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Population ecology and prey consumption by fathead minnows in prairie wetlands: importance of detritus and larval fish

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Abstract – The fathead minnow *Pimephales promelas* occurs in high densities in wetlands of the prairie pothole region (PPR) of North America, but food resources sustaining these populations are poorly known. We assessed population dynamics and prey consumption of fathead minnow populations in three PPR wetlands for 2 years. Fish density peaked at 107 fish per m² for all age classes combined. Larval and juvenile fish dominated these populations in terms of abundance and accounted for 83% of total prey consumption. Detritus dominated fish diets, representing 53%, 40% and 79% of diet mass for larval, juvenile and adult fish respectively. Detritus consumption was positively related to minnow density and negatively related to invertebrate abundance, but only for adult fish. Seasonal production:biomass ratios were unrelated to proportions of detritus in the diet for all ages of fish, indicating that detritus is an important food resource capable of meeting metabolic demands and sustaining fish growth in high-density populations. Detritus consumption may also weaken links between abundance of invertebrate prey and minnows, promoting dense fish populations with strong, consistent influences on wetland ecosystems.

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Key words: fathead minnow; *Pimephales promelas*; bioenergetics models; consumption estimates; fish production; larval fish; detritus

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Introduction

Fathead minnow *Pimephales promelas* is a common resident of semipermanent and permanently flooded wetlands throughout much of the prairie pothole region (PPR) in North America (Stewart & Kantrud 1971; Peterka 1989). Aquatic invertebrates are also abundant in these habitats, and comprise an important food resource for vertebrate consumers, including fish, birds and amphibians (Euliss et al. 1999). However, recently, fathead minnow populations have been shown to strongly influence community characteristics in Minnesota's PPR wetlands, including reducing invertebrate populations, and creating conditions that favour high phytoplankton biomass, low water transparency and reduced submerged aquatic vegetation (Zimmer et al. 2000, 2001a, 2003).

Natural history characteristics (omnivory – Held & Peterka 1974; Price et al. 1991; high tolerance to hypoxic conditions – Klinger et al. 1982; rapid growth – Held & Peterka 1974; high recruitment potential – Payer & Scalet 1978) make the fathead minnow well adapted to shallow wetland habitats, and contribute to their widespread occurrence in PPR wetlands. The fathead minnow is also a fractional spawner, with populations producing multiple cohorts of larvae throughout the summer once water temperatures reach 18 °C (Dobie et al. 1956). These fish grow quickly and can reach sexual maturity and spawn at the end of their first summer (Markus 1934; Held & Peterka 1974). Zooplankton, macroinvertebrates, and detritus have all been found to be important components of fathead minnow diets at various times of the year (Held & Peterka 1974; Price et al. 1991; Zimmer et al.

2006). These characteristics all contribute to high fathead minnow densities and biomass in prairie wetlands, as well as high consumption rates of aquatic invertebrates (Duffy 1998). However, to date, research on prey consumption by the fathead minnow has largely ignored consumption by larval fish. Furthermore, the overall importance of detritus as a food resource for all ages of minnows is poorly understood.

Patterns of metabolic allometry for fish show that mass-specific consumption rates are inversely related to fish size (Post 1990). Thus, gram for gram, larval fish have the potential to exert greater impacts on prey populations and energy flow in wetland ecosystems than do older, large-bodied adults. Implications of this relationship are particularly important in PPR wetlands as young-of-the-year (YOY) and larval fish often dominate fathead minnow populations in these systems. Payer & Scalet (1978) estimated 99% of the annual production of a fathead minnow population was contributed by YOY fish, and estimated that 194 adult fish resulted in over 126,000 recruits in just 3 months.

The role of detritus as a food resource for fathead minnows is poorly known. Consumption of detritus weakens the link between the abundance of invertebrate prey and abundance of fish by allowing higher population-level survival during times of lean invertebrate abundance, resulting in higher, more consistent predation pressure on invertebrates relative to fish populations feeding solely on invertebrates (Polis & Strong 1996; Schaus & Vanni 2000; Schindler & Scheuerell 2002). Additionally, consumption of detritus and subsequent excretion translocates nutrients and represents a 'new' source of nutrients for phytoplankton, potentially increasing their overall abundance (Schaus & Vanni 2000; Zimmer et al. 2006). Thus, influences of fathead minnow populations on wetland ecosystems may depend, in part, on the relative importance of detritus in the diet. Consumption of detritus may also influence dynamics of minnow populations (such as mass-specific production rates of the fish), as detritus has lower concentrations of both energy and protein relative to invertebrate prey (Bowen et al. 1995). Consequently, detritus has usually been considered a supplemental food source that allows the fathead minnow to survive when other more nutritional food sources are low (Held & Peterka 1974; Price et al. 1991). More recently, it has been suggested that consumption of lower quality, readily available detritus, combined with higher quality, difficult-to-catch invertebrate prey may serve as a mechanism for rapid growth of fathead minnows (Lemke & Bowen 1998).

Here, we describe population characteristics, and estimate consumption of invertebrate and detrital food resources in adult, juvenile and larval fathead minnow

cohorts in three prairie wetlands. Our goals were to: (1) estimate and contrast consumption of detritus and invertebrate prey among larval, juvenile, and adult fish; (2) estimate rates of biomass and energy flow through the fathead minnow populations; (3) test whether consumption of detritus was related to abundance of invertebrate prey; and (4) test whether mass-specific production rates of minnow populations were related to the amount of detritus in fish diets.

Methods

We studied fathead minnow populations in three wetlands in western Minnesota. Study wetlands ranged in size from 6.4 to 13.0 ha, and maximum wetland depths were 1.9–2.6 m (Table 1).

Fathead minnow population characteristics and growth

Density estimates of juvenile (20–40 mm TL) and adult (>40 mm TL) fathead minnows were obtained using square 1-m² pop nets (Dewey et al. 1989) fitted with 0.5 mm (bar measure) mesh. Pop nets consist of a buoyant top frame (PVC pipe and foam insulation) fitted with 1 m² netting attached to four sides and the bottom, but open on top. The net is then temporarily secured to a weighted bottom frame and deployed. After a waiting period, the device is triggered remotely sending the top frame and netting rapidly up through the water column, capturing small fishes and thus providing a quantitative estimate of minnow density in the selected area sampled. Twelve samples were collected using pop nets that were randomly distributed in the 0.1- to 1.0-m depth zone of each wetland on each sampling date. Populations were sampled once every 2 weeks in 2001 and once every 3 weeks in 2002 from mid-May to mid-September each year. Pop nets were allowed to sit undisturbed on the wetland sediment for 1 h prior to being triggered. Although our sampling was restricted to 0.1- to 1-m water depths, our previous work with pop nets has indicated densities of larval, juvenile and adult minnows do not differ with depth in these systems (B.R. Herwig and K.D. Zimmer, unpublished data). Minnows captured in the pop nets were counted, and up to 40 fish per sample were measured for total length to

Table 1. Classification, surface area, maximum depth and other fish species present for the three study sites located in west-central Minnesota.

