

Predation on zebra mussels (*Dreissena polymorpha*) by captive-reared map turtles (*Graptemys geographica*)

Robert Serrouya, Anthony Ricciardi, and Fred G. Whoriskey

Abstract: The suitability of the Eurasian zebra mussel, *Dreissena polymorpha*, as prey for the common map turtle, *Graptemys geographica*, was tested under laboratory conditions. The turtles, which were reared in captivity without contact with molluscs, readily consumed zebra mussels in every feeding trial. Mussels were ingested whole. Repeated exposure to zebra mussels in successive trials did not increase consumption rates (ca. 11 mussels/turtle per day), suggesting that the turtles required little time to recognize and efficiently utilize zebra mussels as prey. The turtles were offered zebra mussels ranging from 4 to 34 mm in length and consumed mussels as large as 32 mm, but mussels larger than 25 mm were consumed at lower rates. Turtles consumed lower numbers of zebra mussels in the presence of an alternative prey, the prosobranch snail *Bithynia tentaculata*, which is common in map turtle habitats in the Great Lakes – St. Lawrence River system. Populations of map turtles and zebra mussels are sympatric in the upper St. Lawrence River, Lake Champlain, the lower Great Lakes, and the upper Mississippi River basin. Our results suggest that map turtles may forage on zebra mussels in nature, but zebra mussels will be important prey only when preferred or more profitable prey are scarce.

Résumé : La consommation de Moules zébrées (*Dreissena polymorpha*) par des Tortues géographiques, *Graptemys geographica*, a été évaluée en laboratoire. Les tortues, élevées en captivité sans contact avec des mollusques, se sont avérées friandes de moules dans toutes les expériences. Les moules étaient consommées entières. De nouvelles expositions à la présence de moules au cours d'expériences successives n'ont pas augmenté les taux de consommation (ca. 11 moules/tortue par jour), ce qui indique que les tortues mettent peu de temps à reconnaître leurs proies et à les consommer. Les tortues ont été mises en présence de moules de 4 à 34 mm, mais les tortues mangeaient moins de moules de plus de 25 mm, même si elles pouvaient consommer des moules de taille allant jusqu'à 32 mm. Les tortues ont mangé moins de Moules zébrées lorsqu'elles avaient le choix d'une autre proie, le gastropode prosobranch *Bithynia tentacula*, une espèce commune dans les habitats qu'occupe la Tortue géographique dans le haut Saint-Laurent, le lac Champlain, les Grands Lacs inférieurs et le bassin supérieur du Mississipi. Nos résultats indiquent que les Tortues géographiques peuvent consommer des Moules zébrées en nature, mais que les moules ne deviendront des proies importantes que lorsque les proies préférées ou plus profitables se font rares.

[Traduit par la Rédaction]

Introduction

Since the beginning of its invasion of North America in the mid-1980s, the Eurasian zebra mussel (*Dreissena polymorpha*) has spread rapidly throughout the Great Lakes and into several major rivers in eastern North America, including the St. Lawrence, Hudson, Mississippi, Illinois, Tennessee,

Ohio, and Arkansas rivers (New York Sea Grant 1994). The zebra mussel tends to dominate macroinvertebrate numbers and biomass wherever it becomes established (Stanczykowska 1977). The establishment of large mussel populations (up to $10^5/m^2$) has been accompanied by dramatic changes in the composition and structure of macroinvertebrate communities at several locations throughout the Great Lakes – St. Lawrence River system (Griffiths 1993; Dermott et al. 1993; Stewart and Haynes 1994; A. Ricciardi, personal observation), including the extirpation of native unionid mussel populations in Lake St. Clair (Gillis and Mackie 1994; Nalepa 1994), Lake Erie (Schloesser and Nalepa 1994), and the upper St. Lawrence River (Ricciardi et al. 1996). The impact of zebra mussels on benthic food webs has scarcely been studied. However, it seems reasonable to expect that changes in the availability of preferred prey will impact higher trophic levels, and zebra mussels have been shown to alter the diets and foraging patterns of certain predators (French and Bur 1993; Wormington and Leach 1992). The mussels themselves may offer preda-

Received June 6, 1995. Accepted August 10, 1995.

R. Serrouya. Department of Natural Resource Sciences, Macdonald Campus of McGill University, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada.

