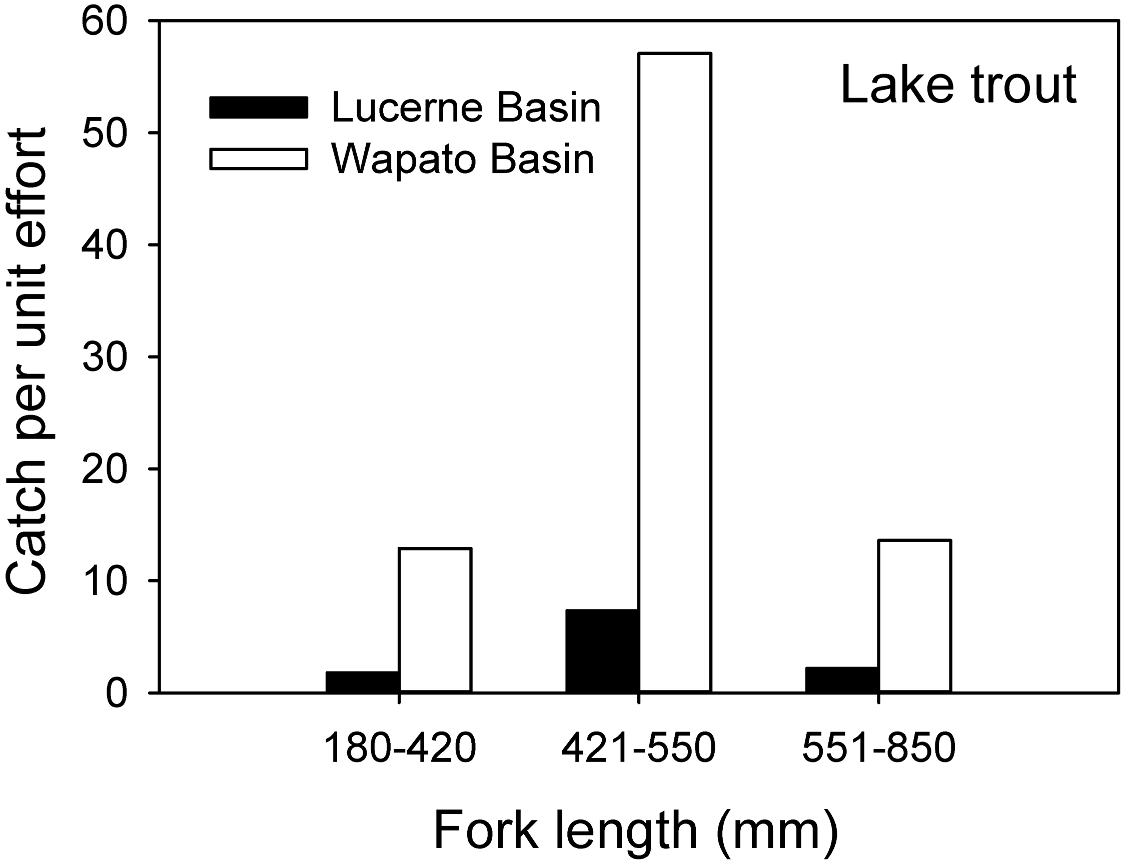

Figure 4.D1. Mean annual catch per unit effort of lake trout in sinking gill nets set in the two lake basins. One unit of effort represented four large mesh and four small mesh nets set overnight at standardized depths during February, May/June, August, and November.

Chapter 5. Bathymetric effects on bentho-pelagic food webs: Does access to deep-water refuge reduce the vulnerability of mysids to lake trout predation?

ABSTRACT

Introductions of mysid shrimp (*Mysis diluviana*) and lake trout (*Salvelinus namaycush*) have caused widespread ecological impacts in western North America. Energetic support from introduced mysid prey has allowed some lake trout populations to expand in density, extirpate other fish species, and drive cascading effects on aquatic and terrestrial food webs. Yet, mysids appear to provide more limited benefits to lake trout in other systems, and the factors mediating these interactions are poorly understood. We recently proposed a deep-water refuge hypothesis that mysids are more vulnerable to lake trout predation, and thus provide greater energetic support to lake trout, in shallower habitats where they aggregate on the lake bottom during daylight than in extremely deep habitats. In this study, we tested whether the proportion of mysids in the diet of lake trout could be explained by 1) mysid density, 2) the density of kokanee, a preferred alternative prey of lake trout, or 3) the vulnerability of mysids to benthic predation (i.e., the deep-water refuge hypothesis). We captured lake trout at five sites across a bathymetric gradient in Lake Chelan, Washington and quantified their diet composition using Bayesian stable isotope mixing models. We quantified mysid density with net sampling in the pelagic zone at night and kokanee density with hydroacoustics. We developed a simple model of mysid vulnerability, based on the proportion of time mysids spent on the lake bottom, using an existing diel vertical migration model. The model predicted the depth distribution and vulnerability of mysids at each site based on the latitude, longitude, and light extinction of the lake, and bathymetry of the site. The predicted vulnerability of mysids explained most of the

spatial variability in the proportion of mysids in the diet of lake trout ($r^2 = 0.86$). The data did not support mysid density or kokanee density as predictors of lake trout diet. These results provide support and a mechanistic basis for the deep-water refuge hypothesis. Further research should test whether this pattern is also evident in other systems, and if it can explain the variable impacts of introduced mysids and lake trout on hundreds of lake and reservoir food webs.

INTRODUCTION

Introductions of mysid shrimp (*Mysis diluviana*) and lake trout (*Salvelinus namaycush*) have caused widespread ecological impacts on aquatic communities throughout western North America (Lasenby et al. 1986, Spencer et al. 1991, Donald and Alger 1993, Crossman 1995, Ruzycki et al. 2003, Vander Zanden et al. 2003). Mysids can influence lake food webs by preying heavily on cladoceran zooplankton (Rieman and Falter 1981, Spencer et al. 1999, Koksvik et al. 2009) and competing with planktivorous fishes for food (Johannsson et al. 1994, Hyatt et al. 2005, Johnson and Martinez 2012). In some systems, they also enhance densities of profundal-feeding fishes such as lake trout (Bowles et al. 1991, Martinez et al. 2009), indirectly boosting predation on alternative prey (Ellis et al. 2011, Schoen et al. *In press*). A long-lived, generalist apex predator, introduced lake trout have extirpated native fish species, eliminated popular sport fisheries, and caused cascading effects on aquatic food webs and adjacent terrestrial communities (Ellis et al. 2011, Middleton et al. 2013). Although lake trout appear to have greater predatory impacts in lakes with mysids (Martinez et al. 2009), surprisingly little is known about factors mediating energy flow from mysids to lake trout. Understanding which lakes and reservoirs are most vulnerable to enhanced predation impacts is an important step towards efficiently prioritizing conservation and management efforts (Schoen et al. *In press*).

In a recent paper, we proposed that lake bathymetry mediates the vulnerability of mysids to lake trout predation because mysids are more vulnerable to predation when they are aggregated on the lake bottom than suspended in open water (Schoen et al. *In press*). Mysids exhibit diel vertical migration (DVM), swimming up into the water column after dusk, and descend before dawn (Juday and Birge 1927, Levy 1990). During daylight, mysids aggregate on the lake bottom or suspend in diffuse layers in the water column in very deep habitats (e.g., > 100 m; Beeton and Bowers 1982, Levy 1991). Lake trout appear to feed effectively on mysids in benthic habitats. Recent experiments showed age-0 lake trout fed easily on mysids in the benthos, even at low light levels and low mysid densities (Holbrook et al. 2013). Larger lake trout have also been observed from a remotely operated vehicle feeding on interstitial prey, presumably mysids, in cobble substrates during the day (D. A. Beauchamp, personal observation). However, we are not aware of evidence of lake trout feeding extensively on mysids in the pelagic zone, either at night or during the day in extremely deep lakes. In near darkness, search volumes would be small (Beauchamp et al. 1999), and feeding on low volumetric densities of mysids dispersed across tens of vertical meters of open water would likely be inefficient.

A case study in Lake Chelan, Washington supported the deep-water refuge hypothesis: lake trout of all size classes consumed more mysids in a relatively shallow lake basin than in a deep, steep-sided basin, and lake trout consumed more mysids at shallower sampling sites within each basin (Schoen et al. *In press*). This bathymetric diet shift was associated with important differences in food-web structure. Lake trout catch per unit effort was seven times greater, and kokanee faced 4-5 times greater predation risk in the shallow basin than in the deep basin. Thus, the stronger energetic link from mysids to lake trout appeared to enhance the predatory impacts of lake trout through apparent competition (Holt 1977).

In this paper, we tested whether the strength of the energetic link between mysids and lake trout could be explained by 1) mysid density, 2) the density of kokanee, a preferred alternative prey of lake trout, or 3) the vulnerability of mysids to lake trout predation, as predicted by a mechanistic model representing the deep-water refuge hypothesis.

STUDY AREA

Lake Chelan is a deep, glacially carved lake (maximum depth 453 m) located in the Cascade Range in north-central Washington (48° N, 120° W). The lake is ultraoligotrophic (extremely low in productivity), monomictic (thermally stratifies once per year), and composed of two basins joined by a narrow channel (our Figure 5.1; Pelletier et al. 1989). Wapato Basin is moderately deep and gradually sloping (mean depth 43 m and maximum depth 122 m), while Lucerne Basin is extremely deep and steep-sided (mean depth 180 m and maximum depth 453 m; Kendra and Singleton 1987). Mysids were introduced in 1967 (Brown 1984) and are now the dominant planktivorous species in the lake (Schoen et al. In press). An introduced, naturally reproducing population of kokanee supports the most popular sport fishery in the lake (Hagen 1997, Duke Engineering and Services 2000). Lake trout were introduced beginning in 1980, were heavily stocked from 1990-2000, and are now a major predator of mysids, kokanee, and other fishes in the lake (Martinez et al. 2009, Schoen et al. 2012).

METHODS

We collected field data and developed a model of mysid vulnerability to identify factors mediating the dietary utilization of mysids by lake trout in Lake Chelan, Washington. We quantified mysid density using net sampling in the pelagic zone at night, and we quantified kokanee density with hydroacoustic surveys. Using a mysid DVM model (Boscarino et al. 2009), we estimated the vulnerability of mysids to benthic predation in different habitats, based on the proportion of time they spent on the lake bottom. We applied this model using light and water transparency data from Lake Chelan at five sites along a bathymetric gradient ranging from shallow, gradually sloping habitats to deep, steep-sided habitats. Finally, we augmented an existing lake trout stomach content dataset with stable isotope analysis to quantify spatial variability in lake trout diet composition across this gradient, and we tested whether mysid density, kokanee density, or predicted mysid vulnerability could explain this dietary variability.

