Journal of Fish Biology (2001) **58,** 1137–1148
doi:10.1006/jfbi.2000.1524, available online at http://www.idealibrary.com on IDEAL®

Density, aggregation, and body size of northern pikeminnow preying on juvenile salmonids in a large river

J. H. Petersen

U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605, U.S.A.

(*Received 12 June 2000, Accepted 20 November 2000*)

Predation by northern pikeminnow *Ptychocheilus oregonensis* on juvenile salmonids *Oncorhynchus* spp. occurred probably during brief feeding bouts since diets were either dominated by salmonids (>80% by weight), or contained other prey types and few salmonids (<5%). In samples where salmonids had been consumed, large rather than small predators were more likely to have captured salmonids. Transects with higher catch-per-unit of effort of predators also had higher incidences of salmonids in predator guts. Predators in two of three reservoir areas were distributed more contagiously if they had preyed recently on salmonids. Spatial and temporal patchiness of salmonid prey may be generating differences in local density, aggregation, and body size of their predators in this large river.

Key words: predation; juvenile salmon; patchy prey; *Ptychocheilus oregonensis*; feeding bouts; Columbia River.

INTRODUCTION

Adult northern pikeminnow *Ptychocheilus oregonensis* (Richardson), formerly called northern squawfish, are 30–60 cm native cyprinids that occur in lakes, streams, rivers and reservoirs in the north-western U.S.A. and south-western Canada (Wydoski & Whitney, 1979). In many bodies of water, northern pikeminnow are important predators of juvenile anadromous salmonids *Oncorhynchus* spp. that are migrating towards the Pacific Ocean (Foester & Ricker, 1941; Jeppson & Platts, 1959; Thompson & Tufts, 1967; Rieman *et al.*, 1991; Ward *et al.*, 1995). In the Columbia River system, for example, northern pikeminnow are widespread and are assumed to be the major source of mortality for juvenile salmonids apart from dam passage mortality (Raymond, 1979; Rieman *et al.*, 1991; Ward *et al.*, 1995).

The magnitude and intensity of northern pikeminnow predation on migrating salmonids has been estimated using several modelling and analytical approaches (Rieman & Beamesderfer, 1990; Rieman *et al.*, 1991; Petersen & DeAngelis, 1992; Ward *et al.*, 1995; Beamesderfer *et al.*, 1996). Often, mortality or loss calculations in these models depend on estimates of salmonid density and the response of northern pikeminnow to changes in prey density (the functional response). Predation rates may vary an order of magnitude or more among different areas or at the same location from one day to the next, presumably due to local changes in prey density (Petersen & DeAngelis, 1992; Petersen, 1994;

Tel.: +1 509 538-2299 x236; fax: +1 509 538-2843; email: jim_petersen@usgs.gov

0022–1112/01/041137+12 $35.00/0

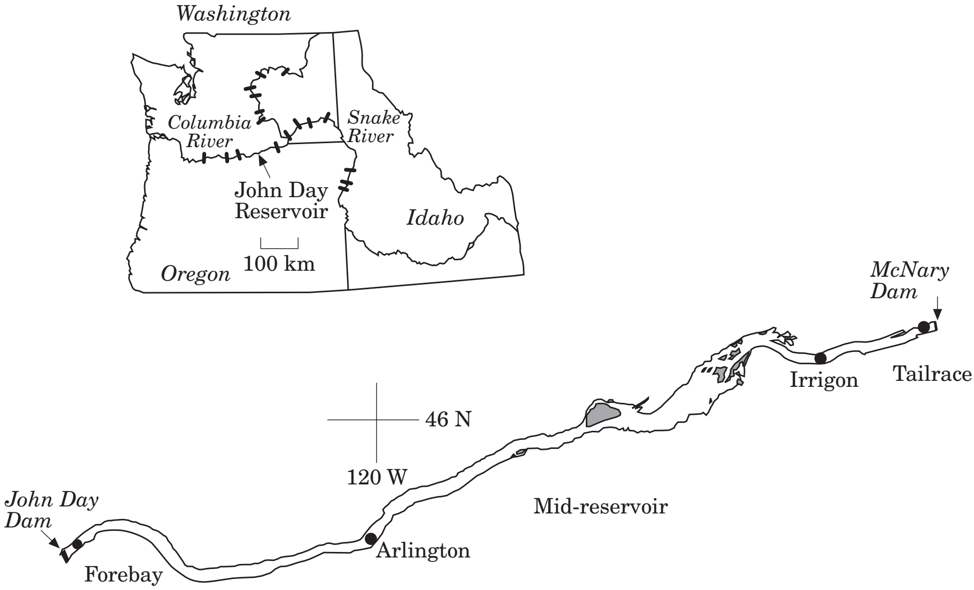

FIG. 1. Sampling locations (●) within John Day Reservoir on the Columbia River (north-western U.S.A.). Samples collected at Arlington and Irrigon were pooled and are referred to as Mid-reservoir in the text. John Day Reservoir is *c.* 123 km in length.