A. Ricciardi.¹ Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montréal, QC H3A 1B1, Canada.

F.G. Whoriskey. Department of Natural Resource Sciences, Macdonald Campus of McGill University, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada.

¹ Author to whom all correspondence should be sent.

tors an abundant, energy-rich food source (Walz 1979), providing they prove to be palatable.

Documented predators of zebra mussels include a few fish, crayfish, and waterfowl species in both Europe (Piesik 1974; Stein et al. 1975; Stanczykowska 1977) and North America (Mitchell and Carlson 1993; Wormington and Leach 1992; French and Bur 1993; Love and Savino 1993; MacIsaac 1994; Martin and Corkum 1994; French and Morgan 1995). Predation of zebra mussels in North America has only begun to be investigated. Thus far, there have been no reports of predation on zebra mussels by reptiles, although molluscivorous turtles, which are known to occasionally feed on native mussels (Ernst and Barbour 1972; Fuller 1974; Conant and Collins 1991), are common in eastern North America. The common map turtle (*Graptemys geographica*), which occurs along rocky shorelines (where suitable basking sites exist) in sheltered, lentic areas (Ernst and Barbour 1972; Gordon and MacCulloch 1980; Flaherty and Bider 1984) and feeds primarily on molluscs, including unionids (Ernst and Barbour 1972; Vogt 1981; Flaherty 1982; Conant and Collins 1991), is a potential predator of the zebra mussel. The ability of map turtles to use zebra mussels may play an important role in their conservation because the zebra mussel has become abundant in areas where map turtle populations are locally endangered (Bider and Matte 1991; Beaulieu 1992; Mellina and Rasmussen 1994).

The objectives of this study were to determine if zebra mussels are palatable to map turtles, and if turtles will consume zebra mussels when given an alternative prey choice: the prosobranch "faucet snail," *Bithynia tentaculata*, a dominant member of the benthos in map turtle habitats along the upper St. Lawrence and lower Ottawa rivers (Magnin 1970; Vincent et al. 1981) and in the lower Great Lakes (Clarke 1973). Snails are an important component of map turtle diets in these and other regions (Vogt 1981; Flaherty 1982; Conant and Collins 1991). We tested the following hypotheses: (i) map turtles would accept zebra mussels as a food source even when offered an alternative prey item (*B. tentaculata*) simultaneously, because of their ability to recognize and crush molluscs; (ii) zebra mussels would be consumed with increasing frequency as the turtles were repeatedly exposed to (i.e., became familiar with) this new food source; (iii) turtles would decrease their consumption of zebra mussels as the size of the zebra mussels increased, because of handling costs associated with both jaw-gape limitation and increased shell strength (Prejs et al. 1990); and (iv) the selection of zebra mussels relative to snails would be determined by the relative foraging benefit (energy gained per unit handling cost) of the two prey items (Pyke et al. 1977; Prejs et al. 1990).

Methods

Twenty-one captive-reared female map turtles (plastron length 6.1–9.5 cm, mean \pm SE = 7.1 \pm 0.2 cm), fed only trout chow pellets since birth, were maintained in fresh water at 23 \pm 1.5°C. For all experiments, turtles were placed individually in 32-L aquaria that also served as experimental arenas. Each aquarium contained 4 L of water and was inclined approximately 15° to provide a dry basking area. Zebra mussels and snails were collected from the upper

St. Lawrence River by a SCUBA diver in August and September 1993. Prior to their use in experiments, mussels and snails were maintained in aquaria at 20°C with an abundant supply of phytoplankton and homogenized powdered *Chlorella* solution.