Wetland	Classification	Area (ha)	Max depth (m)	Other fish species present
Stammer	4	9.1	1.88	<i>Culaea inconstans</i>
Froland	5	6.4	2.08	None
Bellevue	5	13.0	2.55	<i>Culaea inconstans</i>

Classification of Stewart & Kantrud (1971).

the nearest 1 mm. Larval (<20 mm) fathead minnow density estimates were obtained using a larval ichthyoplankton push net (0.5 m diameter, 0.8 mm mesh) at three fixed transects running parallel to shore, thus providing a spatially integrated estimate of abundance in each wetland. The water depth along each transect was approximately 1 m, and we collected each sample by pushing the ichthyoplankton net alongside the bow of the boat at approximately 5 km h⁻¹ just below the surface for 120 s. A calibrated flow meter mounted inside the net was used to determine the volume of water sampled for larval fish density estimates. The sampling schedule for larval minnows was identical to that used for sampling juveniles and adults. Larval minnows captured in the ichthyoplankton samples were preserved in 95% ethanol in the field, and were later counted and measured (TL to the nearest 1 mm; up to 100 fish per date). We estimated the wetland-wide population size of adults and juveniles by multiplying the density estimates from pop netting by wetland surface area. Larval population size was estimated by multiplying larval densities from ichthyoplankton tows by wetland volume. Depth profiles of each wetland were mapped with a GPS, and wetland surface area and volume were estimated using Surfer software (Golden Software 1997).

The fathead minnow spawns fractionally and is capable of producing multiple cohorts each year; therefore, standard aging methods cannot be used to identify cohorts in fathead minnow populations (Duffy 1998). Thus, we used the length–frequency distribution estimated from our population sampling to identify and track the growth of individual cohorts throughout the sampling season (Duffy 1998). Length–frequency histograms were constructed for each sampling date and modal lengths were identified based on visual inspection (see Fig. 1 for an example). Fish whose sizes were within $\pm 20\%$ of a mode were grouped as a cohort (Duffy 1998; Fig. 1). Mean lengths of cohorts were converted to mean weights based on weight–length regressions developed for fathead minnow populations across the three study wetlands (B.R. Herwig, unpublished data), and growth of individuals in each cohort was measured as the increase in average weight between one sampling date and the next.

Fathead minnow diets

Diets of adult, juvenile and larval fathead minnow were assessed in June, July and August of each year. Ten fish were collected from each size class in each wetland on each date. Larvae were collected using an ichthyoplankton net, while juveniles and adults were collected using a beach seine. Fish were anaesthetised

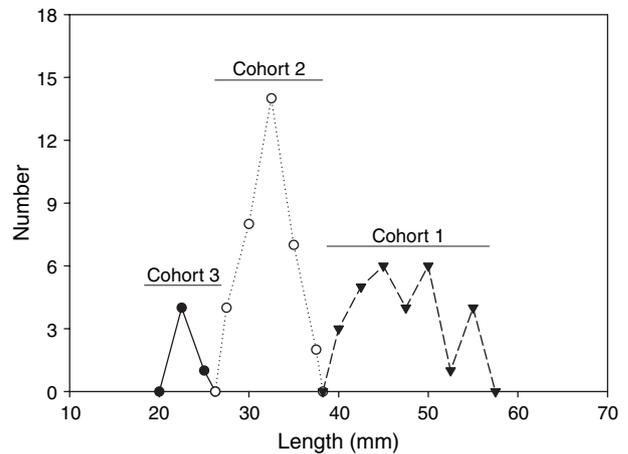


Fig. 1. Length frequency distribution of fathead minnow collected from Bellevue wetland on 22 July 2002 to illustrate the method of cohort separation. Horizontal lines indicate $\pm 20\%$ of the modal value for each cohort.

with a lethal dose of MS-222TM, preserved in a 10% formalin solution, and later transferred to 95% ethanol. Only the anterior one-third of the intestinal tract was dissected and analysed because items lower in the intestinal tract are severely digested and difficult to identify (Duffy 1998). We identified diet items to the lowest feasible taxonomic level (typically genus for zooplankton, and either family or order for macroinvertebrates) and, where possible, measured body lengths of individual items. Lengths were then converted to weights using length–weight regressions (Smock 1980; McCauley 1984, B.R. Herwig & K.D. Zimmer, unpublished data). After all invertebrates were removed from the sample the remaining detritus was filtered onto a preweighed 0.7 μm glass–fibre filter to obtain both wet and dry weights. To obtain an accurate wet weight, excess water was removed by placing the filter on a perforated funnel, and a light vacuum was applied using an electric pump. Filters were then placed in a drying oven at 60 °C for 24 h to obtain dry weights.

Bioenergetics modelling

We estimated prey consumption for fathead minnow populations using Fish Bioenergetics 3.0 (Hanson et al. 1997). Modelling consumption using the bioenergetics model requires constructing energy budgets via the mass balance equation $C = G + R + F + U$ where C is the energy ingested, G the observed growth, R the energy used in metabolism, F the egestion and U the excretion (Hewett & Johnson 1987). We used physiological parameters developed by Duffy (1998) for our adult and juvenile fathead minnow cohorts, but these adult-derived parameters did not fit larval fish metabolism due to metabolic

allometry (Post 1990). We used bioenergetics parameters developed by Post (1990) for larval yellow perch *Perca flavescens* to model our larval fathead minnow cohorts, the most similar freshwater species for which larval modelling parameters have been developed. The complete lists of bioenergetics parameters used to model juvenile and adult minnows, and larvae, can be found in Duffy (1998) and Post (1990) respectively. We modelled individual cohorts, and then compiled estimates for larval, juvenile and adult fish. We modelled all three age groups from 15 May to 30 August in 2001 and from 15 May to 2 September in 2002.

Field data required to parameterise the model include fathead minnow diet composition, population size, growth and mortality rates, predator and prey energy densities, and water temperature. Diet composition was modelled as the proportion of wet weight of each diet item consumed by each life stage on each of the three sampling dates. Diets were assumed to remain constant between sampling periods. When a cohort grew into a subsequent life stage, the diet data appropriate to that life stage was applied. Population size for each cohort was specified as the proportion of the total population represented by that cohort. Each cohort was then tracked from one sampling period to the next, providing a measure of fish growth (change in mass), production (accumulation of biomass) and mortality (loss of biomass). Energy density for the fathead minnow was taken from Duffy (1998), energy density for invertebrates from Cummins & Wuychek (1971), Schindler et al. (1971), Driver et al. (1974) and Vijverberg & Frank (1976), and energy in detritus from Penczak (1985). Water temperatures were recorded hourly in each wetland using temperature loggers suspended 1 m below the surface. Mean daily water temperatures were entered into the model for each wetland for each model day. We modelled spawning losses as a discrete event, where females lost 11% body mass upon reaching 55 mm TL. This was based on observations made by Duffy (1998), who found that 55 mm was the most common length for gravid females and that on average females lost 11% of their mass following spawning.

All calculations were performed on a daily interval. We combined the model outputs for each cohort to estimate prey consumption by larval, juvenile, adult and the entire fathead minnow population in each wetland on each day. Model output was also used to determine gross and net production, production:biomass ratios, biomass turnover time (TT) (calculated as biomass:gross production), and mortality rates of each age class.

Relative abundance of aquatic invertebrates in each wetland was measured using vertically oriented activity traps (ATs) (Murkin et al. 1983) that were deployed

at the same time we assessed fathead minnow diets. Ten ATs were set 30 cm below the water in each wetland, retrieved after 24 h, and contents concentrated by passage through a 140- μ m mesh. We then determined the total number of invertebrates captured in the ATs (summed across taxa) that were also observed in diets of the fish. The total number of invertebrates for each wetland-date ($N = 18$) was subsequently used to reflect relative abundance of invertebrate prey on each date we sampled fish diets.