Shively *et al.*, 1996). Also, predation losses may depend on the local density and movements of predators toward high-density patches of juvenile salmonids (Thompson & Tufts, 1967; Collis *et al.*, 1995; Isaak & Bjornn, 1996; Shively *et al.*, 1996; Martinelli & Shively, 1997).

Direct observation of the interaction between northern pikeminnow and juvenile salmonids is impractical in the Columbia River because of its large size (average annual flow *c.* 6655 $m^3 s^{-1}$) and turbid water. Inferences about this predator–prey interaction have been based on data pooled across relatively large areas or reaches, which influence specific conclusions (Petersen, 1994; Petersen & DeAngelis, 2000). For example, Petersen (1994) demonstrated that estimated mortality of juvenile salmonids due to northern pikeminnow predation could change by >50% based on the spatial pattern used to pool data. In this paper, 4 years of field data were used to test hypotheses that body size, local density, and local aggregation were similar between predators that had consumed salmonids recently and predators without salmonids in their gut. Understanding size effects and the local behaviour of predators may be necessary for predicting mortality of juvenile salmonids that migrate through the Columbia and other rivers (Beamesderfer *et al.*, 1996; Petersen & DeAngelis, 1992, 2000; Friesen & Ward, 1999).

MATERIALS AND METHODS

FIELD METHODS

Northern pikeminnow ($\geq$250 mm L_F, *c.* 190 g) were sampled in John Day Reservoir of the lower Columbia River (Fig. 1). This is the largest reservoir (122·9 km long, 19 781 ha) on the Columbia River and had *c.* 87 000 northern pikeminnow in 1983–1986 (Beamesderfer *et al.*, 1990). For 4 years (1983–1986), northern pikeminnow were collected monthly from April through August at four locations within the reservoir, the forebay of John Day Dam, Arlington, Irrigon, and the tailrace of McNary Dam.

Sampling was conducted at each location using boat electrofishing. Within a location, the shoreline was divided into permanent stations along a shore, which ranged in length from *c.* 0·5 to 2·0 km. A fishing run started at a haphazardly selected point within a station and ran parallel to the shore for 15 min. Northern pikeminnow do not occur commonly in water deeper than 4 m (Martinelli & Shively, 1997; J. H. Petersen, unpubl. data), so no sampling was conducted away from shorelines. During the 15 min sampling period, all predators stunned by the electrical current were netted and placed in a live-well on the boat. Sampling was interrupted during a run only to allow adult salmonids to escape the electrical field; this was fairly uncommon. The distance along a shore covered on an individual sampling run varied considerably because of variable water velocity, obstacles, and the rate at which northern pikeminnow were being caught (higher catch rates usually slowed the boat speed to allow the netter time to retrieve all shocked fish). Sampling was conducted during day and night periods and on both sides of the river. All predators collected during a 15 min run are referred to as a catch. Further details on field methods can be found in Poe *et al.* (1991).

Northern pikeminnow were killed, weighed (wet weight), and digestive tracts were removed and preserved. In the laboratory, gut contents were sorted into major taxa or groups and weighed (wet weight). Many prey fish, including salmonids, can be identified to genus or species using diagnostic bones (Hansel *et al.*, 1988). Specific methods on laboratory procedures are presented in Poe *et al.* (1991) and Vigg *et al.* (1991).

ANALYTICAL METHODS

Data were divided into an early season (April–May), which corresponds to the major out-migration of yearling spring chinook salmon *Oncorhynchus tshawytscha* (Walbaum), steelhead *O. mykiss* (Walbaum), and coho salmon *O. kisutch* (Walbaum), and a late season (June–August), which corresponds to out-migration of sub-yearling fall chinook salmon (Vigg *et al.*, 1991). Data were partitioned into tailrace, forebay, and mid-reservoir zones for analysis; the Arlington and Irrigon locations were pooled for analyses and are referred to as the Mid-reservoir location (Fig. 1; see Petersen, 1994 for justification).

It was assumed that northern pikeminnow encountered fluctuating densities or patches of juvenile salmonids, which varied probably hourly, daily and seasonally (Vigg *et al.*, 1991; Petersen & DeAngelis, 1992, 2000). Measurement of prey patchiness is difficult in this large river, so the presence or absence of salmonids in the gut contents of northern pikeminnow was used as an indicator of recent predator encounters with salmonid patches. A northern pikeminnow with at least one salmonid in its gut obviously would have encountered one or more salmonids during a relatively short period prior to sampling, the period required to digest the prey and evacuate indigestible parts such as bones. Therefore individual predators and catches were divided according to presence (with salmon) or absence (without salmon) of salmonid prey in the predator's gut.