Size-selective predation experiments

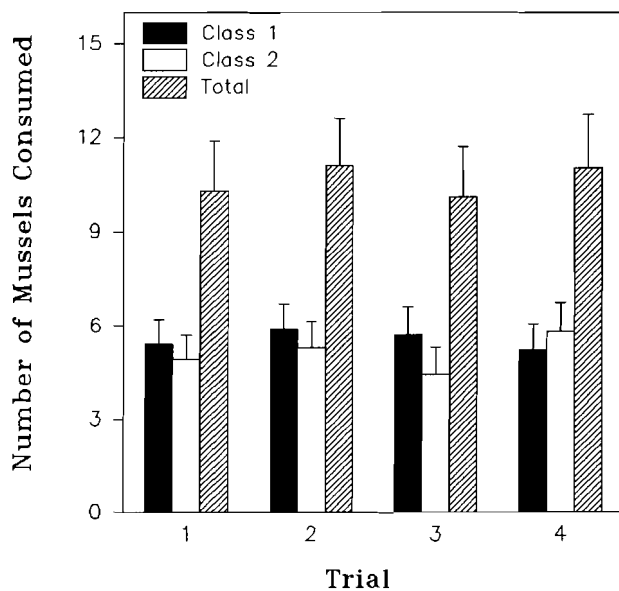
To evaluate size-selective predation upon zebra mussels, three series of experiments were conducted. All 21 turtles were starved for 24 h to increase their appetite prior to the presentation of prey (zebra mussels and snails). Zebra mussels were allowed 24 h to byssally attach to petri dishes, which were placed in each aquarium prior to the introduction of turtles. Following the starvation period, turtles were individually placed in these arenas with zebra mussels for 24 h, after which they were removed and the remaining mussels counted and remeasured. This was the first time that the captive-reared turtles had come into contact with a mollusc of any kind. In the first series of experiments, each of the 21 turtles was presented with 15 young-of-the-year mussels (mean length 9.1 \pm 0.1 mm, range 4–11 mm) and 15 one-year-old mussels (mean length 14.6 \pm 0.1 mm, range 12–18 mm). These age-classes were used because they are the most abundant in the St. Lawrence River (A. Ricciardi, unpublished data), and we assumed a priori that turtles of the size range we used would not be able to consume larger prey. The experiments were replicated four times for each turtle over a period of 2 months (September 1 to November 4, 1993) to determine if the consumption of zebra mussels increased with increased familiarity or handling practice; Spearman's rank correlation was used to test whether repeated exposure had a significant effect on consumption rate. Within each trial, differences in the consumption of both mussel size classes ($\log_{10}(x + 1)$ transformed) were tested with a *t* test.

The results of this first series of experiments suggested that the turtles were capable of consuming larger mussels. Two additional series of experiments were carried out to investigate this possibility. Four turtles were presented with 15 zebra mussels ranging in length from 20.0 to 34.0 mm (mean 23.0 \pm 0.1 mm; *n* = 60). Zebra mussels larger than 34.0 mm are very rare in the Great Lakes – St. Lawrence River system (Mackie 1993; A. Ricciardi, personal observation). The protocol was the same as in the first series of experiments. Having established that the turtles may consume larger mussels, we then examined size-selective predation by presenting 10 randomly selected turtles, placed in individual aquaria, with 3 mussels from each of the following size classes: 4–11.9 mm (mean 7.1 \pm 0.3; *n* = 30), 12–17.9 mm (mean 15.5 \pm 0.2; *n* = 30), 18–24.9 mm (mean 20.5 \pm 0.2; *n* = 30), 25–32 mm (mean 28.1 \pm 0.3; *n* = 30). Differences in consumption rates among mussel size classes were tested using multiple *t* tests with the standard Bonferroni adjustment for a 5% experimentwise error rate.

Prey-selection experiments

A final series of experiments was conducted to evaluate the prey preference of turtles given a choice of zebra mussels and snails (*Bithynia tentaculata*). Eighteen turtles (1 turtle per trial) were presented with 10 zebra mussels (mean length = 11.0 \pm 0.3 mm; *n* = 180) and 10 snails (mean length = 9.4 \pm 0.1 mm; *n* = 180) simultaneously. To determine whether significant prey selection existed, the mean con-

Fig. 1. Numbers of mussels (mean \pm SE) consumed by turtles in each of four successive trials. Class 1 is 4- to 12-mm mussels; class 2 is 13- to 18-mm mussels; the total is classes 1 and 2 combined.