We used simple linear regression to test whether fish density or abundance of aquatic invertebrates influenced consumption of detritus by larval, juvenile and adult fathead minnow populations across sampling dates. Consumption of detritus was expressed as the proportion of total consumption for each age class on the 18 wetland-date combinations, and was arcsine transformed to meet the assumptions of linear regression. Fish density in each age class and the total number of aquatic invertebrates captured in ATs on each wetland-date were both log-transformed to homogenise variance. We then regressed log invertebrate abundance for each wetland-date combination against arcsine-transformed proportion of detritus in the diet on the same date. Similarly, we regressed log fish abundance against arcsine-transformed proportion of detritus in the diet on the same date. This analysis used six samples from each wetland, and autocorrelation among the six samples may cause biased estimates and significance tests in the regression analysis using all 18 samples (Bence 1995). Thus, we used the Durbin-Watson test for first-order autocorrelation to assess the degree of autocorrelation for larval, juvenile and adult fish samples within each wetland (Bence 1995). This analysis was done for both the regression of log fish density on arcsine proportion of detritus and the log invertebrate abundance on arcsine proportion of detritus. We detected no significant autocorrelation among any samples (all $P > 0.05$), and the overall autocorrelation was weak among samples (average Durbin-Watson P -value = 0.40). However, autocorrelation is difficult to detect with sample sizes as small as ours, so the subsequent regression analyses should still be considered approximate.

We also assessed the influence of detritus consumption on production rates for each of our three age classes by regressing the log-transformed, seasonal fish P:B ratio in each wetland in each year on the arcsine-transformed, proportion of diet represented by detritus.

Results

Larval and juvenile fathead minnow densities in Stammer and Bellevue were substantially higher in

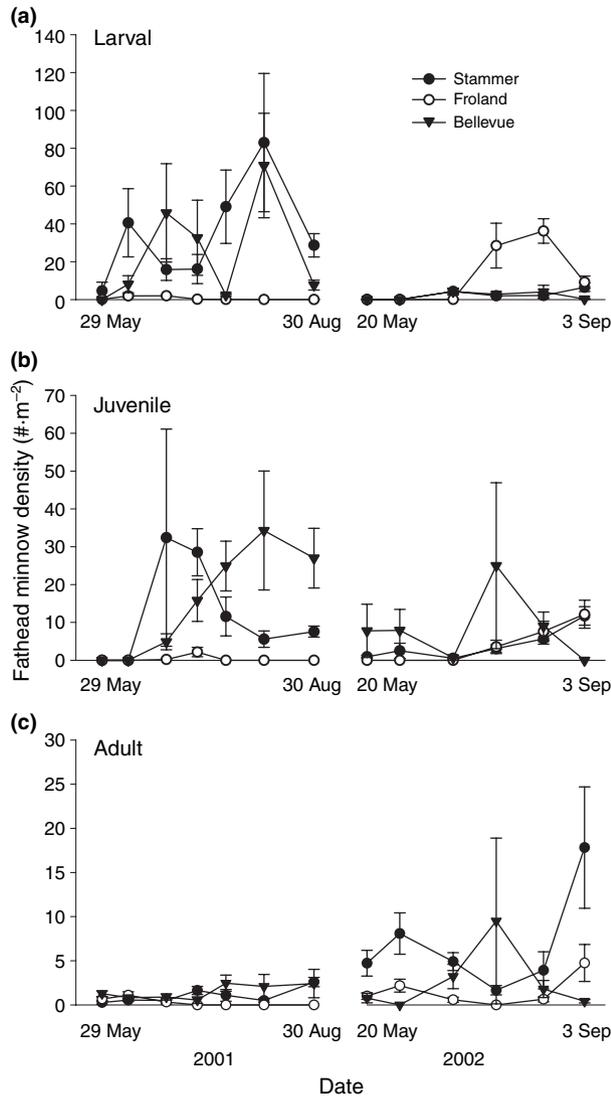


Fig. 2. Density estimates for (a) larval (no. of fish <20 mm m⁻²), (b) juvenile (no. of fish 20–40 mm m⁻²) and (c) adult (no. of fish >40 mm m⁻²) fathead minnow populations in Stammer (filled circles), Froland (open circles) and Bellevue (filled triangles) wetlands throughout summer 2001 and 2002 (± 1 SE).

2001 than in 2002 (Fig. 2). Larval and juvenile fish dominated in these wetlands in 2001, with adult densities seldom exceeding two fish per m². In 2002, juvenile and adult fish dominated in Stammer and Bellevue. Population trends differed considerably in Froland, where densities of all size classes remained low throughout 2001 and during early 2002, but densities of all size classes increased during the later part of 2002.

Larval and juvenile densities fluctuated dramatically in all sites during 2001 and 2002. By early August 2001, summed fish density exceeded 65 fish per m² in both Stammer and Bellevue (Fig. 2). Peak biomass was observed on the same dates as peak density, with 156 kg ha⁻¹ in Bellevue and 63 kg ha⁻¹ in Stammer.

During 2002, juvenile and adult densities reached a combined maximum of 17 fish per m² in Froland, 30 fish per m² in Stammer (both in early September) and 34.5 fish per m² in Bellevue in mid-July (Fig. 2). Biomass peaked in mid-July in Bellevue (167 kg ha⁻¹), in mid-May in Stammer (252 kg ha⁻¹), and in both mid-May and early September in Froland (60 kg ha⁻¹).

The fathead minnow populations within each wetland produced four to seven larval cohorts each year, but recruitment to the juvenile stage was highly variable. At least some recruitment to juvenile was observed for most wetland-years, except for Froland in 2001 where all seven cohorts failed to recruit to juvenile sizes. Growth was variable among wetlands, but we generally observed fast growth, with some fish reaching 2 g in their first growing season. Few adult fish exceeded 4 g, with the exception of one cohort from Stammer in early 2002, which resulted in high standing stock biomass and prey consumption on this date (Fig. 3).

Average standing stock biomass of fathead minnow populations summed across age classes ranged from 5 to 76 kg ha⁻¹ (Table 2). Average biomass was high in Stammer in both years (40 and 76 kg ha⁻¹) and in Bellevue in 2001 (59 kg ha⁻¹), but was low in Froland in 2001 (5 kg ha⁻¹). Gross production (GP) summed across age classes in 2001 was highest in Stammer and Bellevue (3.12 and 2.97 kg ha⁻¹ day⁻¹ respectively), but was only 0.04 kg ha⁻¹ day⁻¹ in Froland (Table 2). In 2002, total GP was similar among all wetlands and ranged from 0.93 to 1.43 kg ha⁻¹ day⁻¹. Gross production was dominated by larval and juvenile fish. Averaged across all wetland-years, larval and juvenile fish accounted for 41% and 37% of total GP, respectively, while representing just 19% (larval) and 28% (juvenile) of the average biomass. Mortality rates were generally high for all age classes in all wetlands, and rates across age classes ranged from 5% to 10% per day (Table 2). High production rates coupled with relatively small standing stock biomass resulted in rapid TT in all age classes, and was highest in larval fish, ranging from 7 to 29 days (mean = 14 days) (Table 2). Scaled allometrically, TT ranged from 15 to 28 days in juvenile fish (mean = 20 days) and from 41 to 163 days in adults (mean = 72 days).

