Fishery Science

The Unique Contributions of Early Life Stages

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Blackwell
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Iowa State Press, a Blackwell Publishing
Company, 2121 State Avenue, Ames, Iowa
50014-8300, USA
Tel: +1 515 292 0140
Blackwell Science Asia Pty, 54 University Street,
Carlton, Victoria 3053, Australia
Tel: +61 (0)3 9347 0300
Blackwell Wissenschafts Verlag,
Kurfürstendamm 57, 10707 Berlin, Germany
Tel: +49 (0)30 32 79 060

First published 2002 by Blackwell Science Ltd

Library of Congress
Cataloging-in-Publication Data
is available

ISBN 0-632-05661-4

A catalogue record for this title is available from the British Library

Set in Times by Gray Publishing, Tunbridge Wells, Kent
Printed and bound in Great Britain by
MPG Books, Bodmin, Cornwall

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(4) The number of age 1 immatures was not correlated with the abundance of feeding larvae. This suggested that mass mortality after the first feeding stage, probably up to 8–10 months of age, was responsible for recruitment failure from 1988 to 1991.

(5) Spawning grounds expanded offshore over the strong flow field of the Kuroshio Current in proportion to the amount of egg production, and presumably, spawning-stock biomass. A particle-tracking model of dispersal of eggs and larvae demonstrated that a large proportion of egg production was transported from the spawning grounds to the downstream Kuroshio Extension area in 2–3 weeks.

(6) Food availability for larvae and early juveniles was higher in the waters north of the Kuroshio Extension than in the spawning grounds. Otolith-based daily growth rates in early juvenile sardines were higher in the Kuroshio Extension area than in the Kuroshio Current area. The Kuroshio Extension area is thought to constitute a nursery of late larval and early juvenile sardines. Transport of eggs and larvae from the spawning grounds to the nursery area is an important component of early life history of the sardine.

(7) Spawning-stock biomass of sardines and other pelagic egg spawners can be estimated based on daily or annual egg production. A rough estimate of spawning-stock biomass may be obtained from the area of the spawning grounds. Biomass estimates based on egg and larval surveys are independent of commercial catch data and, therefore, one of the important pieces of information for management of fish stocks.

Cascading Effects of Human Impacts on Fish Populations in the Laurentian Great Lakes

James A. Rice

11.6 Introduction

The biological communities of the Laurentian Great Lakes have undergone dramatic changes over the last 200 years, many induced directly or indirectly by human behavior. Overharvest of fisheries and the establishment, both intentional and accidental, of exotic species have dramatically altered the food web and community structure of the lakes. Forest clear-cutting, shifts in land use, and changes in nutrient loading have altered the productivity of the Great Lakes system. Chemical pollution and waste disposal practices of the past continue to affect ecosystem functions today. These changes have presented extraordinary management challenges, and continue to do so.

Early work on fishes of the Great Lakes, dating back to the 1920s and 1930s, provided a basic foundation of knowledge concerning species distributions, early life histories, and basic biology. Unfortunately, over much of this time fish early life-history studies were not a major factor in fishery research and management. Historically, adult fishes were the primary focus of attention; larger fishes naturally drew people's interest and were the target of subsistence and commercial fisheries, which provided data from harvest records. They were more obvious than eggs and larvae and, in many respects, easier to sample. Even stock–recruitment analyses emphasized the role of spawning adults in determining recruitment.

More recently, fishery biologists have come to understand that events occurring during early life often are the primary forces that dictate the dynamics we observe in adult populations and communities. Over the last 20 years, an understanding of fish early life history has played a significant role in almost every major Great Lakes fishery management issue. How did this change in perspective come about, and how has it changed the way we approach fishery science and management? The Great Lakes story, far too rich a history to relate in full detail here, offers a wealth of opportunities to illustrate many of the concepts presented in this book. In the following pages I will share several examples that show how early life-history studies have been critical to understanding and managing the dynamics of Great Lakes fisheries, and have fundamentally changed our thinking about fishery management in general.

11.7 First, some background

The emergence of early life-history studies as a force in Great Lakes fishery management is best understood in the context of the history of Great Lakes fisheries. Until about 200 years ago, the fish communities of the Great Lakes were relatively stable. Lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) were the dominant predators, and a substantial portion of the fish population consisted of endemic species. Commercial fishing began in the early 1800s and was a major industry by 1850. Harvest continued to increase throughout the 19th century as better nets and improvements in fishing technology, such as the steam engine, allowed fishermen to range farther afield and harvest fishes more efficiently.

During this same period a growing lumber industry was deforesting much of the Great Lakes region. The reduced forest canopy increased water temperatures in tributaries, and increased erosion smothered spawning grounds in silt. Massive amounts of sawdust waste from sawmill operations were disposed of in rivers and floated 30–50 km out into the lakes, sinking and covering feeding and spawning grounds. The development of major cities and ports along the shore of the lakes led to increasing pollution and loss of wetlands. Construction of dams on tributaries impeded spawning migrations. By the late 1800s these impacts had already led to major declines in Great Lakes fisheries.

With further development of shipping came a new invasion, still going on today – colonization of the lakes by exotic species. In 1829 the Welland Ship Canal was built around Niagara Falls to allow ships to reach the four upper Great Lakes. Shortly after its enlargement in 1919, sea lampreys (*Petromyzon marinus*) began their march through the Great Lakes. These ancient parasites attach to large fishes and suck their blood, often until their victim dies. With no natural predators to control them, lampreys decimated populations of lake trout, lake whitefish (*Coregonus clupeaformis*), and other large species by the 1950s.