Field sampling

We measured physical parameters and collected mysids, lake trout, and other fish species at five sampling sites in Lake Chelan, including three sites in Lucerne Basin and two sites in Wapato Basin. We sampled these sites during February, May, June, August, and November during a two-year period from summer 2004 to summer 2006. We measured light extinction profiles of the photosynthetically active radiation (PAR) wavelength range (400-700 nm) at 1-m intervals from the surface to 40 m depth with a spherical underwater quantum sensor (LI-193, Li-Cor, Inc.). Surface irradiance levels were measured simultaneously with a LI-190 surface quantum cell to standardize the underwater readings to the available surface light. We sampled mysids at night with vertical hauls from 80 m to the surface using a conical 1-m-diameter, 1-mm-mesh ring net. These hauls started below the mysid scattering layer as observed on an echosounder. We calculated the areal density of mysids in the water column at each site (mysids / m^2 of lake surface) by dividing the count by the area of the net opening, assuming 100% net efficiency (Nero and Davies 1982). We previously reported these mysid densities broken down by lake basin and season (Schoen et al. *In press*), and for this analysis we calculated the annual mean mysid density at each site.

We captured lake trout and other fish species with sinking gill nets fished overnight at four depth strata ranging 0-70 m. These depths encompassed the epilimnion, metalimnion, and two depths below the hypolimnion during stratified periods (Schoen et al. 2012). We collected small littoral fishes using minnow traps deployed with a subset of the sinking gill nets, and we sampled kokanee by angling and with mid-water gillnets. We recorded the length and mass of each collected fish and collected the stomachs of lake trout. For stable isotope analysis, we retained whole mysids, a sample of dorsal white muscle tissue from fish larger than approximately 50 mm fork length (FL), and fillets from smaller fish. All stable isotope samples were frozen for transportation to the lab. We quantified kokanee densities with mobile hydroacoustic surveys conducted at night and analyzed the data by echocounting single targets. We previously reported kokanee densities broken down by lake basin and season (Schoen et al. *In press*), and for this analysis we calculated the annual mean kokanee density at each site, as estimated from the two nearest hydroacoustic transects. We excluded age-0 kokanee from the density estimates because they were nearly nonexistent in lake trout stomach contents. Further information about the field sampling protocol is available in previous publications (Schoen and Beauchamp 2010, Schoen et al. 2012, Schoen et al. In press).

Model of mysid vulnerability to benthic predation

We estimated the vulnerability of mysids to benthic predation at each site using a DVM model for mysids (Boscarino et al. 2009). This model estimates the vertical distribution of a mysid population based on light- and thermal-preference functions estimated from field observations and controlled experiments, and has accurately predicted the vertical distribution of mysids in Lake Ontario (Boscarino et al. 2009). In our application, the benthic vulnerability of mysids was determined by the light-preference function alone because we assumed that mysids would actively avoid shallow near-shore areas where light levels or temperatures above their thermal tolerance reached all the way to the lake bottom (Johannsson 1995). We did not account for the possibility that currents advected mysids into these shallow areas, a process that occurs due to unusually strong, turbulent flow in the West Arm of Kootenay Lake, BC, but is unlikely to strongly influence mysid distributions in most other lakes (Martin and Northcote 1991).

To accurately determine the depth-specific light levels perceived by mysids, we accounted for depth-based changes in the underwater light spectrum and the spectral sensitivity of mysids. The light-preference function of the DVM model uses units of mylux, a measure of light intensity relevant to the vision of *Mysis diluviana* (Gal et al. 1999). Mysids prefer light levels of 3.0×10^{-8} mylux in laboratory experiments, and this light preference explains their DVM patterns in natural environments as well (Boscarino et al. 2009). One mylux is approximately equal to 175 lux (lx) or 2.35 microeinsteins / m^2 / sec of photosynthetically active radiation (PAR; i.e., the flux of photons within the 400-700 nm waveband) under the light spectrum at the water's surface (Gal et al. 1999). However, these conversions depend on the spectrum of ambient light and can change by as much as an order of magnitude in the underwater optical environment, due to shifts in the spectrum of ambient light relative to the spectral sensitivity of the mysid eye (Boscarino et al. 2009).

We estimated light intensity at the water's surface at Lake Chelan using a model of illuminance (lx) from the sun and moon (Janiczek and DeYoung 1987). Surface light levels vary with time of day, season, and cloud cover. To account for the full annual range of this variability in a relatively simple model, we estimated surface light levels on 5-min intervals over a 24-hour diel cycle on the winter solstice, spring equinox, and summer solstice of 2005 (the first year of field sampling), under clear sky conditions. We considered the spring equinox data as a proxy for the autumnal equinox, which has a nearly identical solar light regime. We estimated light levels under thin cloud cover and heavy overcast skies by reducing the light levels under clear skies by 50% and 90%, respectively (our Figure 5.2; Janiczek and DeYoung 1987, Hansen and Beauchamp 2015). We converted these illuminance values to irradiance of PAR using the following conversion for daylight conditions: PAR (microeinsteins / m^2 / sec) = 54.3 lux (Thimijan and Heins 1983). We subdivided this total irradiance into 10 nm wavelength increments using the solar spectral irradiance standard ASTM G173-03 (http://www.astm.org/Standards/G173.htm). This standard was applicable during both day and night because the spectral composition of daylight and moonlight are similar (Munz and McFarland 1973, Gal et al. 1999).

We estimated the vertical distribution of mysids under different conditions based on the underwater light environment. We calculated wavelength-specific light extinction coefficients using the mean light extinction coefficient k_{PAR} measured in the field (0.161 / m, n = 16, SD = 0.026) and a relationship between wavelength-specific light extinction rates and k_{PAR} determined for Lake Superior, a similarly low-productivity lake (Jerome et al. 1983). We calculated depth-and wavelength-specific light intensities according to the Beer-Lambert equation (Kirk 2010). We calculated the light intensity perceived by mysids at each depth based on the wavelength-specific intensities and the mysid spectral sensitivity (mylux) curve (Gal et al. 1999). Finally, we estimated the mean depth of the mysid population as the depth corresponding to the preferred mylux level under the given optical conditions.

To compare the vulnerability of mysids among the five sampling sites, we quantified the bathymetry of each site. We generated site-specific hypsographic (depth-area) curves from bathymetric maps (Kendra and Singleton 1987). For these purposes, we defined each site with a 1-km radius around the center of the actual sampling area. We measured the area of each depth contour within each site using ImageJ version 1.47 (http://imagej.nih.gov/ij/), and fit these data with cubic spline curves (Figure 5.3). After subtracting land area within the radii, this procedure resulted in lake surface areas of 1.3-2.2 km^2 at each site. These sites were approximately 10 times larger than the core utilization areas (50% density kernels) of 14 lake trout tracked during a 57-day period in a telemetry study in Lake Louisa, Ontario (Morbey et al. 2006). We used larger areas to allow for potentially greater lake trout movements during the annual time frame of this study.

We estimated the vulnerability of mysids to benthic predation at each site by applying the preferred mysid depth from the DVM model to the bathymetry of each site. First, we assumed that mysids actively avoided shallow, near-shore areas, based on our observations during hydroacoustic surveys (E. R. Schoen personal observation) and similar patterns in other lakes (Johannsson 1995, Whall and Lasenby 2009, Sierszen et al. 2014). We do not imply that these habitats could not support mysids (e.g., in a shallower lake where no deeper habitat was available), only that mysids are generally absent from shallow areas in deep systems. Therefore, we excluded these shallow, unsuitable habitats from our calculations of areas where mysids were vulnerable to predation. We defined unsuitable habitat as being shallow enough that the light intensity at the lake bottom constantly exceeded the preferred light level of mysids, even at night, during a given season. The depth threshold specifying unsuitable habitat ranged from 36 m in winter to 58 m in summer. For comparison, warm water temperatures unsuitable for mysids (≥ 14˚ C) reached 25-29 m deep at all sites in late August (Schoen et al. *In press*); thus, light was more limiting than temperature in defining unsuitable shallow habitat. We assumed that the mysid population was randomly distributed throughout the remaining, deeper habitat within each site.

We quantified mysid vulnerability as the proportion of the mysid population distributed on the lake bottom under a given set of conditions (Figure 5.4). A vulnerability value of 0 indicated mysids were suspended in the water column throughout a site, a vulnerability of 1 indicated mysids were aggregated on the lake bottom throughout a site, and intermediate values indicated that a fraction of the population was on the bottom in the shallower habitats within a site. We compared patterns of vulnerability graphically as a function of time of day, season, and cloud cover at the different sites. Finally, we calculated the mean annual vulnerability for each site, averaged across the 24-hour period, four seasons, and the clear sky and thin cloud cover scenarios. We excluded the heavy overcast scenario from the annual mean because such weather patterns are unusual at Lake Chelan, due to its location in the rain shadow of the Cascade Mountains.

Spatial patterns in lake trout diet composition

We quantified spatial variability in the contribution of mysids to the diet of lake trout using Bayesian stable isotope mixing models MixSIAR, version 2.1.2 (Semmens et al. 2014), implemented in a scripted form in R version 3.2.0 (R Core Team 2015). We initially ran a suite of hierarchical mixing models (Semmens et al. 2009) to test whether the isotopic data supported calculating diet composition separately for each site, or whether diet composition could be estimated more parsimoniously at the broader spatial scale of lake basins. The data indicated the greater support for a model incorporating basin- and site-level variability (Deviance Information Criterion [DIC] = 1664), than for a model including only an effect of basin (DIC = 1667), and more complex models including individual-level variation were not supported. Based on these preliminary findings, we proceeded by running separate mixing models to estimate diet composition for each site. The advantage of this approach was that we could use site-specific prior information from stomach contents to improve the diet composition estimates.

Inputs to the mixing models included the $\delta^{13}C$ and $\delta^{15}N$ signatures of individual consumer and prey specimens, the mean and SD of the fractionation rate for each prey type, and prior information on diet composition from stomach content analysis. We restricted the analysis to lake trout < 600 mm FL because stomach contents indicated larger lake trout consumed few mysids throughout the lake (Schoen et al. *In press*). The stable isotope samples were rinsed under distilled water, oven dried for ≥ 48 h at 60° C, ground to a fine powder with a stainless steel mortar and pestle, and weighed to 1.00 ± 0.2 mg in a tin capsule. We shipped the samples to Northern Arizona University for analysis. Stable carbon and nitrogen isotopes were measured via continuous flow using a Carlo Erba 2100 elemental analyzer interfaced with a Thermo-Finnagan Delta^{plus} isotope ratio mass spectrometer.

We corrected the $\delta^{13}C$ signatures of consumers and prey to account for differences in lipid content among samples. The atomic C:N ratios of our samples ranged from 3-9, indicating enough variability in lipid content to bias the stable isotope analysis (Kiljunen et al. 2006, Sweeting et al. 2006, Post et al. 2007). To correct for this potential bias, we adjusted fish signatures using an equation developed for freshwater fishes with a wide range of C:N values (Logan et al. 2008; equation 1a), and we adjusted mysid signatures with an equation developed specifically for *Mysis diluviana* (Leggett 1998; p. 234). We used trophic fractionation rates of 0.4 ± 1.3 ‰ (mean ± SD) for δ^{13}C and 3.4 ± 1.0 ‰ for δ^{15}N (Post 2002), which closely matched values reported specifically for lake trout (Vander Zanden and Rasmussen 2001, Harvey et al. 2002). We excluded one lake trout sample from the analysis with a δ^{15}N value that was over 5 standard deviations below the mean of the other lake trout samples, which prevented models from converging.