Total daily consumption rates summed across age classes ranged from 0.01 to 38.91 kg ha⁻¹ day⁻¹ (Table 3). Total prey consumption varied greatly between years in all three wetlands, reflecting substantial differences in fish abundance (Fig. 2). Inter-annual differences were most pronounced in Froland, where prey consumption increased approximately 28-fold from 2001 to 2002, concurrent with increases in densities of all fathead minnow size classes during 2002 (Table 3, Fig. 2). Larval fish accounted for the

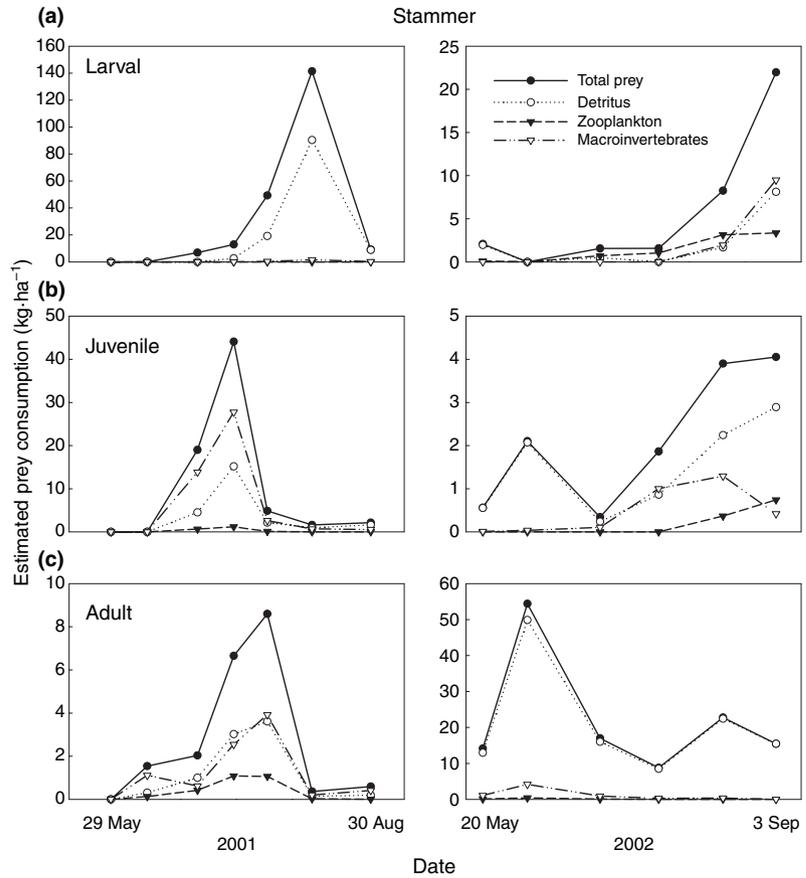


Fig. 3. Estimated prey consumption ($\text{kg ha}^{-1} \text{day}^{-1}$) from a bioenergetics model applied to (a) larval, (b) juvenile and (c) adult fathead minnow size classes in Stammer wetland in 2001 (left panel) and 2002 (right panel). Data points shown are for those dates when population size was directly estimated in the field.

Table 2. Mean biomass (B), gross production (GP), turnover time (TT, biomass/gross production) and natural mortality (M) for larval, juvenile and adult fathead minnow populations from three Minnesota study wetlands in 2001 and 2002.

	Wetland								
	Stammer			Froland			Bellevue		
	Larval	Juvenile	Adult	Larval	Juvenile	Adult	Larval	Juvenile	Adult
2001									
B ($\text{kg}\cdot\text{ha}^{-1}$)	15.62	15.57	9.19	0.20	0.04	4.89	17.84	20.44	21.01
GP ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$)	1.87	1.04	0.21	0.03	0.01	0.03	1.30	1.16	0.51
M ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$)	1.51	1.29	0.97	0.01	0.03	0.34	0.87	0.94	1.95
TT (days)	8.35	14.97	43.76	6.67	20.00	163.00	13.72	17.62	41.20
2002									
B ($\text{kg}\cdot\text{ha}^{-1}$)	3.61	5.51	67.15	5.71	7.10	13.28	1.76	16.43	8.31
GP ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$)	0.17	0.20	1.06	0.42	0.32	0.19	0.10	0.80	0.12
M ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$)	0.01	0.14	3.66	0.33	0.02	0.95	0.02	1.33	1.31
TT (days)	21.24	27.55	63.35	17.84	22.19	69.89	17.60	20.54	69.25

majority (69%) of total food consumption by fathead minnows, despite representing only 19% of the total biomass in the population.

Fathead minnow diets were highly variable and included diverse prey items, including 31 different taxonomic items in total, plus detritus. It is notable that all size classes of minnows consumed each of the major food categories (rotifers, zooplankton, macroinvertebrates and detritus) in their diet at some point during the study. Detritus was an important food resource for all fish sizes, and averaged across

wetland-years it accounted for 53%, 40% and 79% of diet by mass for larval, juvenile and adult fish respectively. Overall, detritus accounted for 55% of total fish consumption (Table 3). Larval fish accounted for 66% of the total mass of consumed detritus, despite the higher selectivity for detritus by adult fish and the higher biomass of adult fish. In contrast to the ubiquitous reliance on detritus, consumption of invertebrate prey differed substantially among fish size classes. In addition to detritus, larval minnows primarily consumed non-rotifer zooplankton (21% of

Table 3. Estimated cumulative consumption (kg ha⁻¹ day⁻¹) of major prey types from mid-May to mid-September by larval, juvenile and adult fathead minnow populations in three Minnesota study wetlands in 2001 and 2002.

Life stage	Major prey taxa				Total prey
	Zooplankton	Rotifers	Macroinvertebrates	Detritus	
Stammer 2001					
Larval	0.83	12.96	0.25	15.00	29.04
Juvenile	0.15	0	3.67	2.25	6.06
Adult	0.16	0	0.62	0.54	1.32
Stammer 2002					
Larval	1.95	0.92	1.36	1.54	5.77
Juvenile	0.11	0	0.46	1.29	1.86
Adult	0.07	0.01	0.87	15.77	16.73
Froland 2001					
Larval	0.33	0	0	0	0.33
Juvenile	0	0	0.01	0	0.01
Adult	0.04	0	0.31	0.10	0.44
Froland 2002					
Larval	2.71	1.05	0	13.34	17.11
Juvenile	0.39	0.04	0.23	2.02	2.68
Adult	0.02	0.01	0.81	0.76	1.59
Bellevue 2001					
Larval	14.33	4.96	0	19.6	38.91
Juvenile	1.08	0	2.17	0.75	4.00
Adult	0.32	0	1.16	0.87	2.36
Bellevue 2002					
Larval	0.49	0.17	2.32	0	2.97
Juvenile	0.42	0	2.39	1.06	3.87
Adult	0.01	0	0.54	0.28	0.79

total consumption) and rotifers (20%), while juvenile fish consumed macroinvertebrates (48%) and zooplankton (12%) and adult fish consumed mostly macroinvertebrates (19%) (Figs 3–5).

Prey consumption rates reflected population sizes, with peak periods corresponding to maximum fathead minnow densities (Figs 2–5). Abundance of fish in the three size classes fluctuated due to timing of reproduction, such that adult and juvenile consumption rates generally peaked in June to early July, while maximum consumption by larval fish peaked in mid- to late August. Comparing the timing of maximum fish densities and diet composition of the three size classes indicates that consumption of macroinvertebrates peaked in June, zooplankton and rotifers in late July to early August, and detritus in early to late August.