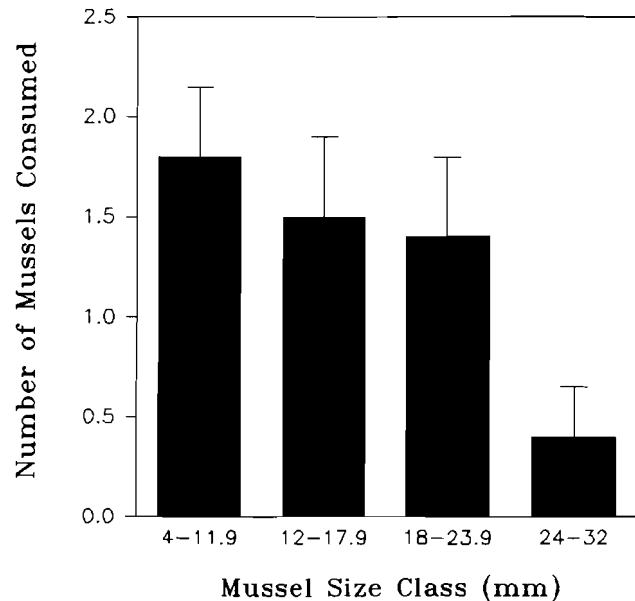
sumption rates of both prey items ($\log_{10}(x + 1)$ transformed) were compared using a *t* test. The protocol used here was similar to those of previous trials, except that the first 8 h were videotaped using a tripod-mounted VHS camera to record turtle behaviour and the handling times of both prey items. Handling time was recorded from the moment that the turtle picked up the mollusc in its jaws until it had finished manipulating it (prior to ingestion). To compare turtle gape size with prey size, we measured the jaw width of each turtle to the nearest millimetre using dial callipers.

We compared the relative net foraging benefit of zebra mussels and snails as prey for map turtles by calculating the ratio of caloric content (energetic benefit) to handling time (energetic cost) for both prey items (Pyke et al. 1977). Handling time was presumed to include the combined costs of rupturing the shell and manipulating the prey item in the turtle's mouth. Zebra mussel tissue caloric content (5130 ± 38 cal/g dry mass; 1 cal = 4.1868 J) was determined by bomb calorimetry of specimens obtained from the Soulanges Canal, a section of the upper St. Lawrence River at Pointe-des-Cascades, Quebec ($45^{\circ}20'N$, $73^{\circ}58'W$); these specimens were from the same population (and collected on the same date) as those used in prey-selection experiments. The caloric content of *B. tentaculata* tissue (5186 cal/g dry mass) was obtained from Prus (1970). Dry tissue masses were determined from length-mass regression equations for both zebra mussels (A. Ricciardi and F.G. Whoriskey, unpublished data) and *B. tentaculata* (Vincent et al. 1981) for St. Lawrence River populations. Net foraging benefit (energy gained per unit handling time) was estimated by the following model:

$$[1] \text{ net benefit (cal/s)} = (\text{energy content of prey item} \\ \times \text{dry tissue mass of prey item}) / \text{handling time}$$

The difference in the proportions of zebra mussels consumed in the presence and absence of snails was tested by a

Fig. 2. Numbers of mussels (mean \pm SE) consumed by turtles in 10 trials in which three mussels from each size class were presented.



t test after the data were normalized using the $\sin^{-1}(x^{0.5})$ transformation (Zar 1984).

Results

Size-selective predation experiments

In the first series of experiments, the mean number of zebra mussels consumed in 24 h by map turtles ranged from 10.0 ± 1.6 (33% of available mussels) in trial 3 to 11.1 ± 1.5 (37% of available mussels) in trial 2 (Fig. 1). Mussel shells and tissues were consumed whole. Throughout each experimental trial, all uneaten mussels remained alive. Contrary to our hypothesis, the total number of zebra mussels consumed did not increase over the four trials (Spearman's correlation, $p > 0.9$). Over 84 encounters (21 within each trial), turtles consumed 5.7 ± 0.4 young-of-the-year mussels and 4.9 ± 0.4 one-year-old mussels. There was no significant difference in consumption between size classes in any trial.

The second series of experiments, in which the turtles were presented with mussels 20–34 mm in length, showed that some turtles were capable of consuming zebra mussels as large as 32.4 mm. When four size classes were presented simultaneously (Fig. 2), mussels of the largest class (24–32 mm) were consumed in lower numbers than each of the smaller classes (Bonferroni-adjusted *t* test, $p < 0.05$).

Prey-selection experiments

When the two prey items were presented simultaneously, map turtles consumed significantly more *Bithynia tentaculata* (4.6 ± 0.9 for 18 turtles) than zebra mussels (1.9 ± 0.8 for 18 turtles) (*t* test, $p < 0.02$). Mean handling times for the two prey items were similar: 34.9 ± 3.0 s ($n = 34$) for *B. tentaculata* and 40.5 ± 6.0 s ($n = 17$) for zebra mussels. The mean dry tissue mass of prey consumed was 0.0143 ± 0.002 g ($n = 35$) for zebra mussels and 0.021 ± 0.001 g ($n = 83$) for *B. tentaculata*. From eq. 1, prey profitability (benefit/cost ratio) for chosen *B. tentaculata* (3.1 cal/s) was

72% higher than for zebra mussels chosen (1.8 cal/s). The presence of snails caused map turtle consumption of zebra mussels to decline from a mean of 35% in trials with no alternative prey to 19% in trials in which snails were available (t test on transformed proportion data, $p < 0.05$).