We analyzed lake trout stomach contents to determine informative priors for each site. We identified the stomach contents of lake trout to the level of species. A subset of otherwise unidentifiable salmonid prey specimens was identified to species using genetic sequencing (Schoen and Beauchamp 2010). We recorded the blotted wet mass of each prey category and calculated diet proportions by mass (Chipps and Garvey 2007). For each site, we specified priors as the diet proportion of each prey type multiplied by the sample size of non-empty stomachs at the site. We also used stomach content data to choose which diet sources to include in the mixing models. We initially included all prey species that contributed ≥ 5% of the overall lake trout diet (averaged across seasons and basins) as indicated by stomach analysis. Five prey species met this criterion: kokanee, mysids, northern pikeminnow (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), and threespine stickleback (*Gasterosteus aculeatus).*

We tested for spatial variability in prey isotopic signatures to determine whether to pool the prey signatures from the entire lake or to use basin- or site-specific prey signatures. We pooled prey signatures *a priori* for kokanee, which migrate seasonally between basins (Brown

1984, Schoen et al. *In press*). For each remaining prey species, we tested for spatial differences in δ^{13}C and δ^{15}N signatures using hierarchical ANOVA models including fixed effects of basin, site, basin + site, or no spatial differences (intercept-only model). We evaluated each model set using AIC_c. Mysid δ^{13}C signatures differed between basins (ΔAIC_c: basin model = 0, intercept-only model = 8.1) but did not differ further among sites ($\Delta AIC_c = 1.5$). Thus, we used separate mysid signatures for the two basins. The signatures of northern pikeminnow, peamouth, and threespine stickleback did not differ between basins or sites ($\Delta AIC_c < 2$ for all intercept-only models), so we used lake-wide mean signatures for these prey species. The mixing models for some sites failed to converge when the prior diet proportion estimates for one or more of the prey types were very small (< 2 %). We iteratively increased these prior estimates to 3% and then dropped the prey species from the model entirely if necessary to allow the model to converge. All models included a residual error term to account for sources of variability in consumer isotopic signatures not explicitly accounted for in the model (Phillips et al. 2014). For each model, we used a burn in of 2,700,000 and a chain length of 3,000,000 for three parallel MCMC chains.

Associations between mysid density, predicted mysid vulnerability, and lake trout diet

We tested whether the proportion of mysids in the diet of lake trout could be explained by the density or predicted vulnerability of mysids using linear regression models. For the response variable, we used the mean diet proportions of mysids at each site as estimated by the site-specific mixing models. We tested three simple models with the following continuous explanatory variables: mysid density, mysid vulnerability, and the product of density and vulnerability. We evaluated the most parsimonious model using AIC_c (Burnham and Anderson

2002), and we quantified their explanatory power using r^2. We performed all statistical analyses with R version 3.2.0 (R Core Team 2015).

RESULTS

Densities of mysids and kokanee

Mysid densities were highly variable among tows, but generally greater at the deeper sites. In ascending order, the annual mean areal densities of mysids (mysids / m^2) were 39.9 (SE = 13.6) at site 1, 53.9 (SE = 13.0) at site 3, 54.9 (SE = 14.0) at site 2, 78.5 (SE = 19.7) at site 5, and 91.7 (SE = 39.8) at site 4. Kokanee densities were similar among sites 1-4, but 4-6 times greater at site 5, where kokanee staged during late summer and autumn prior to spawning in the Stehekin River. In ascending order, the annual mean densities of kokanee (kokanee / ha) were 12.2 (SE = 5.6) at site 4, 16.5 (SE = 6.7) at site 3, 19.1 (SE = 7.8) at site 1, 20.5 (SE = 11.2) at site 2, and 74.0 (SE = 48.1) at site 5.

Predicted vulnerability of mysids to benthic predation

The mysid DVM model predicted that the depth of the mysid population in Lake Chelan varied across a range of 175 m as surface light levels changed with time of day, season, and cloud cover (Figure 5.5), except where their descent was limited by the lake bottom. The depth of the light intensity level preferred by mysids ranged from a minimum of 18 m under the darkest ambient surface light levels (5×10^{-5} lx under heavy overcast at night during the winter) to a maximum of 193 m under the brightest conditions (10^5 lx under clear skies at midday during the summer). Time of day was the dominant factor controlling the magnitude of DVM, and season controlled the duration of time mysids spent at the apex of their migration. Cloud cover caused a relatively minor change in predicted mysid depths, with mysids predicted to ascend approximately 5 m under light clouds and approximately 18 m under heavy overcast, relative to their position under clear skies.

The predicted vulnerability of mysids to benthic predation varied strongly with surface light levels and among sites across the bathymetric gradient (Figure 5.6). At the shallowest, most gradually sloping site (site 1) mysids were predicted to aggregate on the lake bottom throughout the site (vulnerability = 1) during daylight, ascend into the water column after moonset, and descend to the lake bottom after moonrise. By contrast, the DVM model predicted mysids to always remain suspended in the water column across the majority of the steepest site (site 4), which had a maximum vulnerability of 0.39 under the brightest conditions. At site 4, the model predicted mysids were suspended in the water column across nearly the entire site (vulnerability 0-0.1) when the sun was below the horizon. Cloud cover reduced the vulnerability of mysids to varying degrees, depending on the ambient light levels and the bathymetry of the site. Cloud cover reduced mysid vulnerability to a greater extent at shallower sites than deeper sites, and to a greater extent at night than during the day.

Averaging across the temporal variability in light intensity, the five sites exhibited a wide range of predicted mean annual mysid vulnerability levels (0.20-0.84). Vulnerability decreased from shallow, gradually sloping sites where mysids were usually aggregated on the lake bottom to deep, steep-sided sites where they were usually suspended in open water.

Association between predicted mysid vulnerability and lake trout diet composition

Stable isotope mixing models indicated the proportions of mysids in lake trout diets varied substantially along the bathymetric gradient (Figure 5.7). The mean proportion of mysids in the diet ranged from a maximum of 0.51 (95% credible interval [CI]: 0.44-0.59) at the shallowest site 1 to a minimum of 0.002 (95% CI: 0-0.019) at the deepest site 4. Lake trout diets contained intermediate levels of mysids at the remaining sites: in order of increasing depth, the means and 95% credible intervals were 0.46 (95% CI: 0.36-0.57) at site 2, 0.26 (95% CI: 0.04-0.47) at site 5, and 0.17 (95% CI: 0.01-0.46) at site 3.

Mysids contributed a larger fraction of the lake trout diet at sites where they were predicted to be more vulnerable to benthic predation (Figure 5.8; $\Delta AIC_c = 0$; Table 5.1). This relationship had strong predictive power ($r^2 = 0.86$) and was described by a linear regression with a slope of 0.74 (SE = 0.17) and an intercept of -0.11 (SE = 0.10). Neither mysid density nor kokanee density explained lake trout diet composition, based on model selection ($\Delta AIC_c > 4$; Table 5.1).

DISCUSSION

We found that lake trout consumed more mysids in shallower habitats where mysids aggregated on the lake bottom and were predicted to be more vulnerable to benthic predation, thus providing support for the deep-water refuge hypothesis. The spatial differences in diet could not be explained by either the densities of either mysids or kokanee, a preferred alternative prey of lake trout. These results provide a mechanistic basis for our previous findings that lake trout density and predation pressure on kokanee was greater in the shallow lake basin than in the deep basin of our study lake (Schoen et al. *In press*). To our knowledge, these are the first studies to identify an environmental mechanism mediating energy flow from mysids to lake trout.

By using stable isotope data to quantify diets at a small spatial scale, we assumed that lake trout did not perform large-scale movements outside of the sampling sites during the approximately 1-year isotopic turnover time. This assumption was reasonable based on previous telemetry-based evidence of the limited home ranges of lake trout (Morbey et al. 2006), but we did not quantify movements in our study system and could not rule them out. In support of our conclusions, any movements of lake trout among sites would likely have diminished the spatial variability we observed in lake trout isotopic signatures, so our results represent a conservative estimate of the actual spatial variability in lake trout diet.

Energy flows from mysids to lake trout were insensitive to mysid densities across the range we measured (40-92 mysids / m^2), but highly sensitive to whether mysids were distributed on the lake bottom or suspended in the pelagic zone. Similarly, based on feeding experiments, the daily consumption rates of age-0 lake trout feeding on mysids in the benthic zone were predicted to be insensitive to mysid densities as low as 3 mysids / m^2 (Holbrook et al. 2013). This is far lower than the typical densities measured in our study or other studies of introduced mysid populations (reviewed in Northcote 1991), suggesting that the energetic support of lake trout populations by mysids may be largely independent of mysid density across their introduced range. Surprisingly, our data actually showed an inverse relationship between mysid density and the proportion of mysids in the lake trout diet. We interpreted this counterintuitive pattern with caution because pelagic mysid densities were highly variable; however, it could potentially be explained either by top-down or bottom-up processes. First, lake trout predation might have reduced mysid densities at the sites where mysids were most vulnerable. Second, the sites where lake trout consumed the most mysids (sites 1 and 2 in the shallower Wapato Basin) also experienced longer periods of thermal stratification than the other sites, which excluded mysids from the zooplankton-rich epilimnion and could have limited their densities as well (Schoen et al. *In press*).

Our model of mysid vulnerability was purposely simple: we assumed mysids were vulnerable on the lake bottom and invulnerable when suspended in the water column. In reality, lake trout predation rates on any given prey species likely depend on many other factors. However, this simple model had strong predictive power, and its simplicity is an asset for applications in other systems. The only lake-specific model inputs were latitude and longitude (inputs to the surface illuminance model), the light extinction rate (which is available for many lakes and can be approximated by Secchi depth; Koenings and Edmundson 1991), and the hypsographic curves (which can be easily produced from a bathymetric map).

Comparisons with other lakes

Our results indicate that extremely deep habitats provide mysids with a refuge from benthic predation and reduce energy flows to lake trout in Lake Chelan. Diet data from other systems also generally appear to fit this pattern. Lake trout relied heavily on mysids in relatively shallow Flathead Lake, Montana, USA (mean depth = 50 m; Beauchamp et al. 2007, Ellis et al. 2011) and Swan Lake, Montana, USA (mean depth = 16 m; Guy et al. 2011), but consumed few mysids in extremely deep, steep-sided Lake Pend Oreille, Idaho, USA (mean depth = 164 m; Clarke et al. 2005). In contrast to these systems, Lake Tahoe appeared not to support this mechanism: while it is extremely deep (mean depth = 305 m), lake trout consumed large proportions of mysids there (Vander Zanden et al. 2003). Our model of mysid vulnerability suggests this seemingly incongruous pattern could be explained by the extensive 40-100 m deep shelf habitat around the lake margins. Additionally, kokanee and other visually feeding planktivores consume mysids in habitats where upwelling currents or a very shallow lake bottom (e.g., 10-50 m) blocks their downward migration (Lasenby et al. 1986, Bowles et al. 1991). We propose that these overall patterns, which have previously received little attention in the literature, can be explained by the access of mysids to deep-water refuge from predators. Future research should test whether quantitative predictions of the mysid vulnerability model described here can explain the strengths of energetic linkages between introduced mysids and fishes in these and other systems.