Relationships among consumption of detritus, fish density and abundance of aquatic invertebrates were variable, but more robust with increasing fish size (Fig. 6). We detected no relationship between abundance of larval fish and the proportion of detritus in their diet ($F_{1,16} = 3.81$, $P = 0.068$, $r^2 = 0.19$), nor any relationship between invertebrate abundance and consumption of detritus ($F_{1,16} < 0.01$, $P = 0.98$, $r^2 < 0.01$). These relationships were stronger for juvenile fish, with a significant negative relationship observed between detritus in the diet and abundance of

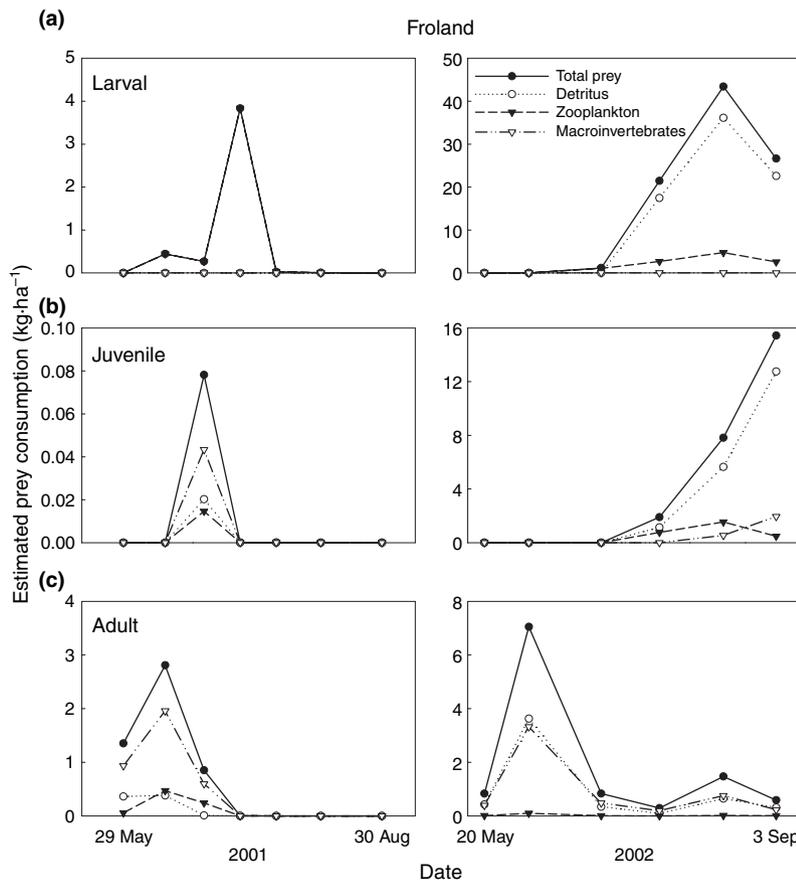


Fig. 4. Estimated prey consumption (kg ha⁻¹ day⁻¹) from a bioenergetics model applied to (a) larval, (b) juvenile and (c) adult fathead minnow size classes in Froland wetland in 2001 (left panel) and 2002 (right panel). Data points shown are for those dates when population size was directly estimated in the field.

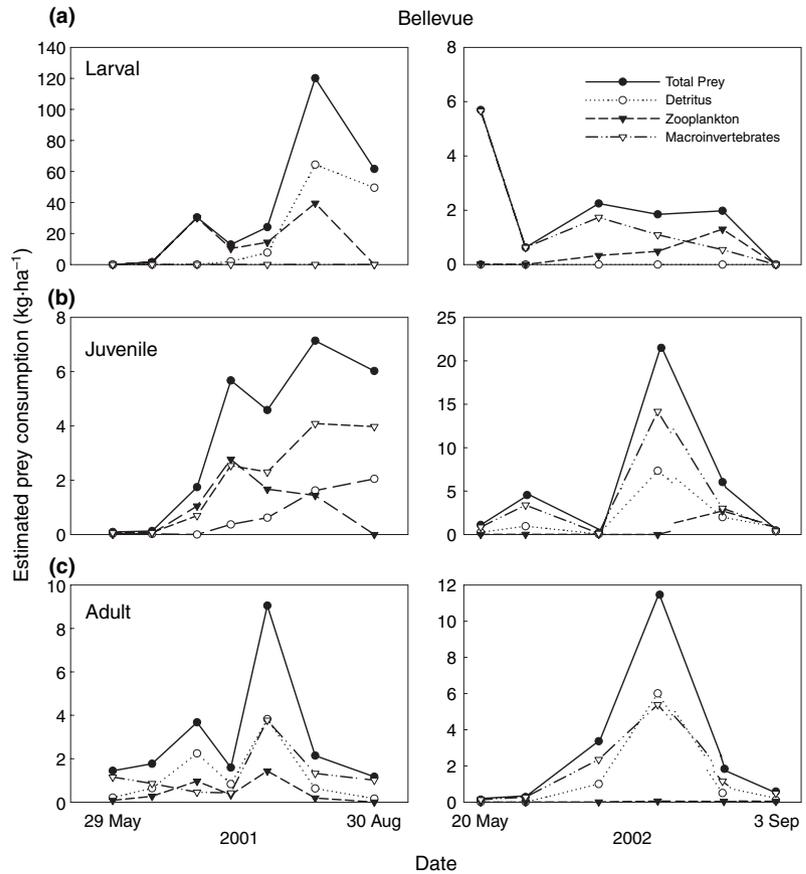


Fig. 5. Estimated prey consumption ($\text{kg ha}^{-1} \text{ day}^{-1}$) from a bioenergetics model applied to (a) larval, (b) juvenile and (c) adult fathead minnow size classes in Bellevue wetland in 2001 (left panel) and 2002 (right panel). Data points shown are for those dates when population size was directly estimated in the field.

invertebrates ($F_{1,16} = 4.84, P = 0.043, r^2 = 0.23$) but no statistically significant relationship between proportion of detritus in the diet and fish density ($F_{1,16} = 4.21, P = 0.056, r^2 = 0.21$). Adult consumption of detritus was positively related to adult fish density ($F_{1,16} = 9.12, P = 0.008, r^2 = 0.36$) and adult consumption of detritus was negatively related to invertebrate abundance ($F_{1,16} = 6.28, P = 0.023, r^2 = 0.28$) (Fig. 6).

Detritus as a proportion of the total diet over the sampling season varied dramatically among the six wetland-years, ranging from 0% to 78% for larval fish, 0–76% for juvenile fish and 23–94% for adult fish. However, consumption of detritus had little effect on fish production, as we detected no significant relationship between seasonal P:B ratios and proportion of detritus in the diet for adult ($F_{1,4} = 0.10, P = 0.769, r^2 = 0.02$), juvenile ($F_{1,4} = 0.57, P = 0.492, r^2 = 0.02$) or larval fish ($F_{1,4} = 0.21, P = 0.668, r^2 = 0.05$) (Fig. 7).