For each location and season, the average predator mass was computed for predators with *v.* without salmonids. Averages were computed using only those catches with at least one salmonid present in a northern pikeminnow gut, assuming catches with no salmonids would not have encountered a prey patch. Pairwise comparisons (with *v.* without salmonid prey) were made with *t*-tests.

Catch data were analysed for differences in local density (catch-per-unit effort) and to see if predators were distributed contagiously. The catch-per-unit of effort for transects with *v.* without salmonids present were compared using Wilcoxon's rank test since these data were highly skewed. Aggregation may suggest that predators were responding to temporally variable prey patches, such as salmonid schools. Frequency distributions of catches from a location and season were tested for deviation from randomness using a χ^2 dispersion test (Pielou, 1977; Ives, 1991). If catches were taken from a population with a random distribution, the frequency distribution of catches would be Poisson distributed. Pielou (1977) shows that an index of randomness can be computed as $\Sigma(x_i - \bar{x})^2\bar{x}^{-1}$ where x_i is the number of individuals in the ith of n units sampled and $\bar{x}$ is the mean of all x_i. This index is equivalent to a variance : mean ratio and is distributed as a χ^2 deviate with $(n - 1)$ degrees of freedom. χ^2 indices were computed for catch data by area, period and diet category (with *v.* without salmon). Catches were not distributed randomly when indices were greater than tabulated χ^2 deviates.

If the null hypothesis of randomness was rejected, an aggregation measure J was examined to determine whether northern pikeminnow were distributed contagiously (positive J) or uniformly (negative J). J is a measure of aggregation, developed by Ives (1991), which is a modification of Lloyd's index of mean crowding (Lloyd, 1967). Intraspecific crowding or patchiness, J, is defined as:

$$J=(L-M)\ M^{-1}$$

where L is Lloyd's index of crowding and M is the mean number of individual pikeminnow for a collection of catches. J, which is a positive or negative proportion, measures the relative deviation of a sample from Poisson expectation. If J is not significantly different from zero, the null hypothesis that the sample was drawn from a population of randomly distributed individuals cannot be rejected. If J is positive, for example $+0{\cdot}75$, there are 75% more individuals per sample than expected based on random and independent assortment. J was used in this analysis because it is density-independent, it is applicable to incomplete samples, and Lloyd's index is not sensitive to the areal size of the sample (quadrat size) (Pielou, 1977; Ives, 1988, 1991). These considerations were important since the samples were collected over different distances of shoreline, using a constant timed effort (15 min) rather than a fixed length of shore. Variance (S.E.) of J were estimated using Tukey's jack-knifing procedure (Ives, 1991).

Paired (with *v.* without salmonid prey) averages of aggregation (J) were compared using a bootstrap resampling procedure analogous to a paired t-test (Westfall & Young, 1993). Tests were conducted with PROC MULTTEST (SAS, 1990) and datasets were resampled 1000 times. The significance criteria for all tests was $P<0{\cdot}05$, with a Bonferroni adjustment to account for multiple testing.

RESULTS

A total of 4998 northern pikeminnow were collected ranging in size from 191 g (250 mm L_F) to 2700 g (590 mm L_F). Although samples were collected throughout the day and night, data were pooled for analyses below. Preliminary examinations showed no consistent differences between day (0600–1800 hours) *v.* night (1800–0600 hours) periods for paired statistics of aggregation (J) or catch. The differences in the average mass of predators with *v.* without salmonids in their guts (see below) were consistent whether individual northern pikeminnow were collected during either day or night.

At all locations, if a predator had salmonids in its gut, then salmonids tended to be the dominant prey item (Fig. 2). When salmonids were found within northern pikeminnow, they were >80% of the diet in the dam tailrace or forebay locations, *c.* 75% of the diet during April–May in the mid-reservoir, and *c.* 30% of the diet during June–August in the Mid-reservoir (Fig. 2).

During the early season, northern pikeminnow were largest at McNary Dam tailrace, intermediate at the Mid-reservoir location, and smallest at the John Day Dam forebay (Fig. 3). During June–August, northern pikeminnow at McNary Dam tailrace were largest, while predators at the Mid-reservoir and