Bathymetry may also mediate energy flow from mysids to lake trout within the native range of these species, but we expect this pattern to be less ecologically important. In similarity to our results, lake trout consumed more mysids in shallower waters (< 64 m) of Lake Superior than in deeper waters (Dryer et al. 1965), although mysid density was greater in deeper waters (Sierszen et al. 2014). However, Lake Superior contains three morphotypes of lake trout distributed at different depths, which confounds simple relationships between diet composition and bathymetry (Sierszen et al. 2014). Further, although the energetic benefits of introduced mysids typically flow predominantly to other nonnative species such as lake trout and lake whitefish (*Coregonus clupeaformis*) (Nesler and Bergersen 1991, Ellis et al. 2011), mysids provide energetic benefits to a wide range of coevolved species in their native range, including planktivorous fishes such as ciscoes (*Coregonus* spp.), which can follow the DVM of mysids (Jensen et al. 2006) and feed on them in complete darkness (TeWinkel and Fleischer 1999). Thus, the food-provisioning benefits of mysids are spread across multiple trophic levels and likely less strongly tied to bathymetry. Mysids and other vertically migrating macroinvertebrates such as amphipods strengthen energetic links between benthic and pelagic communities and are considered integral to the functioning of many large, complex lake food webs (Eshenroder et al. 1999, Sierszen et al. 2014). It is perhaps not unexpected that the development of such strong links in lake ecosystems that previously lacked them can have profound ecological consequences (Bowles et al. 1991, Vander Zanden et al. 2003, Ellis et al. 2011).

Implications for conservation and management

If lake bathymetry mediates the flow of energy from mysids to lake trout, as our results suggest, this would have important ecological and management implications for hundreds of lakes and reservoirs in the introduced range of these species. Resource managers might adopt several potential approaches for conserving native fishes and maintaining productive fisheries in these systems, including bottom-up strategies such as lake fertilization (Ashley et al. 1997) or thermal management of reservoirs (Johnson and Martinez 2012), or top-down strategies such as liberalized sport harvest or active suppression of lake trout (Ruzycki et al. 2003, Martinez et al. 2009, Hansen et al. 2010). However, each of these approaches involves significant costs and the potential for unintended consequences. Complicating these decisions, the impacts of lake trout appear to vary substantially among systems, and strong impacts can be masked from detection for years due to high predatory inertia, creating uncertainty about whether these populations are likely to expand enough to pose a risk in any given system (Schoen et al. 2012). Developing general principles about which lakes and reservoirs are most vulnerable to strong impacts and which strategies are most likely to lead to desired outcomes in these systems are important steps towards efficiently prioritizing management efforts.

Theory predicts that energetic subsidies to predators generally enhance predation rates on alternative prey (Holt 1977, Courchamp et al. 2000, Vander Zanden et al. 2005). Thus, our results suggest introduced mysids should boost lake trout predation on other species more strongly in relatively shallow lakes than in extremely deep, steep-sided lakes where mysids are less vulnerable to predation (also see Schoen et al. *In press*). Given the potential for expanding lake trout populations to extirpate native fishes, eliminate popular sport fisheries, radically alter aquatic food webs, and influence terrestrial ecosystems (Martinez et al. 2009, Ellis et al. 2011, Middleton et al. 2013), understanding how environmental factors mediate these interactions is an important step towards informed conservation and management.

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REFERENCES

Ashley, K., L. C. Thompson, D. C. Lasenby, L. McEachern, K. E. Smokorowski, and D. Sebastian. 1997. Restoration of an interior lake ecosystem: The Kootenay Lake fertilization experiment. Water Quality Research Journal of Canada 32:295-323.

Beauchamp, D. A., C. M. Baldwin, J. L. Vogel, and C. P. Gubala. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences 56 Suppl. 1:128-139.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 in C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Beeton, A. and J. Bowers. 1982. Vertical migration of Mysis relicta Loven. Pages 53-61 in M. D. Morgan, editor. Ecology of Mysidacea. Springer, Netherlands.

Boscarino, B. T., L. G. Rudstam, E. R. Loew, and E. L. Mills. 2009. Predicting the vertical distribution of the opossum shrimp, Mysis relicta, in Lake Ontario: a test of laboratory-based light preferences. Canadian Journal of Fisheries and Aquatic Sciences 66:101-113.

Bowles, E. C., B. E. Rieman, G. R. Mauser, and D. H. Bennett. 1991. Effects of introductions of Mysis relicta on fisheries in northern Idaho. American Fisheries Society Symposium 9:65-74.

Brown, L. G. 1984. Lake Chelan fishery investigations. Chelan County Public Utility District No. 1 and Washington Department of Game, Olympia.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Chipps, S. R. and J. E. Garvey. 2007. Quantitative assessment of food habits and feeding patterns. Pages 473-514 in C. S. Guy and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267-277.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. Journal of Animal Ecology 69:154-164.

Crossman, E. J. 1995. Introduction of the lake trout (Salvelinus namaycush) in areas outside its native distribution: A review. Journal of Great Lakes Research 21, Supplement 1:17-29.

Donald, D. B. and D. J. Alger. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.

Dryer, W. R., L. F. Erkkila, and C. L. Tetzloff. 1965. Food of lake trout in Lake Superior. Transactions of the American Fisheries Society 94:169-176.

Duke Engineering and Services. 2000. Lake Chelan Fisheries Investigation, Lake Chelan Hydroelectric Project No. 637., Prepared for Chelan County Public Utility District No. 1, Bellingham, Washington.

Ellis, B., J. Stanford, D. Goodman, C. Stafford, D. Gustafson, D. Beauchamp, D. Chess, J. Craft, M. Deleray, and B. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108:1070-1075.

Eshenroder, R. L., V. G. Sideleva, and T. N. Todd. 1999. Functional convergence among pelagic sculpins of Lake Baikal and deepwater ciscoes of the Great Lakes. Journal of Great Lakes Research 25:847-855.

Gal, G., E. R. Loew, L. G. Rudstam, and A. M. Mohammadian. 1999. Light and diel vertical migration: spectral sensitivity and light avoidance by Mysis relicta. Canadian Journal of Fisheries and Aquatic Sciences 56:311-322.

Guy, C. S., T. E. McMahon, W. A. Fredenberg, C. J. Smith, D. W. Garfield, and B. S. Cox. 2011. Diet overlap of top-level predators in recent sympatry: bull trout and nonnative lake trout. Journal of Fish and Wildlife Management 2:183-189.

Hagen, J. E. 1997. An Evaluation of a Trout Fishery Enhancement Program in Lake Chelan. Master's thesis. University of Washington, Seattle.

Hansen, A. G. and D. A. Beauchamp. 2015. Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. Journal of Animal Ecology 84:532-544.

Hansen, M., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator–prey dynamics in Lake Pend Oreille, Idaho, USA. Hydrobiologia 650:85-100.

Harvey, C. J., P. C. Hanson, T. E. Essington, P. B. Brown, and J. F. Kitchell. 2002. Using bioenergetics models to predict stable isotope ratios in fishes. Canadian Journal of Fisheries and Aquatic Sciences 59:115-124.

Holbrook, B. V., T. R. Hrabik, D. K. Branstrator, and A. F. Mensinger. 2013. Foraging mechanisms of age-0 lake trout (Salvelinus namaycush). Journal of Great Lakes Research 39:128-137.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197-229.

Hyatt, K. D., C. R. Ramcharan, D. J. McQueen, and K. L. Cooper. 2005. Trophic triangles and competition among vertebrate (Oncorhynchus nerka, Gasterosteus aculeatus) and macroinvertebrate (Neomysis mercedis) planktivores in Muriel Lake, British Columbia, Canada. Ecoscience 12:11-26.

Janiczek, P. and J. A. DeYoung. 1987. Computer programs for sun and moon illuminance with contingent tables and diagrams. DTIC Document.

Jensen, O. P., T. R. Hrabik, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community II. Modeling trade-offs at an intermediate trophic level. Canadian Journal of Fisheries and Aquatic Sciences 63:2296-2307.

Jerome, J. H., R. P. Bukata, and J. E. Bruton. 1983. Spectral Attenuation and Irradiance in the Laurentian Great Lakes. Journal of Great Lakes Research 9:60-68.

Johannsson, O. E. 1995. Response of Mysis relicta population dynamics and productivity to spatial and seasonal gradients in Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52:1509-1522.

Johannsson, O. E., L. G. Rudstam, and D. C. Lasenby. 1994. Mysis relicta: Assessment of metalimnetic feeding and implications for competition with fish in Lakes Ontario and Michigan. Canadian Journal of Fisheries and Aquatic Sciences 51:2591-2602.

Johnson, B. M. and P. J. Martinez. 2012. Hydroclimate mediates effects of a keystone species in a coldwater reservoir. Lake and Reservoir Management 28:70-83.

Juday, C. and E. A. Birge. 1927. Pontoporeia and Mysis in Wisconsin lakes. Ecology 8:445-452.

Kendra, W. and L. R. Singleton. 1987. Morphometry of Lake Chelan. Water Quality Investigations Section, Washington State Dept. of Ecology, Olympia.

Kiljunen, M., J. Grey, T. Sinisalo, C. Harrod, H. Immonen, and R. I. Jones. 2006. A revised model for lipid-normalizing delta C-13 values from aquatic organisms, with implications for isotope mixing models. Journal of Applied Ecology 43:1213-1222.

Kirk, J. 2010. Light and photosynthesis in aquatic ecosystems. 3rd edition. Cambridge University Press, Cambridge, UK.

Koenings, J. and J. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: Effects of yellow color and turbidity. Limnology and Oceanography:91-105.

Koksvik, J. I., H. Reinertsen, and J. Koksvik. 2009. Plankton development in Lake Jonsvatn, Norway, after introduction of Mysis relicta: a long-term study. Aquatic Biology 5:293-304.

Lasenby, D. C., T. G. Northcote, and M. Furst. 1986. Theory, practice, and effects of Mysis relicta introductions to North American and Scandinavian lakes. Canadian Journal of Fisheries and Aquatic Sciences 43:1277-1284.

Leggett, M. F. 1998. Food-web dynamics of Lake Ontario as determined by carbon and nitrogen stable isotope analysis. Ph.D. dissertation. University of Waterloo.

Levy, D. A. 1990. Reciprocal Diel Vertical Migration Behavior In Planktivores And Zooplankton In British-Columbia Lakes. Canadian Journal of Fisheries and Aquatic Sciences 47:1755-1764.

Levy, D. A. 1991. Acoustic analysis of diel vertical migration behavior of Mysis relicta and kokanee (Oncorhynchus nerka) within Okanagan Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 48:67-72.

Logan, J. M., T. D. Jardine, T. J. Miller, S. E. Bunn, R. A. Cunjak, and M. E. Lutcavage. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. Journal of Animal Ecology 77:838-846.

Martin, A. D. and T. G. Northcote. 1991. Kootenay Lake: an inappropriate model for Mysis relicta introduction in north temperate lakes. Pages 23-29 in T. P. Nesler and E. P. Bergersen, editors. Mysids in fisheries: Hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, Maryland.

Martinez, P., P. Bigelow, M. Deleray, W. Fredenberg, B. Hansen, N. Horner, S. Lehr, R. Schneidervin, S. Tolentino, and A. Viola. 2009. Western lake trout woes. Fisheries 34:424-442.