Discussion

Fathead minnow populations in our study exhibited prolific recruitment (up to seven cohorts per summer), reached high standing stock biomass (up to

252 kg ha^{-1}), and experienced high levels of natural mortality. As a consequence, smaller bodied larval and juvenile fish often dominated the minnow populations in terms of numbers, biomass and production. Typically, larval fish have been considered ‘too dilute’ to have significant impacts on prey populations (Cushing 1983), and are often ignored in models describing the roles of fish in shallow lakes. However, metabolic allometry generates an inverse relationship between mass-specific consumption rates and fish body size, causing influences of larval and juvenile fish on prey populations to be potentially much higher compared with similar adult biomass (Post 1990). Larval and juvenile production was appreciable in our study sites (78% of total GP), and accounted for 83% of total consumed prey, despite comprising only 47% of the total fish mass. To our knowledge, Duffy (1998) represents the only other attempt to estimate prey consumption by fathead minnow populations, but his consumption estimates were restricted to fish classified as adults in our study ($>40 \text{ mm TL}$). Across four South Dakota wetlands, Duffy estimated average prey consumption rates of adult minnows ranging from 4.3 to $16.7 \text{ kg ha}^{-1} \text{ day}^{-1}$ with a mean of $8.3 \text{ kg ha}^{-1} \text{ day}^{-1}$. In contrast, our average daily consumption rates summed across larval, juvenile and adult fish ranged

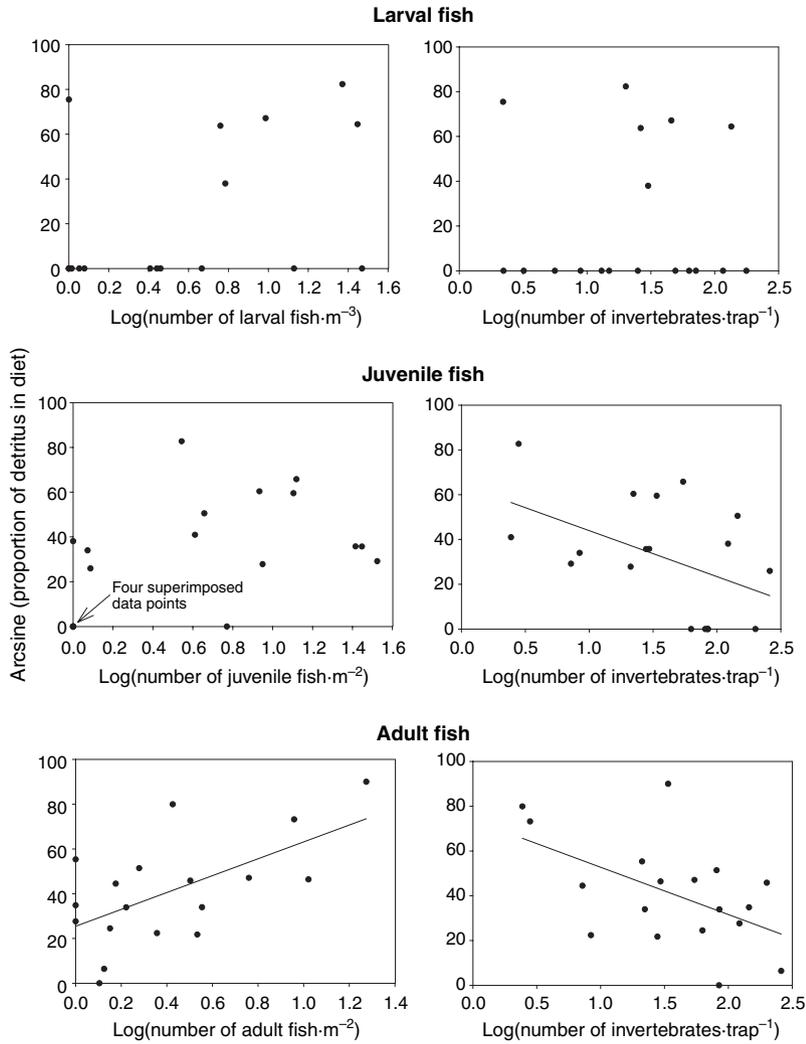


Fig. 6. Relationships between fish density and consumption of detritus (left panels), and abundance of aquatic invertebrates and consumption of detritus (right panels) by larval, juvenile and adult minnows. Data points represent three estimates for each of three wetlands in two separate years.

from 0.8 to 36.4 kg ha⁻¹ day⁻¹, and the mean of 22.6 kg ha⁻¹ day⁻¹ was 2.7-fold higher than reported by Duffy (1998). Despite being largely ignored in previous studies, our results highlight the importance of larvae and juveniles when describing the effects of fathead minnow populations on aquatic ecosystems.

We observed a maximum density and biomass of fathead minnow of 107 fish per m² and 252 kg ha⁻¹, respectively, which was generally lower than estimates for other prairie wetlands. Duffy (1998) reported that standing stock biomass of adult fathead minnows in three South Dakota wetlands exceeded 300 kg ha⁻¹ on one or more sampling dates, with a maximum biomass of 482 kg ha⁻¹ and density of 43 fish per m². In contrast, Zimmer et al. (2001a) estimated populations of all fish sizes and observed peaks of 369 kg ha⁻¹ and densities of 570 fish per m² in one Minnesota wetland. In aquatic systems outside of the prairie pothole region, fathead minnow density has been reported to range from 1.8 fish per m² in an Alberta

pond (Price et al. 1991) to 25 fish per m² in Michigan ponds (Spencer & King 1984). In culture settings, annual production of fathead minnow of up to 368 kg ha⁻¹ is regularly attainable (Dobie et al. 1948). Factors driving differences in minnow density among regions has not been assessed, but abundance of predatory fish, lake productivity and probability of winterkill are all probably important.

Zooplankton, macroinvertebrates (especially chironomids and amphipods) and detritus have all been found to be important components of fathead minnow diets at various times of the year (Held & Peterka 1974; Price et al. 1991; Duffy 1998). Similarly, we found that all size classes of minnows consumed each of these food categories in their diet at some point during the study. The exception was that we found rotifers were also important at times, especially for larval and juvenile fish. In addition to ubiquitous consumption of detritus, larval fish consumed rotifers and non-rotifer zooplankton, juvenile fish consumed a large percentage of zooplankton and macroinverte-

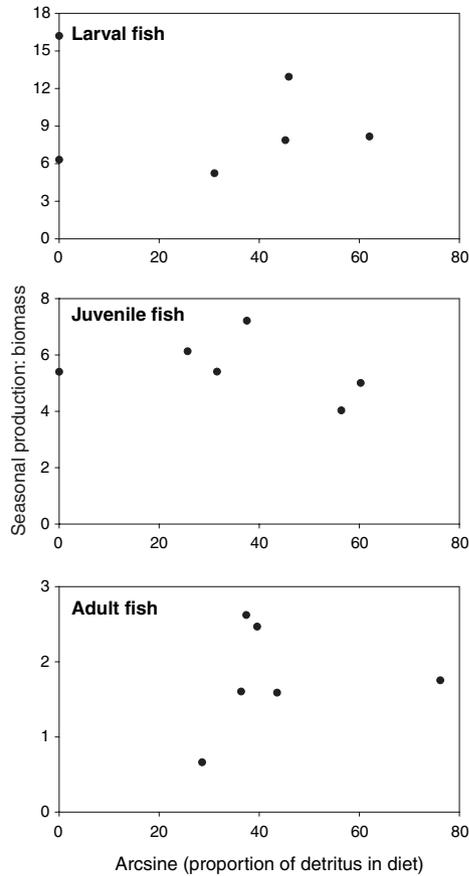


Fig. 7. Relationships between proportion of detritus in diets and production: biomass ratios in larval, juvenile and adult fish. Data points represent seasonal means for three wetlands in two separate years.

brates, and adult fish focused primarily on macroinvertebrates.

The predation pressure exerted by fathead minnow for invertebrate resources shared with waterfowl and other wetland-dependent species suggests potential for competition (Duffy 1998), and reduced invertebrate food resources could have negative consequences for duckling growth and survival (Cox et al. 1998). Duffy (1998) estimated that consumption of aquatic invertebrates by adult fathead minnow populations ranged from 333 to 1104 kg ha⁻¹ year⁻¹ in South Dakota wetlands. Our estimates ranged from 74 to 2596 kg ha⁻¹ throughout the growing season in 2001 and from 584 to 699 kg ha⁻¹ in 2002. Our maximum estimates were higher than those of Duffy (1998) in 2001, but fell within his reported range in 2002. Additionally, aquatic invertebrate production rates in prairie wetlands have been estimated to range from 100 to 500 kg ha⁻¹ year⁻¹ (Duffy 1998, based on literature values) and from 1139 to 1836 kg ha⁻¹ year⁻¹ (Zimmer et al. 2001b, based on allometric models). Thus, estimates of consumption rates of aquatic invertebrates by fathead minnow populations in this

study and Duffy (1998) approximate production rates of invertebrates in these systems. This potentially strong predatory influence of fathead minnow populations is consistent with several recent studies in the PPR documenting strong negative influences of fathead minnow on invertebrate populations (Hanson & Riggs 1995; Zimmer et al. 2000, 2001b, 2003).