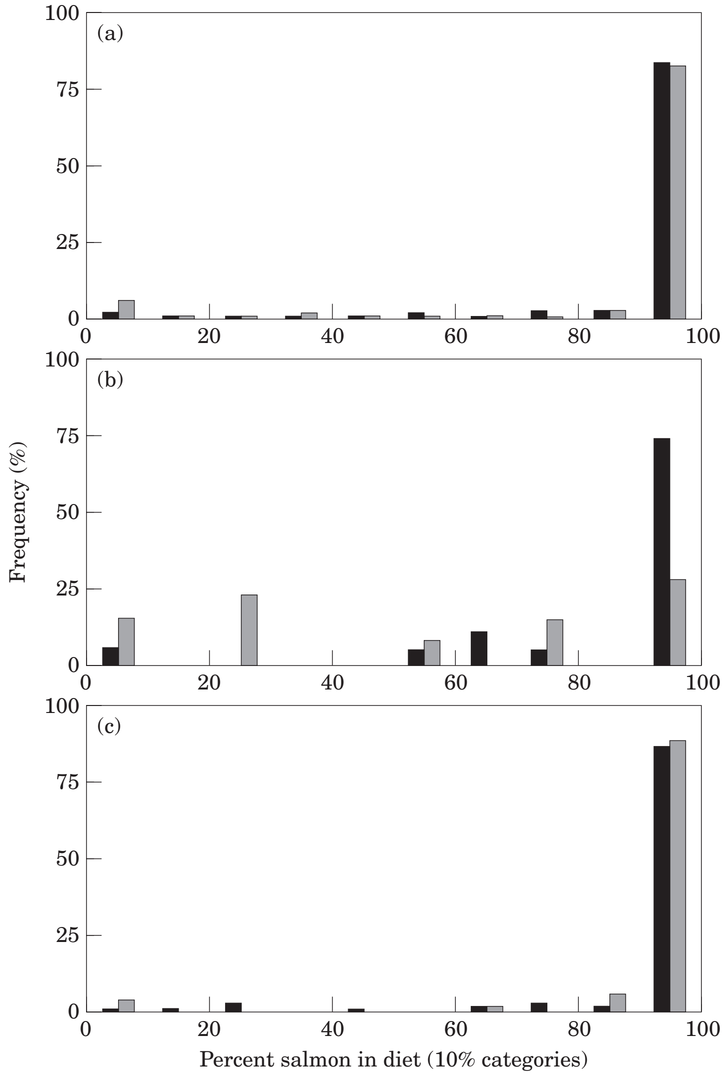

FIG. 2. Frequency of northern pikeminnow from John Day Reservoir (1983–1986) whose diets were various percentages (0–10, 10–20, 20–30, . . .) of salmonids. Separate distributions are shown for the April–May (■) and the June–August (□) periods, and for the three reservoir locations sampled. (a) McNary Dam tailrace; n=356 and 590 for April–May and June–August, respectively; (b) Mid-reservoir; n=19 and 13; (c) John Day Dam forebay, n=99 and 54.

John Day Dam forebay location were of similar mass (Fig. 3). The average size of predators with salmonid prey were significantly greater than the size of predators without salmonid prey in five of six comparisons; only in the Mid-reservoir during June–August were predator sizes not significantly different (Fig. 3).

In pairwise comparisons, the median catch of predators with salmonid prey was significantly higher than the median catch of predators without salmonid prey in their guts at all areas and times [Fig. 4(a), (b)]. The highest median catch

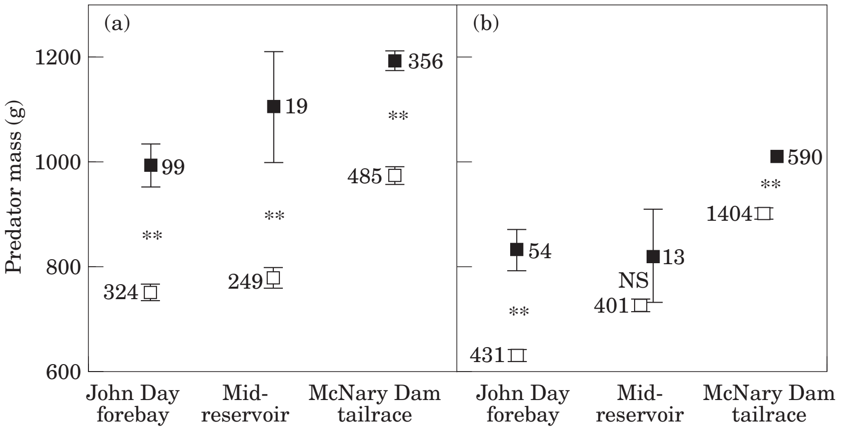

FIG. 3. Mass (mean ± S.E.; *n* beside symbol) of northern pikeminnow with (■) *v.* without (□) juvenile salmonid prey by season and reservoir location, John Day Reservoir during 1983–1986. Asterisks between paired statistics (with *v.* without salmonid prey) indicate results of pairwise comparisons (*NS*, not significant at $P=0.05$; $^{**}P<0.01$). (a) April–May; (b) June–August.

occurred at the McNary Dam tailrace during summer for predators with salmonid prey. Catch distributions with salmonid prey present tended to be highly skewed with as many as 42 northern pikeminnow being collected during a 15 min run. At the Mid-reservoir location, median catches of pikeminnow with salmonids were only two pikeminnow (Fig. 4).