Discussion

Map turtles consumed zebra mussels in repeated trials, even in the presence of a conventional prey item (*Bithynia tentaculata*), which suggests that the turtles will include zebra mussels in their diet in the wild. This appears encouraging for conservationists, as map turtle populations are threatened in parts of their range (Beaulieu 1992; Bider and Matte 1991), and the inability of turtles to adapt to changing abundances of prey resources would have exacerbated their situation in many habitats. However, map turtles and other potential predators of zebra mussels may be exposed to toxic concentrations of mussel-borne contaminants, including heavy metals, organochlorines, and polycyclic aromatic hydrocarbons (Bruner et al. 1994), which may be several times higher in zebra mussels than in unionid mussels (M. Pilote, Département des Sciences Biologiques, Université du Québec à Montréal, personal communication). Therefore, the impact of this new and abundant food source on threatened map turtle populations deserves further study.

In our laboratory trials, map turtles readily consumed young-of-the-year (4–11 mm) and 1-year-old (12–18 mm) zebra mussels; these are the two most abundant size classes of zebra mussels currently found in map turtle habitats in the upper St. Lawrence River (A. Ricciardi, unpublished data). Although turtles did not show any preference between mussels 4–11.9 and 12–17.9 mm long, they consumed significantly fewer mussels of the largest size class (25–32 mm), which suggests that either foraging efficiency or prey profitability declined above a critical prey size. MacIsaac (1994) observed a similar pattern when crayfish (*Orconectes propinquus*) were presented with three size classes of zebra mussels spanning 3–14 mm in length; mussels ≤ 5 mm were preferentially consumed. Martin and Corkum (1994), also working with *O. propinquus*, found that crayfish of a wide range of sizes foraged primarily on zebra mussels ≤ 8 mm in length, although they were capable of consuming mussels as large as 17 mm. By contrast, diving ducks in Lake Erie followed optimal foraging predictions by selecting medium-sized to large mussels (> 11 mm) over the more abundant smaller (< 5 mm) mussels (Hamilton et al. 1994).

We predicted an increase in zebra mussel consumption by turtles over time because of a hypothesized increase in predation efficiency, but found that mussels were consumed at similar rates in all successive trials (Fig. 1). There is often a lag time before a novel prey item is recognized and an effective foraging strategy is learned by a potential predator (Tinbergen 1960; Smith 1990). This lag time may have been partially or completely eliminated in the laboratory trials by presenting the prey to the turtles in an artificial setting in which the mussels were conspicuous. Conversely, the turtles may require little time to recognize or learn to efficiently utilize zebra mussels as a food source because they are well adapted to foraging on molluscs. Their large skull length to carapace length ratio (Vogt 1981) and masticatory surface (Garman 1890; Hay 1892) are both considered specific adap-

tations to crushing molluscs. Map turtles may have an innate mechanism for recognizing molluscs and thus could immediately identify zebra mussels in nature as suitable prey. Therefore, in habitats where zebra mussels are causing declines in native mussels (Nalepa 1994; Schloesser and Nalepa 1994) or large grazing snails (Dusoge 1966; Tucker 1994), map turtles may be able to quickly shift their prey selection to the dominant mollusc. Because zebra mussels rapidly build up a large population after invading a habitat (Stanczykowska 1977), predators should expend little time searching for available mussel prey.