Detritus was an important food resource for all sizes of fish. Averaged across wetland years, it accounted for 40–79% of diet mass for larval, juvenile and adult fish. Larval fish accounted for 66% of the total mass of consumed detritus, despite the higher selectivity for detritus by adult fish and the higher biomass of adult fish. Price et al. (1991) also found that detritus was important in the diet of fathead minnow, with 54% of fish sampled containing detritus in their gut. Price et al. (1991) neither reported differences in the frequency of occurrence of detritus among fish life stages or sex, nor did they identify temporal patterns in detritus consumption.

If a choice between animal and detrital food exists and costs of capturing animals are not high, foraging models would predict that the fathead minnow should select animal prey (high protein and energy) over detritus to maximise foraging efficiency (Ahlgren 1990). We found support for this prediction in juvenile and adult minnows, as both ages of fish showed a negative relationship between consumption of detritus and abundance of aquatic invertebrates. We also detected a positive relationship between consumption of detritus and abundance of adult minnows. Taken together, these results suggest that juvenile and adult minnows choose invertebrate prey over detritus when invertebrate prey are available and intra-specific competition is low, consistent with optimal foraging theory (Schoener 1971). The absence of these relationships for larval fish was somewhat surprising. Perhaps the increased energetic needs associated with breeding and nest defence for maturing males (Unger 1983) and egg production in maturing females (Grant & Tonn 2002) increase their selectivity for the higher quality invertebrate prey relative to larval fish. Or perhaps the cost/benefit ratio for consuming invertebrate prey is simply larger for larval fish relative to juvenile and adult fish.

The quality of detritus as a food source depends on its level of bacterial conditioning, but it is typically lower in energy and protein relative to invertebrate prey (Bowen et al. 1995). Detritus has historically been considered a food supplement that allows the fathead minnow to survive when more nutritional food sources are low (Held & Peterka 1974; Price et al. 1991). Reduced quality of detritus, although, is presumably compensated to some degree by higher overall availability. More recently, it has been suggested that consumption of high-availability, poor-quality detritus, in

conjunction with availability of high-quality invertebrates may help sustain rapid growth and high survival in fathead minnow populations (Bowen et al. 1995; Lemke & Bowen 1998). Our data support this hypothesis in that inclusion of detritus in the diet has no negative effect on production. Despite consumption of detritus (as percentage of total diet) ranging from 0% to 78% for larval fish, 0–76% for juvenile fish and 23–94% for adult fish, we detected no relationships between seasonal P:B ratios and consumption of detritus for any age class of fish. Taken together, Lemke & Bowen's (1998) laboratory results, and our field data, indicate that detritus is an important food resource capable of supporting metabolic processes and growth in fathead minnow populations. Consumption of detritus may be especially important for maintaining the extremely high minnow densities observed in PPR wetlands, as it weakens the link between abundance of invertebrate prey and minnow populations (Polis & Strong 1996; Schaus & Vanni 2000; Schindler & Scheuerell 2002). The ability to consume detritus results in consistently high densities of minnows despite fluctuations in the abundance of invertebrate prey.

The greatest source of uncertainty in this study is our imprecise estimates of fish density. The large error bars in Fig. 2 would lead to error propagation and large error bars in Figs 3–5, and introduce error into the regressions in Figs 6 and 7. Our estimates of population density are supported by the fact that our estimates fall within the ranges estimated for fathead minnow populations in other studies (Duffy 1998; Zimmer et al. 2001a), but imprecision undoubtedly influences estimates and analyses in Figs 3–7. A second source of uncertainty is our use of bioenergetics parameters developed for larval perch to model larval fathead minnow populations. These two species of fish are in different orders, and have vastly different natural histories. However, allometric patterns of fish metabolism are strong, and application of adult bioenergetics parameters to larval fish is inappropriate (Post 1990). Given the strong pattern of metabolic allometry, we feel the bioenergetics parameters developed for larval perch are likely a good approximation for fathead minnow larvae. Overall, however, imprecise estimates of fish density, coupled with our use of larval perch parameters, reduce the precision of our overall estimates. Thus, our estimates and results should be considered approximate attempts to assess the role of larval fish and detritus in the population ecology of the fathead minnow.

At intermediate nutrient concentrations, shallow water ecosystems are thought to exist in one of two alternative states, either a clear water, macrophyte-dominated state, or a turbid water, phytoplankton-dominated state (Scheffer et al. 1993; Scheffer 1998). Recent work has indicated that this model also applies

to PPR wetlands, as these ecosystems exhibit a dichotomy of dominance by either phytoplankton or macrophytes (Zimmer et al. 2003; Herwig et al. 2004). The stable-state model suggests that fish stabilise the turbid state through two main mechanisms: resuspension of sediment, and the suppression of zooplankton populations. While appreciable resuspension of sediment by fathead minnow feeding is unlikely, our results suggest that the high levels of zooplankton consumption exhibited by minnow populations could function to stabilise the turbid water state. Additionally, our results also suggest fathead minnow populations may stabilise the turbid-state in PPR wetlands through bottom-up influences on phytoplankton, where excreted nutrients originating from wetland detritus contributes to high, stable algal densities (Braband et al. 1990; Schindler et al. 1993; Zimmer et al. 2006).

Overall, the ability to consume and utilise detritus as a food resource likely increases ecological influences of the fathead minnow on wetland ecosystems relative to other fish species. Detritus helps sustain high densities of minnows and contributes to a substantial flux of nutrients and energy from wetland sediments into the water column. High density of minnows and strong benthic–pelagic coupling, in turn, has potential to influence nutrient fluxes, water transparency and abundance of invertebrates, phytoplankton and submerged macrophytes in wetland ecosystems.

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References

Ahlgren, M.O. 1990. Diet selection and the contribution of detritus to the diet of the juvenile white sucker (*Catostomus*