For samples with salmonid prey present, all frequency distributions of catches collected near dams were distributed contagiously [Table I; Fig. 4(c), (d); $J>0$]. The relatively high values for J in the McNary Dam tailrace [Fig. 4(c), (d)] suggest a fairly high degree of aggregation. The degree of aggregation was significantly greater for samples with salmonids than for comparable samples without salmonids at John Day Dam forebay (spring and summer) and at McNary Dam tailrace (spring only) (Fig. 4). At Mid-reservoir locations, predator aggregations was not significantly different for samples with and without salmonids (Fig. 4).

DISCUSSION

Several types of evidence suggest that northern pikeminnow capture juvenile salmonids during brief feeding bouts. In the present study, high percentages (>80%) of salmonids were found in pikeminnow diets especially during April–May. These high percentages suggest that predators had not consumed a mixed diet of salmonids and other prey types prior to sampling, but instead had eaten salmonids almost exclusively. Petersen & DeAngelis (1992) back-calculated the time of ingestion of salmonids by northern pikeminnow in the McNary Dam tailrace and compared intercapture frequency distributions to predictions from models of random and contagious feeding events. The intercapture frequency distributions were most similar to the contagious feeding model, suggesting that northern pikeminnow consumed salmonids during discrete feeding bouts. In

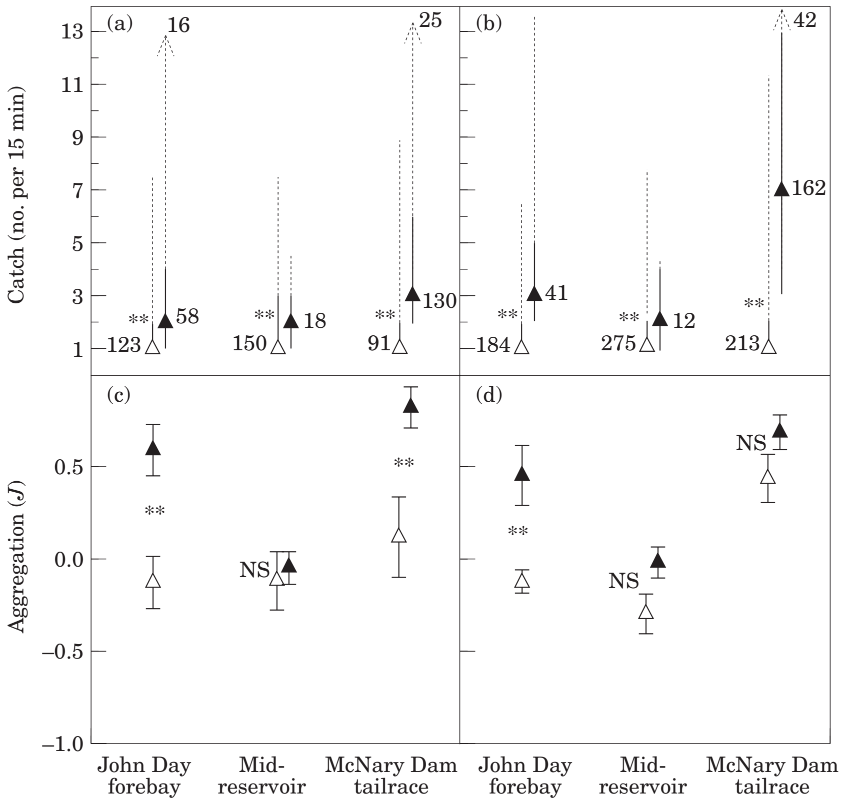

FIG. 4. Catch [(a), (b); median, ± 1 quartile (——), maximum (· · · · ·)] and aggregation index [(c), (d); mean ± 1 S.E.] of northern pikeminnow with (▲) and without (△) juvenile salmonid prey in a sample. Samples were collected during two seasons at three locations in John Day Reservoir, 1983–1986. Asterisks between paired statistics (with *v.* without salmonid prey) indicate results of pairwise comparisons (*NS*, not significant at $P=0{\cdot}05$; $^{**}P<0{\cdot}01$). Sample sizes beside symbols in (a), (b) are the same in (c), (d), respectively. (a), (c) April–May; (b), (d) June–August.

large tanks or raceways, 1 day starved northern pikeminnow often attacked and consumed several salmonids within a few minutes after prey were added to the system (Petersen & Gadomski, 1994; pers. obs.). Other fish feed during discrete bouts (Beukema, 1968; Brett, 1971; Grove *et al*., 1978).