Middleton, A. D., T. A. Morrison, J. K. Fortin, C. T. Robbins, K. M. Proffitt, P. White, D. E. McWhirter, T. M. Koel, D. G. Brimeyer, and W. S. Fairbanks. 2013. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. Proceedings of the Royal Society of London B: Biological Sciences 280:20130870.

Morbey, Y. E., P. Addison, B. J. Shuter, and K. Vascotto. 2006. Within-population heterogeneity of habitat use by lake trout Salvelinus namaycush. Journal of Fish Biology 69:1675-1696.

Munz, F. and W. McFarland. 1973. The significance of spectral position in the rhodopsins of tropical marine fishes. Vision research 13:1829-1874.

Nero, R. W. and I. J. Davies. 1982. Comparison of two sampling methods for estimating the abundance and distribution of Mysis relicta. Canadian Journal of Fisheries and Aquatic Sciences 39:349-355.

Nesler, T. P. and E. P. Bergersen, editors. 1991. Mysids in fisheries: hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, Maryland.

Northcote, T. G. 1991. Success, problems, and control of introduced mysid populations in lakes and reservoirs. Pages 5-16 in T. P. Nesler and E. P. Bergersen, editors. Mysids in fisheries: Hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, Maryland.

Pelletier, G., C. R. Patmont, E. B. Welch, D. Bandon, and C. C. Ebbesmeyer. 1989. Lake Chelan Water Quality Assessment. Washington Department of Ecology, Olympia.

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823-835.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montana. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179-189.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rieman, B. E. and C. M. Falter. 1981. Effects of the establishment of Mysis relicta on the macrozooplankton of a large lake. Transactions of the American Fisheries Society 110:613-620.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Schoen, E. R. and D. A. Beauchamp. 2010. Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: Implications for prey species and fisheries management. Washington Cooperative Fish and Wildlife Research Unit, US Geological Survey, University of Washington, Seattle.

Schoen, E. R., D. A. Beauchamp, A. R. Buettner, and N. C. Overman. In press. Temperature and depth mediate resource competition and apparent competition between Mysis diluviana and kokanee. Ecological Applications 10.1890/14-1822.1.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: Pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society 141:1191-1206.

Semmens, B. X., B. C. Stock, E. Ward, J. W. Moore, A. Parnell, A. L. Jackson, D. L. Phillips, S. Bearhop, and R. Inger. 2014. MixSIAR: A Bayesian stable isotope mixing model for characterizing intrapopulation niche variation.

Semmens, B. X., E. J. Ward, J. W. Moore, C. T. Darimont, and W. M. Getz. 2009. Quantifying Inter- and Intra-Population Niche Variability Using Hierarchical Bayesian Stable Isotope Mixing Models. Plos One 4:e6187.

Sierszen, M. E., T. R. Hrabik, J. D. Stockwell, A. M. Cotter, J. C. Hoffman, and D. L. Yule. 2014. Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshwater Biology 59:1197-1212.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. Bioscience 41:14-21.

Spencer, C. N., D. S. Potter, R. T. Bukantis, and J. A. Stanford. 1999. Impact of predation by Mysis relicta on zooplankton in Flathead Lake, Montana, USA. Journal of Plankton Research 21:51-64.

Sweeting, C. J., N. V. C. Polunin, and S. Jennings. 2006. Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Communications In Mass Spectrometry 20:595-601.

TeWinkel, L. M. and G. W. Fleischer. 1999. Vertical migration and nighttime distribution of adult bloaters in Lake Michigan. Transactions of the American Fisheries Society 128:459-474.

Thimijan, R. W. and R. D. Heins. 1983. Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. HortScience 18:818-822.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6:274-288.

Vander Zanden, M. J., T. E. Essington, and Y. Vadeboncoeur. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? Canadian Journal of Fisheries and Aquatic Sciences 62:1422-1431.

Vander Zanden, M. J. and J. B. Rasmussen. 2001. Variation in delta N-15 and delta C-13 trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46:2061-2066.

Whall, J. D. and D. C. Lasenby. 2009. Differences in the trophic role of Mysis diluviana in two intermontane lakes. Aquatic Biology 5:281-292.

Tables

Table 5.1. Model selection results evaluating the effects of mysid areal density (mysids / m^2), the vulnerability of mysids to benthic predation, and kokanee density (kokanee / ha) on the proportion of mysids in the diet of lake trout.

Model	k	LL	AIC_c	ΔAIC_c	r^2
Mysid vulnerability	3	6.15	17.69	0	0.86
Mysid density	3	3.96	22.08	4.39	0.66
Kokanee density	3	1.29	27.41	9.72	0.00

Notes: Values shown for each model include the number of parameters k, the log likelihood LL, the corrected Akaike's information criterion (AIC_c), the differences in AIC_c among models (ΔAIC_c), and the coefficient of determination r^2.

FIGURES

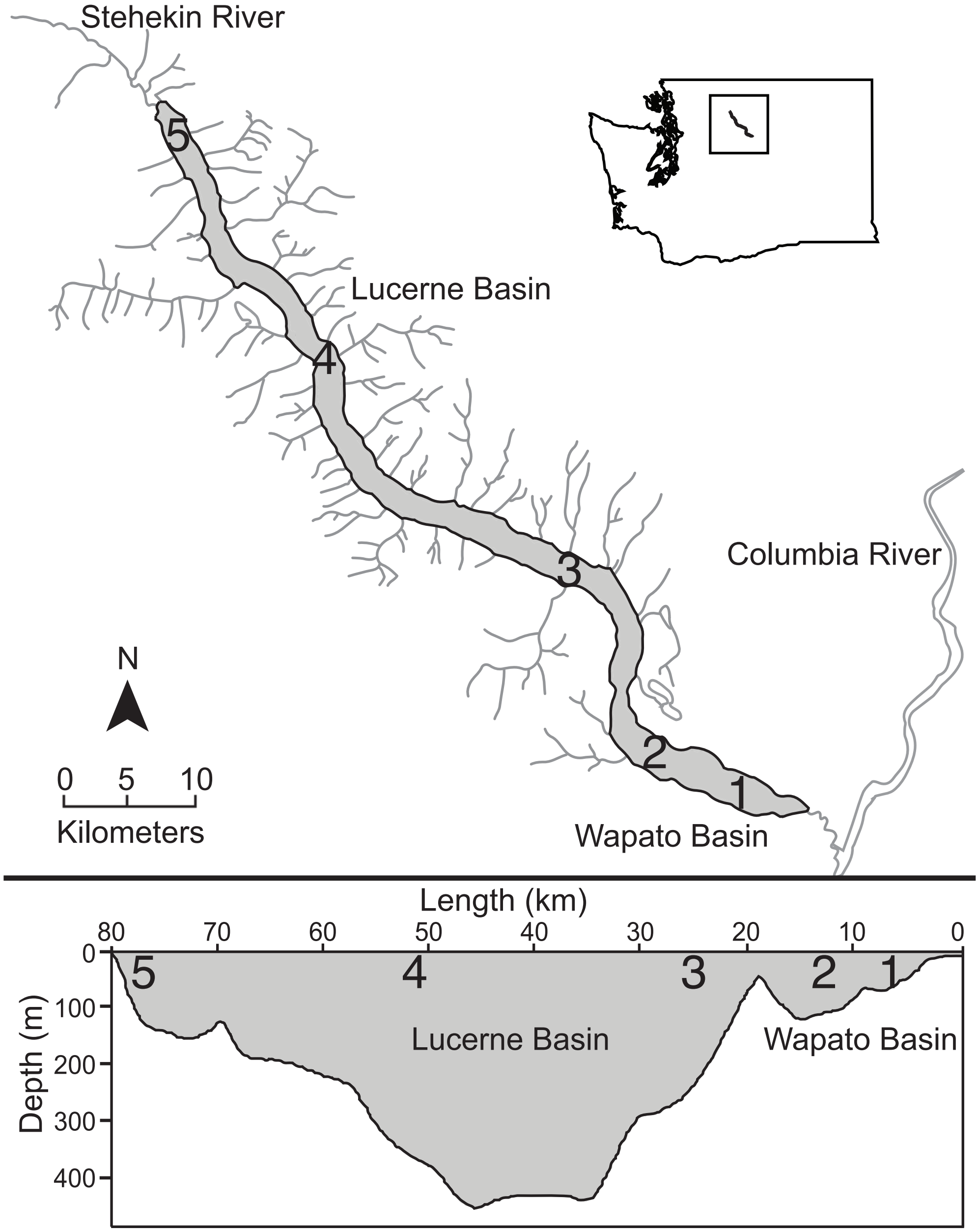

Figure 5.1. (Top panel) Map of Lake Chelan, Washington. (Bottom panel) Longitudinal depth profile of Lake Chelan. Horizontal axis represents distance from the lake outlet along the primary axis of the lake, and vertical axis represents depth. In both panels, numerals within the lake represent sampling sites 1-5.