Map turtles selectively consumed *B. tentaculata* over zebra mussels, which is consistent with our prey profitability estimations. Similar results were obtained by Love and Savino (1993) when crayfish (*Orconectes virilis*) selected rainbow trout (*Oncorhynchus mykiss*) eggs over zebra mussels, which had a lower benefit/cost ratio. According to this simple optimal foraging model, predators should select the largest available mussels because the energy profitability of zebra mussels as prey (measured as the ratio of total caloric content to shell-crushing resistance) increases with increasing mussel size (Stein et al. 1984; Prejs et al. 1990). Predators may select molluscs with shells that are more resistant to crushing than those of zebra mussels if they are more energetically profitable (French and Morgan 1995). However, prey selection may be limited by handling costs regardless of energy content (Covich et al. 1980; Stein et al. 1984; Prejs et al. 1990), and may be mediated by the size of the prey relative to the size of the predator (Stein et al. 1975; Prejs et al. 1990; MacIsaac 1994). Gape size is an important threshold limiting the consumption of larger size classes of zebra mussels and other prey by fish predators (Stein et al. 1975, 1984; Prejs et al. 1990; French and Bur 1993; French and Morgan 1995), and gape-limited predators are common in freshwater systems (Zaret 1980). The greater proportion of snails chosen over zebra mussels by turtles in our experiments may be due to the small and relatively simple shell morphology of *B. tentaculata*. Conspicuous prey movement may also have contributed to the selection of snails over mussels by attracting predator attention. Videotape recordings revealed that the snails moved frequently, whereas zebra mussels remained stationary. Young-of-the-year zebra mussels have the ability to move considerable distances using their retractable foot (Oldham 1930), yet our laboratory observations have shown that they cease movement and siphoning activity when disturbed. Disturbance caused by turtles in their confined environments may have discouraged zebra mussel activity, but did not seem to cause the snails to reduce their movements.

Female map turtles can attain plastron lengths of up to 25 cm (Ernst and Barbour 1972; Gordon and MacCulloch 1980), twice as large as the largest turtle used in our experiments. Since gape size is linearly correlated with plastron length (A. Ricciardi and R. Serrouya, unpublished data), female map turtles may be able to exploit a wide size range of zebra mussels in nature. Turtles in our experiments had a mean gape size of approximately 11.0 mm (range 9.8–13.6 mm) and effectively handled mussels 4–24 mm in length, which include the most frequently encountered size classes in the Great Lakes – St. Lawrence River system (Dermott et al. 1993; Mackie 1993; A. Ricciardi, unpublished data). Some were capable of consuming mussels as large as 32 mm. The minimum width and height of a zebra mussel are normally

less than one-half of its maximum shell length (Stanczykowska 1977). Therefore, given that large map turtles can have gape sizes greater than 20 mm, and assuming that prey size is the primary factor limiting predation, a natural population of map turtles should be capable of exploiting most or all size classes of zebra mussels available within a habitat.

The probability of map turtles encountering zebra mussels will increase as zebra mussels continue to colonize large rivers and inland lakes in eastern North America. The zebra mussel and the map turtle are sympatric in the upper St. Lawrence River (Gordon and MacCulloch 1980; Mellina and Rasmussen 1994), Lake Champlain (Gordon and MacCulloch 1980; New York Sea Grant Extension 1994), the lower Great Lakes, and the upper Mississippi River basin (Conant and Collins 1991; New York Sea Grant Extension 1994). Although much of the exposed shoreline of the Great Lakes is probably unsuitable for map turtles, sheltered areas with suitable basking sites (e.g., river outlets, lagoons) will likely harbour populations of both zebra mussels and map turtles. Several species of *Graptemys* that occur in the lower reaches of rivers draining into the Gulf of Mexico (Conant and Collins 1991) may also act as predators of zebra mussel populations that become established in these regions. We predict that map turtles will prey upon zebra mussels in these areas even when other prey (e.g., snails, insects, crayfish) are available, but zebra mussels may become a dominant prey item only when preferred or more energetically profitable prey are scarce.

Acknowledgements

The authors thank J.R. Bider and the St. Lawrence River Valley Ecomuseum (Ste-Anne-de-Bellevue, Quebec) for providing turtles for this study, and S. Wood and K. Brown for laboratory assistance. Financial support was provided by operating grants from the Natural Sciences and Research Council of Canada and the ELBJ Foundation to F.G.W.