Larger northern pikeminnow within an area appeared to be more successful at capturing salmonids than nearby smaller predators. All northern pikeminnow examined were >250 mm L_F and the great majority of salmonids (*c.* 80–160 mm L_F) could be eaten by predators of this size (Poe *et al*., 1991) so differences in prey vulnerability due to size would not appear to explain this result. The average difference in northern pikeminnow mass with *v.* without salmonids in their gut was *c.* 200 g during April–May and *c.* 100 g during June–August (Fig. 3). This difference in predator size may have been a consequence of differences in prey size between spring (primarily spring chinook salmon and steelhead; *c.* 120–200 mm L_F) and summer (primarily fall chinook salmon; *c.* 80–140 mm L_F; Poe *et al*., 1991). The specific mechanism(s) by which larger predators were more successful is not clear. Larger individuals may be more successful through

Table I. χ^2 tests of dispersion for northern pikeminnow catch distributions in John Day Reservoir during 1983–1986

Season/Area	With salmonid prey		Without salmonid prey	
	χ^2 *P*	*n*	χ^2 *P*	*n*
April–May				
John Day Dam forebay	**	58	NS	123
Mid-reservoir	NS	18	NS	150
McNary Dam tailrace	**	130	NS	91
June–August				
John Day Dam forebay	**	41	NS	184
Mid-reservoir	NS	12	NS	275
McNary Dam tailrace	**	162	**	213

χ^2 *P* is the significance (NS, not significant at 0·05; * = 0·01 < *P* < 0·05; ** = *P* < 0·01) of χ^2 dispersion tests by season and area. Samples were separated into categories based on the presence or absence of salmonid prey in predator's digestive tracts; *n*, sample size.

better visual acuity (Howick & O'Brien, 1983), a higher rate of acceleration during an attack (Webb, 1978), or by causing changes in prey behaviour, such as shoaling, that affect prey vulnerability indirectly (Parrish, 1992; Johannes, 1993; Essington *et al*., 2000).

Near the dams, all four (Table I; Fig. 4) samples of northern pikeminnow with a salmonid present were dispersed non-randomly and the aggregation index was significantly >0, suggesting contagious distributions. Only one of the samples near the dams without salmonids present was aggregated. In the Mid-reservoir, aggregation indices suggested predators were dispersed randomly and there was no difference between catch distributions where salmonids were present or absent (with *v.* without salmonids); however, probably the power to detect differences was low because of small sample sizes ($n = 18$ and 12; Fig. 4). Sampling occurred at only one spatial scale (15 min transects; *c.* 0·5–2·0 km) and the summary statistics on aggregation are applicable only at this scale. It is quite possible that predators in the Mid-reservoir, where no aggregation was detected, were aggregated at either smaller or larger scales. Northern pikeminnow diet in Mid-reservoir areas includes a high proportion of benthic prey, such as crayfish and sculpins (Poe *et al*., 1991; Petersen & Ward, 1999), influencing perhaps spatial patterns or aggregations that were not detected in this study.

Using presence or absence of diagnostic bones in a predator does not provide information on the precise timing of predation, but an approximate estimate of the time prior to sampling that prey were ingested can be made using an evacuation rate model. Using the model of Beyer *et al*. (1988), 90% of a salmonid meal would be evacuated from a 1000 g northern pikeminnow within *c.* 18 h in April–May (*c.* 12° C) and within *c.* 6 h in June–August (*c.* 19° C). Studies with cod *Gadus morhua* L. and rainbow trout *O. mykiss* (Walbaum) have shown that indigestible particles (glass beads and pieces of chitin) may be retained about twice as long as digestible material (Kionka & Windell, 1972; dos Santos & Jobling, 1991). Assuming diagnostic bones observed in northern pikeminnow guts were retained twice as long as most digestible organic matter, salmonid prey were consumed *c.* 0–36 h prior to sampling in April–May and *c.* 0–12 h before sampling in June–August.

Rapid changes in the local density of salmonids may be causing the bout-feeding response observed in northern pikeminnow. Hydroacoustic surveys for juvenile salmonids in the Columbia River suggest salmonids often occur in patches and rarely are distributed evenly throughout a reach or reservoir (Steig & Johnson, 1996; U.S. Geological Survey, unpubl. data). Patchiness of salmonids in this large river may be created through natural shoaling or schooling, by diel passage at dams that creates temporal pulses of prey (Venditti *et al.*, 2000), or by hatchery releases of salmonids. The rate of predation by northern pikeminnow on salmonids increased following hatchery releases into a lake (Thompson & Tufts, 1967), small rivers (Collis *et al.*, 1995; Shively *et al.*, 1996) and large rivers, including one site in the Columbia River (Thompson, 1959; Collis *et al.*, 1995). Shively *et al.* (1996) reported increased feeding by northern pikeminnow 60 km downstream of the release site of 1·1 million chinook salmon, suggesting migratory prey patches remain coherent for considerable distances and thus stimulate predator responses through a river reach (Petersen & DeAngelis, 2000).