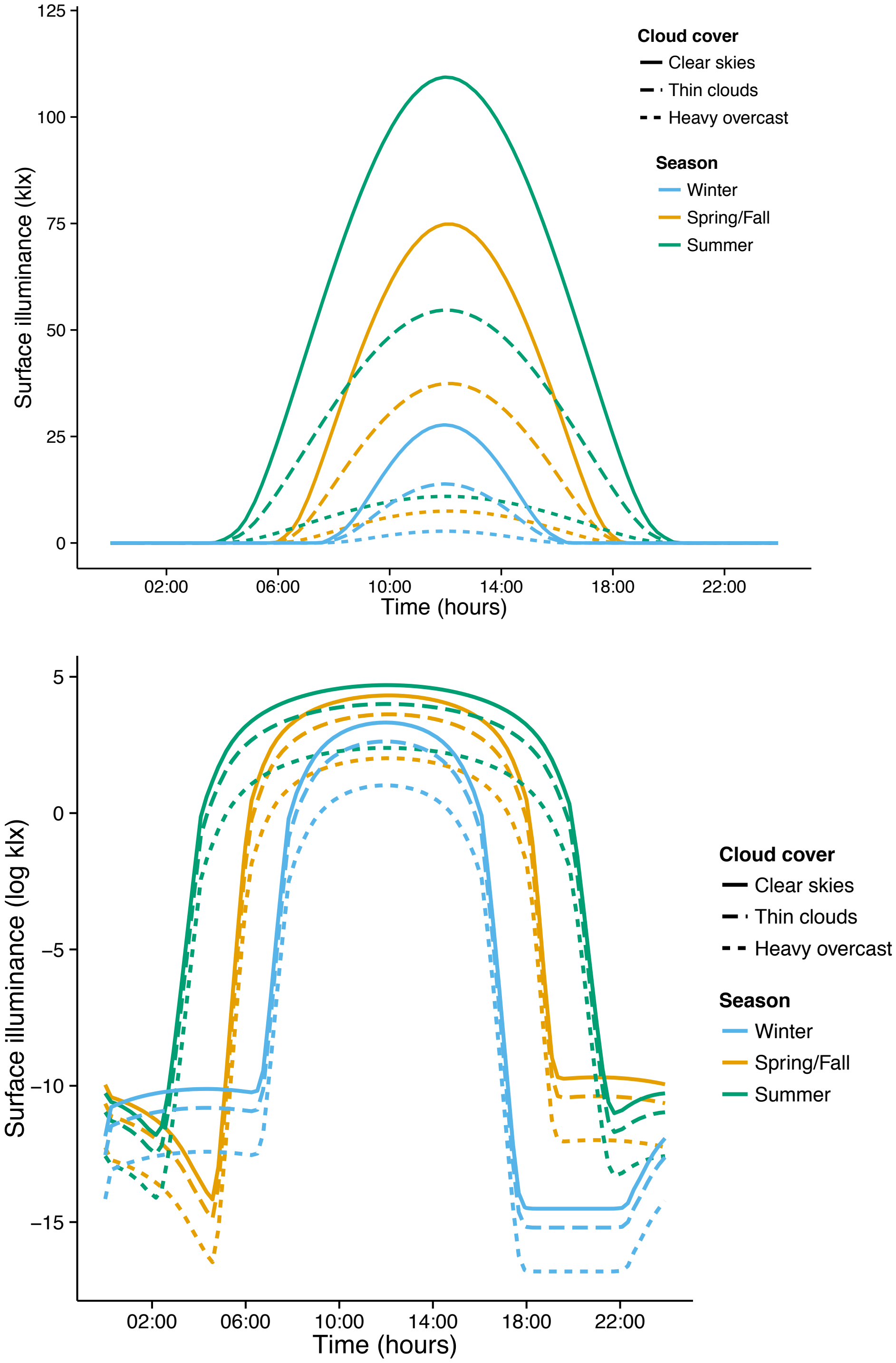

Figure 5.2. (Top panel) Diel light regimes at Lake Chelan, as a function of season and cloud cover, generated with the sun and moon illuminance model of Janiczek and DeYoung (1987). (Bottom panel) Light regimes plotted on a log scale to reveal the effects of moonrise and moonset on illuminance at night.

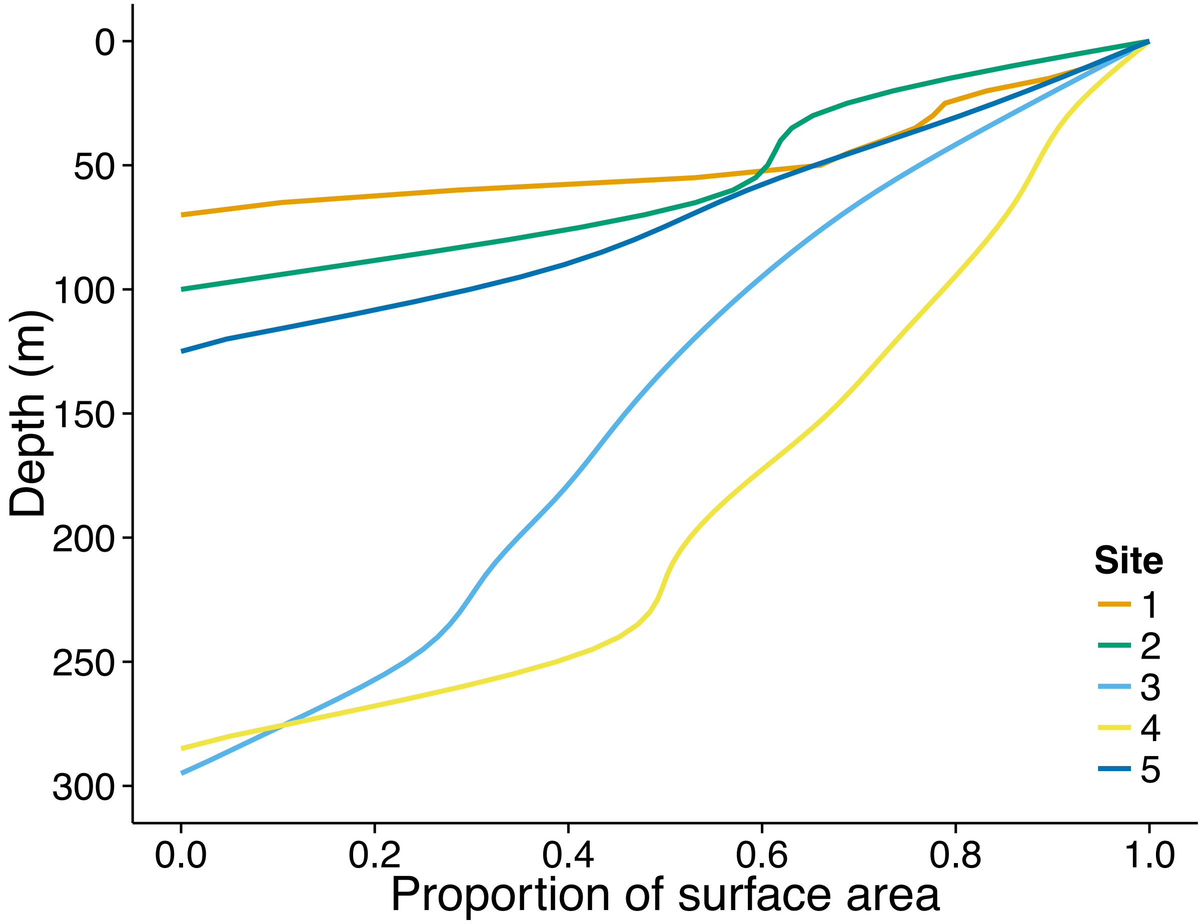

Figure 5.3. Hypsographic (depth-area) curves for five sampling sites in Lake Chelan, Washington.

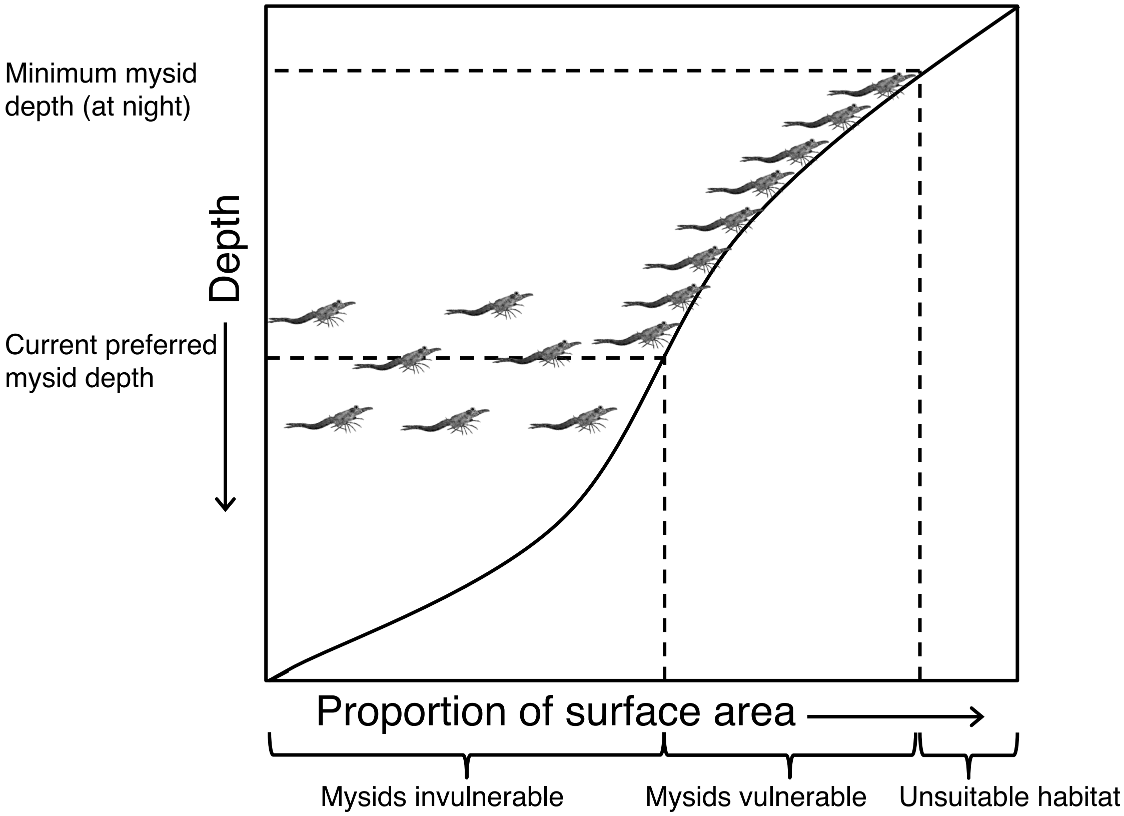

Figure 5.4. Illustration of mysid vulnerability model. The preferred depth of the mysid population under a given set of conditions was determined using a diel vertical migration model (Boscarino et al. 2009). The vulnerability of mysids to benthic predation was defined as the proportion of the mysid population aggregated on the lake bottom, rather than suspended in deep-water refuge habitat. Mysids were assumed to actively avoid shallow nearshore habitats that consistently exceeded their preferred light level. A vulnerability value of 0 indicated mysids were suspended in the water column throughout the site, and a vulnerability of 1 indicated mysids were aggregated on the lake bottom throughout the site.

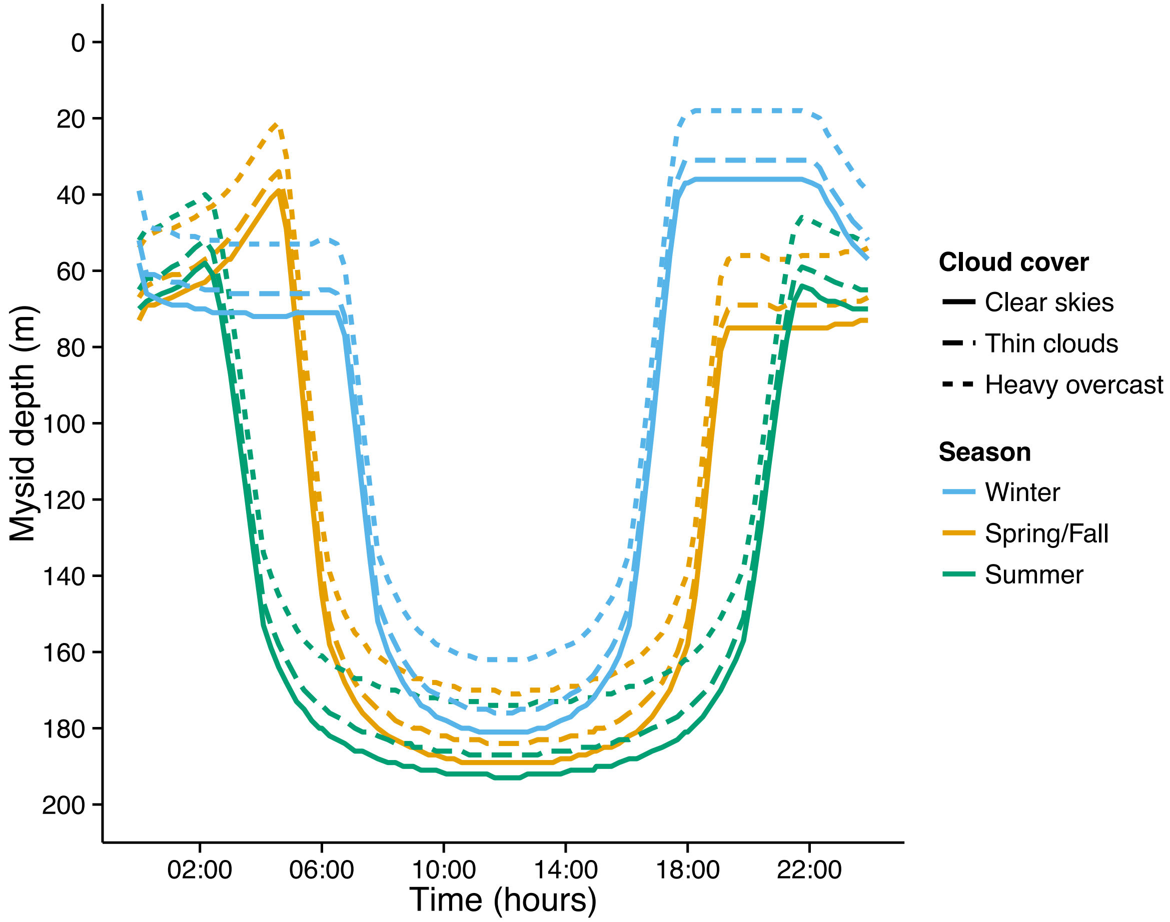

Figure 5.5. Predicted depth distribution of mysids as a function of time of day, season, and cloud cover, as estimated by the mysid diel vertical migration model of Boscarino et al. (2009), using ambient light and light extinction data from Lake Chelan.