References

- Beaulieu, H. 1992. Liste des espèces de la faune vertébrée susceptibles d'être désignées menacées ou vulnérables. Publ. No. 2-550-27104-1, Ministère du Loisir, de la Chasse et de la Pêche, Québec.
- Bider, J.R., and Matte, S. 1991. Atlas des amphibiens et des reptiles du Québec. Société d'Histoire naturelle de la Vallée du Saint-Laurent, Montréal, et Ministère du Loisir, de la Chasse et de la Pêche, Québec.
- Bruner, K.A., Fisher, S.W., and Landrum, P.F. 1994. The role of the zebra mussel, *Dreissena polymorpha*, in contaminant cycling: II. Zebra mussel contaminant accumulation from algae and suspended particles, and transfer to the benthic invertebrate, *Gammarus fasciatus*. *J. Great Lakes Res.* **20**: 735–750.
- Clarke, A.H. 1973. The freshwater molluscs of the Canadian Interior Basin. *Malacologia*, **13**: 1–509.
- Conant, R., and Collins, J.T. 1991. A field guide to reptiles and amphibians (eastern and central North America). 3rd ed. Houghton Mifflin Co., Boston.
- Covich, A.P., Dye, L.L., and Mattice, J.S. 1980. Crayfish predation on *Corbicula* under laboratory conditions. *Am. Midl. Nat.* **105**: 181–188.
- Dermott, R., Mitchell, J., Murray, I., and Fear, E. 1993. Biomass and production of zebra mussels (*Dreissena polymorpha*) in shallow waters of northeastern Lake Erie. *In* Zebra mussels: biology, impacts and control. Edited by T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 399–414.
- Dusoge, K. 1966. Composition and interrelations between macrofauna living on stones in the littoral of Mikolajskie lake. *Ekol. Pol. (Ser. A)*, **14**: 755–762.
- Ernst, C.H., and Barbour, R.W. 1972. Turtles of the United States. University of Kentucky Press, Lexington.
- Flaherty, N. 1982. Home range, movement, and habitat selection in a population of the map turtle, *Graptemys geographica* (Le Sueur), in southwestern Quebec. M.Sc. thesis. Department of Natural Resource Sciences, McGill University, Montréal.
- Flaherty, N., and Bider, J.R. 1984. Physical structures and the social factor as determinants of habitat use by *Graptemys geographica* in southwestern Quebec. *Am. Midl. Nat.* **111**: 259–266.
- French, J.R.P., III, and Bur, M.T. 1993. Predation of the zebra mussel (*Dreissena polymorpha*) by freshwater drum in western Lake Erie. *In* Zebra mussels: biology, impacts and control. Edited by T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 453–464.
- French, J.R.P., III, and Morgan, M.N. 1995. Preference of redear sunfish on zebra mussels and rams-horn snails. *J. Freshwater Ecol.* **10**: 49–55.
- Fuller, S.L.H. 1974. Clams and mussels (Mollusca: Bivalvia). *In* Pollution ecology of freshwater invertebrates. Edited by C.W. Hart, Jr., and S.L.H. Fuller. Academic Press, New York. pp. 215–273.
- Garman, H. 1890. The difference between the geographic turtles *Malaclemys geographica* and *M. lesueuri*. *Essex Inst. Bull.* **22**: 70–83.
- Gillis, P.L., and G.L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. *Can. J. Zool.* **72**: 1260–1271.
- Gordon, D.M., and MacCulloch, R.D. 1980. An investigation of the ecology of the map turtle, *Graptemys geographica* (Le Sueur), in the northern part of its range. *Can. J. Zool.* **58**: 2210–2219.
- Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. *In* Zebra mussels: biology, impacts and control. Edited by T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 415–438.
- Hamilton, D.J., Ankney, C.D., and Bailey, R.C. 1994. Predation of zebra mussels by diving ducks: an enclosure study. *Ecology*, **75**: 521–531.
- Hay, O.P. 1892. Some observations on the turtles of the genus *Malaclemys*. *Proc. U.S. Natl. Mus.* **15**: 379–383.
- Love, J., and Savino, J.F. 1993. Crayfish (*Orconectes virilis*) predation on zebra mussels (*Dreissena polymorpha*). *J. Freshwater Ecol.* **8**: 253–259.
- MacIsaac, H.J. 1994. Size-selective predation on zebra mussels (*Dreissena polymorpha*) by crayfish (*Orconectes propinquus*). *J. N. Am. Benthol. Soc.* **13**: 206–216.
- Mackie, G.L. 1993. Biology of the zebra mussel (*Dreissena polymorpha*) and observations of mussel colonization on unionid bivalves in Lake St. Clair of the Great Lakes. *In* Zebra mussels: biology, impacts and control. Edited by T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 333–358.
- Magnin, E. 1970. Faune benthique littorale du lac Saint Louis près de Montréal (Québec). *Ann. Hydrobiol.* **1**: 181–195.
- Martin, G.W., and Corkum, L.D. 1994. Predation of zebra mussels by crayfish. *Can. J. Zool.* **72**: 1867–1871.
- Mellina, E., and Rasmussen, J.B. 1994. Patterns in the distribution and abundance of zebra mussels (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physico-chemical factors. *Can. J. Fish. Aquat. Sci.* **51**: 1024–1036.
- Mitchell, C.A., and Carlson, J. 1993. Lesser scaup forage on zebra mussels at Cook Nuclear Plant, Michigan. *J. Field Ornithol.* **64**: 219–222.