Local changes in salmonid density also may stimulate short movements in northern pikeminnow, perhaps causing some of the aggregation patterns observed in this study, especially near dams. Radio-tagged northern pikeminnow have been studied in the tailraces of three dams and in each case there appeared to be movements that were associated with foraging on salmonids (Faler *et al.*, 1988; Isaak & Bjornn, 1996; Martinelli & Shively, 1997). Collis *et al.* (1995) observed an increase in the catch-per-unit effort of northern pikeminnow at each of three sites after a hatchery release, which was attributed to predator movement into these areas.

Management models used in the Columbia River assume predators and prey are distributed homogeneously throughout large areas and that encounters occur instantaneously (Beamesderfer *et al.*, 1990, 1996). However, inclusion of the patchy nature of the prey, predator size and movement, and bout-feeding behaviour for predators may change mortality estimates considerably. For example, the model of Petersen & DeAngelis (2000) showed how salmonid mortality estimates depended on the number of prey in a patch, the rate of spread of the prey patch, and the position of the predator within the reach. Better descriptions and quantification of behaviour, combined with spatially explicit models, should improve the ability to estimate the role of predators in this and other systems (Dunning *et al.*, 1995; Jager *et al.*, 1997; Pascual & Levin, 1999; D. L. DeAngelis & J. H. Petersen, unpubl. data).

Helpful comments on earlier versions of the manuscript were provided by D. DeAngelis, A. Ives, D. Gadomski, T. G. Northcote and an anonymous reviewer. This work was supported through contracts with the Bonneville Power Administration, administered by W. Maslen, which I appreciate.

References

Beamesderfer, R. C., Rieman, B. E., Bledsoe, L. J. & Vigg, S. (1990). Management implications of a model predation by resident fish on juvenile salmonids migrating through a Columbia River reservoir. *North American Journal of Fisheries Management* **10,** 290–304.

Beamesderfer, R. C., Ward, D. L. & Nigro, A. A. (1996). Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 2898–2908.

Beukema, J. J. (1968). Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.). The influence of hunger and experience. *Behaviour* **31,** 1–126.

Beyer, J. M., Lucchetti, G. & Gray, G. (1988). Digestive tract evacuation in northern squawfish (*Ptychocheilus oregonensis*). *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 4548–4553.

Brett, J. R. (1971). Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **28,** 409–415.

Collis, K., Beaty, R. E. & Crain, B. R. (1995). Changes in catch rate and diet of northern squawfish associated with the release of hatchery-reared juvenile salmonids in a Columbia River reservoir. *North American Journal of Fisheries Management* **15,** 346–357.

Dunning, J. B. Jr, Stewart, D. J., Danielson, B. J., Noon, D. R., Root, T. L., Lamberson, R. H. & Stevens, E. E. (1995). Spatially explicit population models: current forms and future uses. *Ecological Applications* **5,** 3–11.

Essington, T. E., Hodgson, J. R. & Kitchell, J. F. (2000). Role of satiation in the functional response of a piscivore, largemouth bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Science* **57,** 548–556.

Faler, M. P., Miller, L. M. & Welke, K. I. (1988). Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam. *North American Journal of Fisheries Management* **8,** 30–35.

Foerster, R. E. & Ricker, W. E. (1941). The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. *Journal of the Fisheries Board of Canada* **5,** 315–336.

Friesen, T. A. & Ward, D. L. (1999). Management of northern pikeminnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. *North American Journal of Fisheries Management* **19,** 406–420.

Grove, D. J., Lorizides, L. G. & Nott, J. (1978). Satiation amount, frequency of feeding and gastric emptying rate in *Salmo gairdneri. Journal of Fish Biology* **12,** 507–516.

Hansel, H. C., Duke, S. D., Lofy, P. T. & Gray, G. A. (1988). Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Transactions of the American Fisheries Society* **117,** 55–62.

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

Isaak, D. J. & Bjornn, T. C. (1996). Movement of northern squawfish in the tailrace of a lower Snake River dam relative to the migration of juvenile anadromous salmonids. *Transactions of the American Fisheries Society* **125,** 780–793.

Ives, A. R. (1988). Aggregation and coexistence of competitors. *Annales Zoologici Fennici* **25,** 75–88.

Ives, A. R. (1991). Aggregation and coexistence in a carrion fly community. *Ecological Monographs* **61,** 75–94.

Jager, H. I., Cardwell, H. E., Sale, M. J., Bevelheimer, M. S., Coutant, C. C. & van Winkle, W. (1997). Modelling the linkages between flow management and salmon recruitment in rivers. *Ecological Modelling* **103,** 171–191.