- commersoni*). Canadian Journal of Fisheries and Aquatic Sciences 47: 41–48.
- Bence, J.R. 1995. Analysis of short time series: correcting for autocorrelation. Ecology 76: 628–639.
- Bowen, S.H., Lutz, E.V. & Ahlgren, M.O. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. Ecology 76: 899–907.
- Braband, A., Faafeng, B.A. & Nilssen, J.P.M. 1990. Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. Canadian Journal of Fisheries and Aquatic Sciences 47: 364–372.
- Cox, R.R., Jr., Hanson, M.A., Roy, C.C., Euliss, N.H., Jr., Johnson, D.H. & Butler, M.G. 1998. Mallard duckling growth and survival in relation to aquatic invertebrates. Journal of Wildlife Management 62: 124–133.
- Cummins, K.W. & Wuychek, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen Internationale Vereinigung fuer Theoretische und Angewandte Limnologie 18: 1–158 pp.
- Cushing, D.H. 1983. Are fish larvae too dilute to effect the density of their food organisms? Plankton Research 5: 847–854.
- Dewey, M.R., Holland-Bartels, L.E. & Zigler, S.J. 1989. Comparison of fish catches with buoyant pop nets and seines in vegetated and nonvegetated habitats. North American Journal of Fisheries Management 9: 249–253.
- Dobie, J., Meehan, O.L. & Washburn, G.N. 1948. Propagation of minnows and other bait species. Circular 12. Washington, D.C., USA: U.S. Fish and Wildlife Service. 113 pp.
- Dobie, J., Meehan, O.L., Snieszko, S.F. & Washburn, G.N. 1956. Raising bait fishes. Circular 35. Washington, D.C., USA: U.S. Fish and Wildlife Service. 123 pp.
- Driver, E.A., Sugden, L.G. & Kovach, R.J. 1974. Calorific, chemical and physical values of potential duck foods. Freshwater Biology 4: 281–292.
- Duffy, W.G. 1998. Population dynamics, production, and prey consumption of fathead minnows (*Pimephales promelas*) in prairie wetlands: a bioenergetics approach. Canadian Journal of Fisheries and Aquatic Science 54: 15–27.
- Euliss, N.H. Jr, Wrubleski, D.A. & Mushet, D.M. 1999. Wetlands of the prairie pothole region: invertebrate species composition, ecology, and management. In: Batzer, D.P., Rader, R.P. & Wissinger, S.A. eds. Invertebrates in freshwater wetlands of North America: ecology and management. New York: John Wiley, pp. 471–514.
- Golden Software. 1997. Surfer for Windows, version 6. Golden, Colorado, USA: Golden Software.
- Grant, S.C.H. & Tonn, W.M. 2002. Effects of nutrient enrichment on recruitment of age-0 fathead minnows (*Pimephales promelas*): potential impacts of environmental change on the Boreal Plains. Canadian Journal of Fisheries and Aquatic Sciences 59: 579–767.
- Hanson, M.A. & Riggs, M.R. 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. Wetlands 15: 167–175.
- Hanson, P.C., Johnson, T.B., Schindler, D.E. & Kitchell, J.F. 1997. Fish bioenergetics 3.0. Madison, WI: UW Sea Grant Institute.
- Held, J.W. & Peterka, J.J. 1974. Age, growth, and food habits of the fathead minnow, *Pimephales promelas*, in North Dakota saline lakes. Transactions of the American Fisheries Society 103: 743–757.
- Herwig, B.R., Hanson, M.A., Reed, J.R., Parsons, B.G., Potthoff, A.J., Ward, M.C., Zimmer, K.D., Butler, M.G., Willis, D.W. & Snook, V.A. 2004. Walleye stocking as a tool to suppress fathead minnows and improve habitat quality in semipermanent and permanent wetlands in the prairie pothole region of Minnesota. St Paul, MN: Division of Fish and Wildlife Special Publication Number 159, 42 pp.
- Hewett, S.W. & Johnson, B.L. 1987. A generalized bioenergetics model of fish growth for microcomputers. Madison, WI: UW Sea Grant, Technical Report No. WISSG-87-245, 47 pp.
- Klinger, S.A., Magnuson, J.J. & Gallepp, G.W. 1982. Survival mechanisms of the central mudminnow (*Umbra limi*), fathead minnow (*Pimephales promelas*), and brook stickleback (*Culaea inconstans*) for low oxygen in winter. Environmental Biology of Fishes 7: 113–120.
- Lemke, M.L. & Bowen, S.H. 1998. The nutritional value of organic detrital aggregate in the diet of fathead minnows. Freshwater Biology 39: 447–453.
- Markus, H.C. 1934. Life history of the blackhead minnow (*Pimephales promelas*). Copeia 1934: 116–122.
- McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. In: Downing, J. & Rigler, F., eds. Methods of estimating secondary production in freshwaters, 2nd edn. Oxford, England: Blackwell Scientific. pp. 228–265.
- Murkin, H.R., Abbott, P.G. & Kadlec, J.A. 1983. A comparison of activity traps and sweep nets for sampling nektonic invertebrates in wetlands. Freshwater Invertebrate Biology 2: 99–106.
- Payer, R.D. & Scalet, C.G. 1978. Population and production estimates of fathead minnows in a South Dakota prairie wetland. The Progressive Fish-Culturist 40: 63–66.
- Penczak, T. 1985. Phosphorus, nitrogen, and carbon cycling by fish populations in two small lowland rivers in Poland. Hydrobiologia 120: 159–165.
- Peterka, J.J. 1989. Fishes of northern prairie wetlands. In: Van der Valk, A., (ed). Northern Prairie Wetland. Ames, IA: Iowa State University Press, pp. 302–315.
- Polis, G.A. & Strong, D.R. 1996. Food web complexity and community dynamics. American Naturalist 147: 813–846.
- Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. Canadian Journal of Fisheries and Aquatic Sciences 47: 554–560.
- Price, C.J., Tonn, W.M. & Paszkowski, C.A. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. Canadian Journal of Zoology 69: 2109–2115.
- Schaus, M.H. & Vanni, M.J. 2000. Effects of gizzard shad on phytoplankton and nutrient dynamics: role of sediment feeding and fish size. Ecology 81: 1701–1719.
- Scheffer, M. 1998. Ecology of Shallow Lakes. London, UK: Chapman & Hall.
- Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B. & Jeppesen, E. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8: 275–279.
- Schindler, D.E. & Scheuerell, M.D. 2002. Habitat coupling in lake ecosystems. Oikos 98: 177–189.
- Schindler, D.W., Clark, A.S. & Gray, J.R. 1971. Seasonal calorific values of freshwater zooplankton, as determined

- with a Phillipson bomb calorimeter modified for small samples. *Journal of Fisheries Research Board of Canada* 28: 559–564.
- Schindler, D.E., Kitchell, J.F., He, X., Carpenter, S.R., Hodgson, J.R. & Cottingham, K.L. 1993. Food web structure and phosphorus cycling in lakes. *Transactions of the American Fisheries Society* 122: 756–772.
- Schoener, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369–405.
- Smock, L. 1980. Relationship between body size and biomass of aquatic insects. *Freshwater Biology* 10: 375–383.
- Spencer, C.N. & King, D.L. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1851–1855.
- Stewart, R.E. & Kantrud, H.A. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Washington, DC: Bureau of Sport Fisheries and Wildlife Resources Publication Number 92.
- Unger, L.M. 1983. Nest defense by deceit in the fathead minnow, *Pimephales promelas*. *Behavioral Ecology and Sociobiology* 13: 125–130.
- Vijverberg, J. & Frank, T.H. 1976. The chemical composition and energy contents of copepods and cladocerans in relation to their size. *Freshwater Biology* 6: 333–345.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 76–85.
- Zimmer, K.D., Hanson, M.A., Butler, M.G. & Duffy, W.G. 2001a. Influences of fathead minnows and aquatic macrophytes on nutrient partitioning and ecosystem structure in two prairie wetlands. *Archiv für Hydrobiologie* 15: 411–433.
- Zimmer, K.D., Hanson, M.A., Butler, M.G. & Duffy, W.G. 2001b. Size distributions of aquatic invertebrates in two prairie wetlands, with and without fish, with implications for community production. *Freshwater Biology* 46: 1373–1386.
- Zimmer, K.D., Hanson, M.A. & Butler, M.G. 2003. Relationships among nutrients, phytoplankton, macrophytes, and fish in prairie wetlands. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 721–730.
- Zimmer, K.D., Herwig, B.R. & Laurich, L.M. 2006. Nutrient excretion by fish in wetland ecosystems and its potential to support algal production. *Limnology & Oceanography* 51: 197–207.