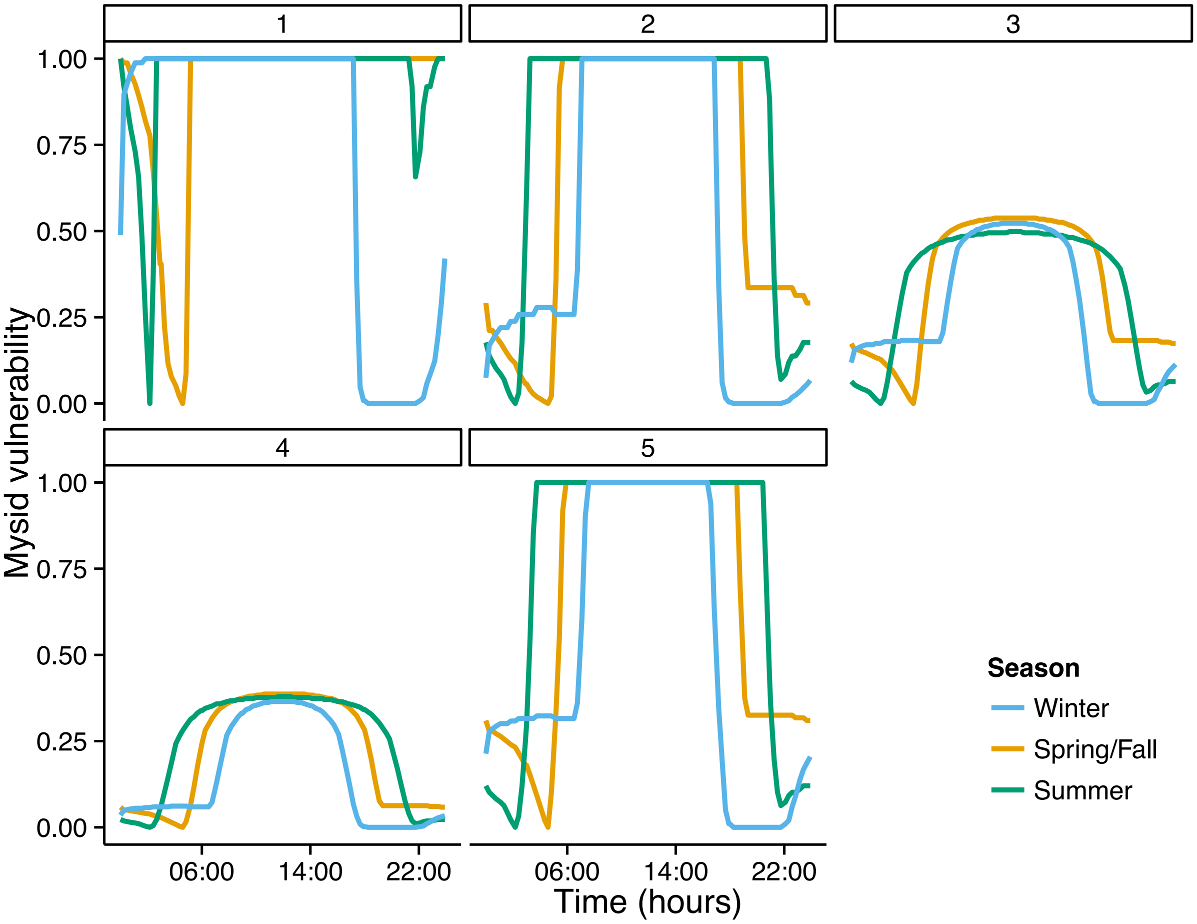

Figure 5.6. Predicted vulnerability of mysids to benthic predation at five sampling sites along a bathymetric gradient in Lake Chelan, as a function of time of day and season, under clear skies. Numerals at the top of each panel indicate site numbers 1-5. Vulnerability was estimated as the fraction of the population that was on the lake bottom under the given conditions. A vulnerability value of 0 indicated mysids were suspended in the water column throughout the site, and a vulnerability of 1 indicated mysids were aggregated on the lake bottom throughout the site.

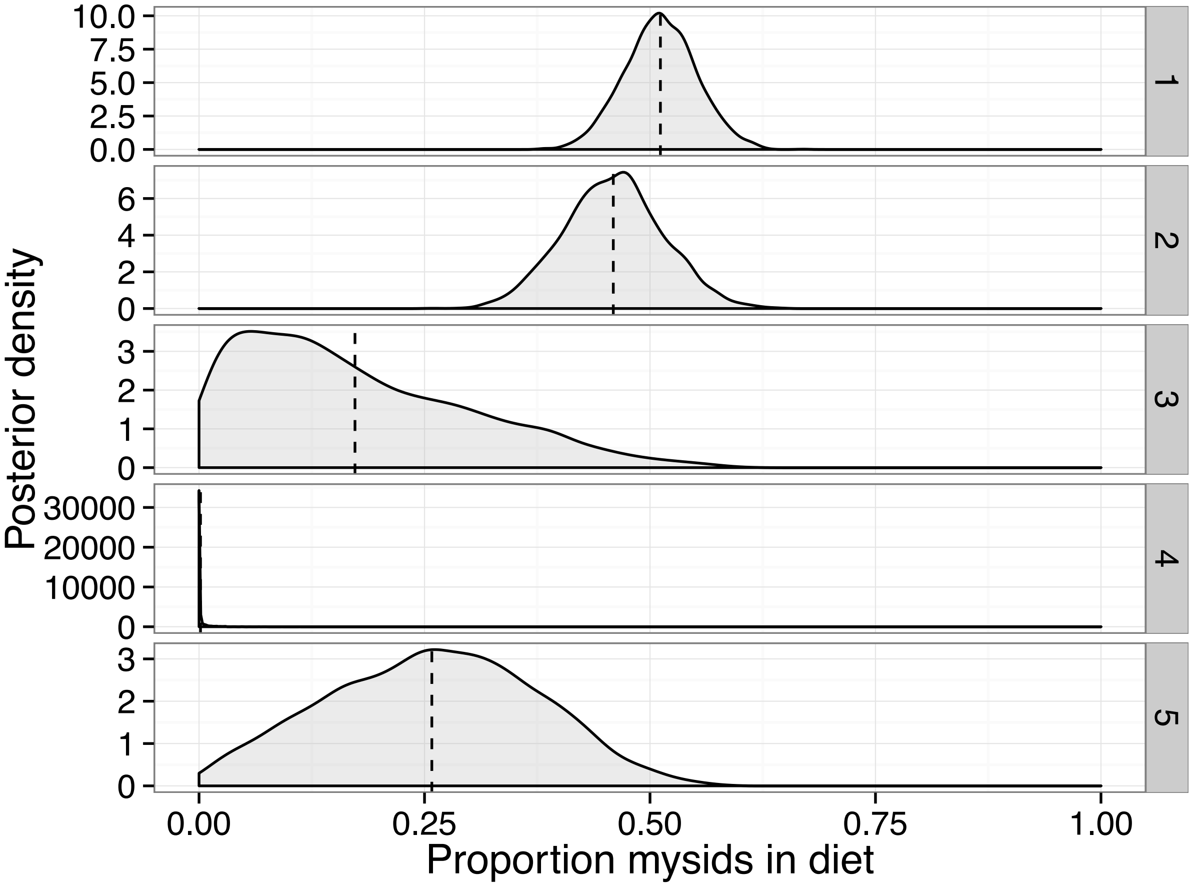

Figure 5.7. Posterior distributions of the proportion of mysids in the diet of lake trout (<600 mm fork length) sampled at five sites in Lake Chelan, Washington. Numerals at right side of each panel indicate site numbers 1-5. Diet proportions were estimated from stomach contents and stable isotope data using a Bayesian stable isotope mixing model (MixSIAR). Dashed lines represent the mean diet proportion of mysids at each site.