Jeppson, P. & Platts, W. S. (1959). Ecology and control of the Columbia River squawfish in northern Idaho lakes. *Transactions of the American Fisheries Society* **88,** 197–202.
Johannes, M. R. S. (1993). Prey aggregation is correlated with increased predation pressure in lake fish communities. *Canadian Journal of Fisheries and Aquatic Science* **50,** 66–73.
Kionka, B. C. & Windell, J. T. (1972). Differential movement of digestible and indigestible food fractions in rainbow trout, *Salmo gairdneri. Transactions of the American Fisheries Society* **101,** 112–115.
Lloyd, M. (1967). Mean crowding. *Animal Ecology* **36,** 1–30.
Martinelli, T. L. & Shively, R. S. (1997). Seasonal distribution, movements and habitat associations of northern squawfish in two lower Columbia River reservoirs. *Regulated Rivers: Research and Management* **13,** 543–556.
Parrish, J. K. (1992). Do predators ' shape ' fish schools: Interactions between predators and their schooling prey. *Netherlands Journal of Zoology* **42,** 358–370.
Pascual, M. & Levin, S. A. (1999). From individuals to population densities: searching for the intermediate scale of nontrivial determinism. *Ecology* **80,** 2225–2236.
Petersen, J. H. (1994). Importance of spatial pattern in estimating predation on juvenile salmonids in the Columbia River. *Transactions of the American Fisheries Society* **123,** 924–930.
Petersen, J. H. & DeAngelis, D. L. (1992). Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 2551–2565.
Petersen, J. H. & DeAngelis, D. L. (2000). Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. *Mathematical Biosciences* **165,** 97–114.
Petersen, J. H. & Gadomski, D. M. (1994). Light-mediated predation by northern squawfish on juvenile chinook salmon. *Journal of Fish Biology* **45,** 227–242.
Petersen, J. H. & Ward, D. L. (1999). Development and corroboration of a bioenergetics model for northern pikeminnow feeding on juvenile salmonids in the Columbia River. *Transactions of the American Fisheries Society* **128,** 784–801.
Pielou, E. C. (1977). *Mathematical Ecology*. New York: John Wiley.
Poe, T. P., Hansel, H. C., Vigg, S., Palmer, D. E. & Prendergast, L. A. (1991). Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* **120,** 405–420.
Raymond, H. L. (1979). Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society* **108,** 505–529.
Rieman, B. E. & Beamesderfer, R. C. (1990). Dynamics of a northern squawfish population and the potential to reduce predation on juvenile salmonids in a Columbia River reservoir. *North American Journal of Fisheries Management* **10,** 228–241.
Rieman, B. E., Beamesderfer, R. C., Vigg, S. & Poe, T. P. (1991). Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* **120,** 448–458.
dos Santos, J. & Jobling, M. (1991). Gastric emptying in cod, *Gadus morhua* L.: emptying and retention of indigestible solids. *Journal of Fish Biology* **38,** 187–197.
SAS Institute (1990). *SAS/STAT User's Guide*, Version 6, 4th edn. Cary, NC: SAS Institute.
Shively, R. S., Poe, T. P. & Sauter, S. T. (1996). Feeding response by northern squawfish to a hatchery release of juvenile salmonids in the Clearwater River, Idaho. *Transactoins of the American Fisheries Society* **125,** 230–236.
Steig, T. W. & Johnson, S. V. (1996). Monitoring fish movement pattern in a reservoir using horizontally split-beam techniques. *ICES Journal of Marine Science* **53,** 435–441.

Thompson, R. B. (1959). Food of the squawfish *Ptychocheilus oregonensis* of the lower Columbia River. *Fishery Bulletin, U.S.* **60,** 43–58.

Thompson, R. B. & Tufts, D. F. (1967). Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. *Transactions of the American Fisheries Society* **96,** 424–427.

Venditti, D. A., Rondorf, D. W. & Kraut, J. M. (2000). Migratory behavior and forebay delay of radio-tagged juvenile fall chinook salmon in a lower Snake River impoundment. *North American Journal of Fisheries Management* **20,** 41–52.

Vigg, S., Poe, T. P., Prendergast, L. A. & Hansel, H. C. (1991). Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* **120,** 421–438.

Ward, D. L., Petersen, J. H. & Loch, J. J. (1995). Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. *Transactions of the American Fisheries Society* **124,** 321–334.

Webb, P. W. (1978). Fast-start performance and body form in seven species of teleost fish. *Journal of Experimental Biology* **74,** 211–226.

Westfall, P. H. & Young, S. S. (1993). *Resampling-based Multiple Testing*. New York: Wiley Interscience.

Wydoski, R. S. & Whitney, R. R. (1979). *Inland Fishes of Washington*. Seattle: University of Washington Press.