- Nalepa, T.F. 1994. Decline of native unionid bivalves in Lake St. Clair after infestation by the zebra mussel, *Dreissena polymorpha*. *Can. J. Fish. Aquat. Sci.* **51**: 2227–2233.
- New York Sea Grant Extension. 1994. North American range of the zebra mussel. *Dreissena polymorpha* information review/ New York Zebra Mussel Information Clearinghouse, **5**(5): 6–7.
- Oldham, C. 1930. Locomotive habit of *Dreissena polymorpha*. *J. Conchol. (Lond.)*, **19**: 25–26.
- Piesik, Z. 1974. The role of the crayfish *Orconectes limosus* (Raf.) in extinction of *Dreissena polymorpha* (Pall.) subsisting on steel-on net. *Pol. Arch. Hydrobiol.* **21**: 401–410.
- Prejs, A., Lewandowski, K., and Stanczykowska-Piotrowska, A. 1990. Size-selective predation by roach (*Rutilus rutilus*) on zebra mussel (*Dreissena polymorpha*): field studies. *Oecologia*, **83**: 378–384.
- Prus, T. 1970. Calorific values of animals as an element of bioenergetical investigations. *Pol. Arch. Hydrobiol.* **17**: 183–199.
- Pyke, G.H., Pulliam, H.R., and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**: 137–154.
- Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B. 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. *Can. J. Fish. Aquat. Sci.* **53**. In press.
- Schloesser, D.W., and Nalepa, T.F. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. *Can. J. Fish. Aquat. Sci.* **51**: 2234–2242.
- Smith, R.L. 1990. *Ecology and field biology*. 4th ed. Harper and Row, New York.
- Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pallas) (Bivalvia) in lakes. *Pol. Arch. Hydrobiol.* **24**: 461–530.
- Stein, R.A., Goodman, C.G., and Marschall, E.A. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology*, **65**: 702–715.
- Stein, R.A., Kitchell, J.F., and Knezevic, B. 1975. Selective predation by carp (*Cyprinus carpio* L.) on benthic molluscs in Skadar Lake, Yugoslavia. *J. Fish Biol.* **7**: 391–399.
- Stewart, T.W., and Haynes, J.M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. *J. Great Lakes Res.* **20**: 479–493.
- Tinbergen, L. 1960. The natural control of insects in pine-woods: 1. Factors influencing the intensity of predation by songbirds. *Arch. Neerl. Zool.* **13**: 265–343.
- Tucker, J.K. 1994. Windrow formation of 2 snails (families Viviparidae and Pleuroceridae) colonized by the exotic zebra mussel, *Dreissena polymorpha*. *J. Freshwater Ecol.* **9**: 85–86.
- Vincent, B., Vaillancourt, G., and Harvey, M. 1981. Cycle de développement, croissance, effectifs, biomass et production de *Bithynia tentaculata* L. (Gastropoda: Prosobranchia) dans le Saint-Laurent (Québec). *Can. J. Zool.* **59**: 1237–1250.
- Vogt, R.C. 1981. Food partitioning in three sympatric species of map turtle, genus *Graptemys* (Testudinata, Emydidae). *Am. Midl. Nat.* **105**: 102–111.
- Walz, N. 1979. The energy balance of the zebra mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. V. Seasonal and nutritional changes in the biochemical composition. *Arch. Hydrobiol. (Suppl.)*, **55**: 235–254.
- Wormington, A., and Leach, J.H. 1992. Concentrations of migrant diving ducks at Pointe Pelee National Park, Ontario, in response to invasion of zebra mussels, *Dreissena polymorpha*. *Can. Field-Nat.* **106**: 376–380.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J.
- Zaret, T.M. 1980. *Predation in freshwater communities*. Yale University Press, New Haven, Conn.