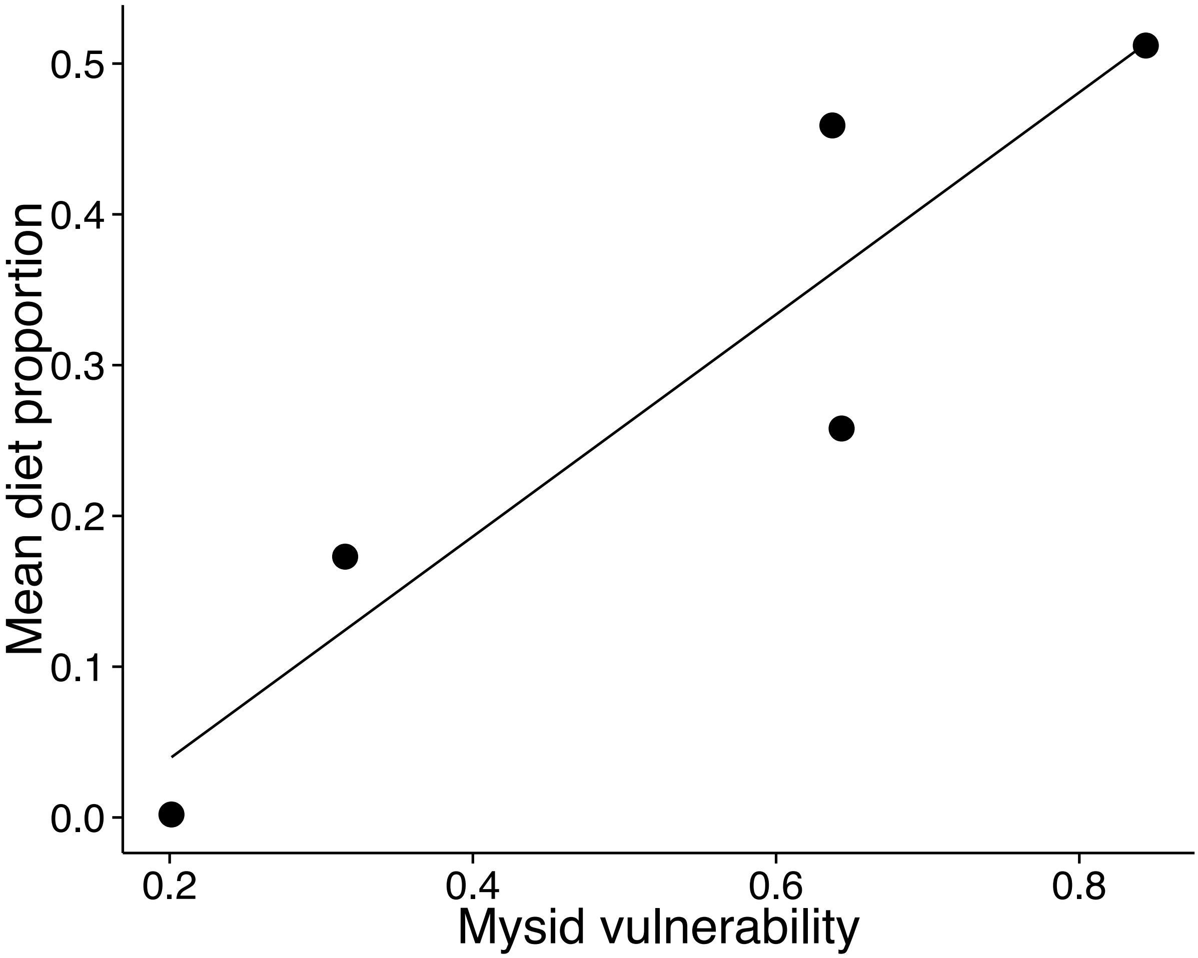

Figure 5.8. The mean proportion of mysids in the diet of lake trout was strongly positively associated with the predicted vulnerability of mysids to benthic predation ($r^2 = 0.86$). Diet proportions of lake trout (<600 mm fork length) were estimated from stomach contents and stable isotope data with a stable isotope mixing model. Mysid vulnerability was estimated from ambient light, water transparency, and bathymetric data with a diel vertical migration model.

APPENDIX

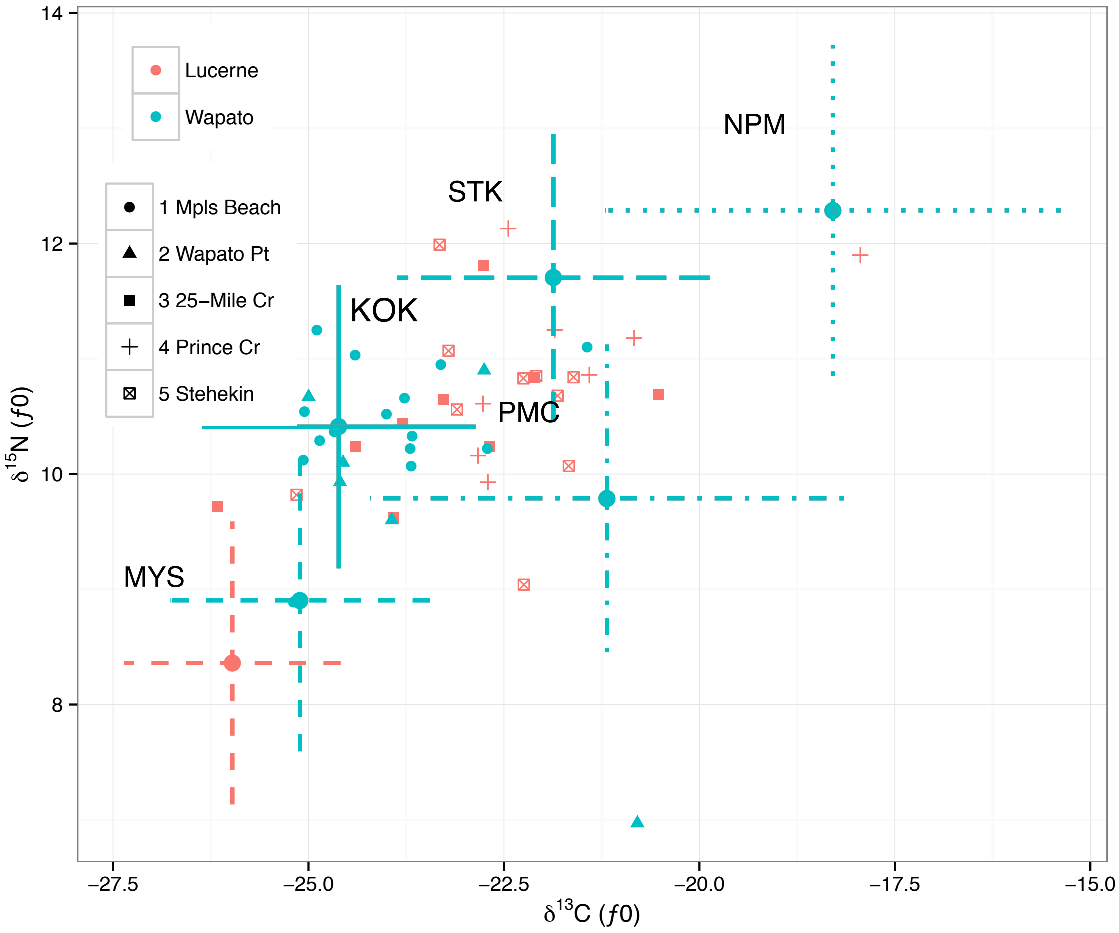

Figure 5.A1. Isospace plot showing the δ^{13}C and δ^{15}N values of individual lake trout from five sampling sites as well as the mean (± SD) of the five predominant species of lake trout prey in Lake Chelan. Lake trout signatures are corrected for trophic discrimination (see Methods). Mysid signatures differed significantly between the two lake basins (Lucerne and Wapato), and are plotted separately. Other prey species did not differ isotopically, so samples were pooled. Prey species are abbreviated as follows: MYS = mysids, KOK = kokanee, PMC = peamouth, NPM = northern pikeminnow, and STK = threespine stickleback.

Conclusion and Synthesis

These studies revealed strong associations between the physical environment, the behaviors of individual predators and prey, and the dynamics of populations and food webs. In particular, they highlighted several mechanisms that strengthened or weakened trophic interactions by decoupling predation rates from the densities of predators and prey. These mechanisms operated at multiple levels of organization. At the behavioral level, shoaling by herring limited their vulnerability to predation by Chinook salmon and diel vertical migration by mysids limited their vulnerability to predation by lake trout. At the population level, high predatory inertia caused the predation impacts of lake trout to increase even as the population declined. At the community level, the availability, rather than the density, of alternative prey (mysids) to apex predators (lake trout) influenced the predation risk of kokanee. Physical habitat gradients also mediated the strength of trophic interactions, interacting with behavioral processes and food-web structure in some cases, but operating independently in others. The capture success of Chinook salmon was limited by turbidity, but this process appeared to be independent from the effect of shoaling. The resource competitive impacts of mysids on kokanee were mediated by water temperature, and this pattern could be explained in part by the slightly reduced density of mysids in warm vs. cold habitats. However, the apparent competitive impacts of mysids were mediated by depth, and this pattern could not be explained by the density of mysids; in fact, mysids provided greater energetics benefits to lake trout in shallow habitats, where they tended to exhibit lower densities.

As predators of highly mobile, patchy prey, the feeding rates of pelagic piscivores are unlikely to vary consistently with prey density. For example, the effect of predator confusion on the capture success of Chinook salmon could not be explained by the densities of herring in the experimental trials, only by the numbers of prey involved in specific encounters with predators. As their densities increased, herring formed larger shoals, which were more difficult for salmon to exploit. Further, when salmon encountered a shoal, they only consumed one herring at most during the encounter. As previously demonstrated for northern pike, a littoral ambush predator, such behavioral processes can cause prey consumption to remain relatively unchanged across a wide range of prey densities (Turesson and Bronmark 2007). Previous research on lake trout showed a similar large-scale pattern: lake trout growth rates were largely insensitive to a 100-fold range of prey fish densities within and among lakes (Eby et al. 1995). Eby and coauthors proposed that this result could be explained if prey consumption by lake trout was more limited by fine-scale behavioral processes than by encounter rates. My findings provide empirical evidence for such processes as a key factor limiting Chinook salmon predation rates, suggesting similar processes may also limit lake trout and other pelagic piscivores.

My results also highlight the importance of considering the food-provisioning and apparent competition interactions of consumers alongside their predation and resource competition interactions, which typically receive far more attention (White et al. 2006, Orrock et al. 2015). If the effects of enhanced predation rates are widespread, this would have broad implications for resource management, including the management of non-native species, where the enemy release hypothesis retains substantial influence. Specifically, the overall impacts of introduced mysids on recipient lakes, reservoirs, and connected ecosystems may in some cases be better explained by enhanced lake trout populations than by depleted zooplankton. If the strengths of these interactions are mediated by separate physical gradients of temperature and depth, as my results suggest, then the hundreds of lakes with introduced mysids, in the presence and absence of lake trout, may represent a large-scale, unplanned experiment testing this hypothesis.

In each of these studies, relatively simple mechanisms yielded valuable insight into broader-scale patterns. In some cases, these mechanisms could be accounted for using little or no additional data beyond what is typically collected in conventional food-web research, and in some cases using even less data (e.g., using bathymetry and water clarity to predict the energetic benefits of mysids to lake trout). In the longstanding tug-of-war in ecology between developing complex models rich in mechanistic detail (e.g., Aksnes and Giske 1993, Hayes et al. 2007) and eschewing complexity to search for broad-scale emergent properties (Ward et al. 2014, Schindler and Hilborn 2015), a profitable middle ground may exist where relatively simple mechanisms with broad explanatory power still remain undiscovered. The interface between environmental gradients, behavioral ecology, and community dynamics is a promising place to search for these mechanisms.

References

Aksnes, D. L. and J. Giske. 1993. A theoretical model of aquatic visual feeding. Ecological Modelling **67**:233-250.

Eby, L. A., L. G. Rudstam, and J. F. Kitchell. 1995. Predator responses to prey population dynamics: An empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences **52**:1564-1571.

Hayes, J. W., N. F. Hughes, and L. H. Kelly. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. Ecological Modelling **207**:171-188.

Orrock, J. L., H. P. Dutra, R. J. Marquis, and N. Barber. 2015. Apparent competition and native consumers exacerbate the strong competitive effect of an exotic plant species. Ecology **96**:1052-1061.

Schindler, D. E. and R. Hilborn. 2015. Prediction, precaution, and policy under global change. Science **347**:953-954.

Turesson, H. and C. Bronmark. 2007. Predator-prey encounter rates in freshwater piscivores: effects of prey density and water transparency. Oecologia **153**:281-290.

Ward, E. J., E. E. Holmes, J. T. Thorson, and B. Collen. 2014. Complexity is costly: a meta−analysis of parametric and non−parametric methods for short−term population forecasting. Oikos **123**:652-661.

White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. Diversity and Distributions **12**:443-455.

VITA

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