The rise of sea lamprey populations paved the way for the advance of another anadromous invader, the alewife (*Alosa pseudoharengus*). First reported in Lake Michigan in 1949, alewife populations exploded in the vacuum created by the decimation of the lakes' piscivorous predators. From 1960 to 1967 alewives increased from 8% of the fish biomass in Lake Michigan to a stunning 80% of the fish biomass, culminating in a massive die-off in the spring of 1967. The alewife invasion, in concert with other stressors, resulted in the extirpation or extinction of several common and endemic planktivorous fish species.

By the middle of the 20th century, the Great Lakes and their fisheries were in total disarray. These events galvanized previously unsuccessful efforts to initiate a comprehensive management strategy for the Great Lakes fisheries, culminating in the formation of the Great Lakes Fishery Commission by the United States and Canada. Their first mission was to find a way to control the sea lamprey.

11.8 In search of a vampire slayer

Clearly, it would be impossible to control lampreys in the large, open lake environment. The key to controlling lamprey lay in understanding their early life history, and, in particular, the concept of ontogenetic habitat shifts (Chapter 7). Because sea lampreys are anadromous, they move into small streams to spawn, depositing their eggs in clean gravel. After the young hatch, they drift downstream to muddy areas, burrow into the sediment, and spend 3–17 years as filter-feeding larvae called ammocoetes. Eventually the ammocoetes transform into parasitic adults and move into the lake where they feed on body fluids of host fishes for 1 or 2 years before returning to spawn.

It was in the spawning or larval stage, when sea lampreys and their young are concentrated in streams, where the battle would have to be joined. Early efforts to block lamprey spawning migrations using mechanical and electrical barriers failed. The focus then shifted to identifying a way to kill lamprey larvae, which were not only confined to streams, but were in the life-history stage when many fishes are most sensitive to toxic substances (Chapter 10). After testing more than 6000 chemicals over 5 years, US Fish and Wildlife Service biologists finally found the chemical TFM (3-trifluoromethyl-4-nitrophenol). It could be dripped into spawning streams to selectively kill lamprey larvae without significant harm to populations of other aquatic organisms. (They later identified a second chemical, Bayer 73, that worked more effectively in still or slowly moving water.) Stream treatments with TFM radically reduced lamprey populations, paving the way for efforts to re-establish lake trout, the primary native piscivore.

11.9 Bring back the lake trout

With lamprey populations greatly reduced, efforts to re-establish naturally reproducing lake trout were begun in the 1950s and 1960s, by rearing millions of lake trout (Figure 1.3d) in hatcheries and stocking them in the lakes. Lake trout populations rebounded as these stocked fish matured, but mysteriously the stocked lake trout failed to reproduce successfully. Restoration efforts are still continuing today, though with limited success except in Lake Superior.

Many hypotheses being explored for this limited success focus on early life stages. For example, naive hatchery fish may deposit eggs in unsuitable habitats because they do not home to historical spawning sites. Predation on eggs and larvae has been observed and may limit survival. There is also concern that chemical contaminants may inhibit egg viability and survival (Selgeby *et al.* 1995).

In recent years, another potentially important factor, called Early Mortality Syndrome (EMS), has been identified. This syndrome results in high mortality in salmonid larvae between hatching and first feeding due to a deficiency of thiamine, a B vitamin, in the eggs. Evidence suggests that this problem stems from the prominence of alewives, which contain high levels of thiaminase (a thiamine-degrading enzyme), in the diets of Great Lakes salmonids (see Box 10.5; Fisher *et al.* 1996, Fitzsimons *et al.* 1999). In some years, some salmonid populations in the Great Lakes Basin have experienced up to 90% mortality due to this deficiency. EMS also appears to be more common in contaminated ecosystems, and when spawning females exhibit deficiencies of vitamin E, an antioxidant. Fortunately, EMS can be prevented in the hatchery by treating eggs with thiamine during incubation.

When it became clear that lake trout populations were not going to rebound rapidly, managers turned to two other exotic species to help fill the void at the top of the food web. They stocked millions of chinook salmon (*Oncorhynchus tshawytscha*; Figure 1.3c) and coho salmon (*Oncorhynchus kisutch*), natives of the Pacific Ocean. These predators flourished, but not before the alewife population, free from predatory control, exploded. The alewife's rise to dominance would prove to have one of the longest lasting impacts on the Great Lakes fish community.

11.10 The secret lives of alewives

As alewives became abundant first in Lake Ontario, then in Lakes Huron and Michigan, native planktivore communities in each lake followed a similar pattern of dramatic decline. For example, by the 1960s all but one of the seven native species in Lake Michigan's coregonid deepwater cisco complex were either extinct or severely reduced. Only bloater (*Coregonus hoyi*), the smallest species, remained relatively abundant, but it too declined in the late 1960s. The emerald shiner (*Notropis atherinoides*) had been extremely abundant in Lake Michigan until the late 1950s, but disappeared in the early 1960s. While fishing and lamprey predation likely contributed to declines in the larger species, alewives were strongly implicated in the decline of all of these species.

Alewives are primarily planktivores, so their main impact was thought to occur via competition. Changes in the plankton community supported this argument; in Lake Michigan, mean zooplankton size decreased sharply from 1954 to 1966 in response to intense planktivory by the increasing alewife population, then increased again following the alewife die-off in 1967 (Wells 1969). These impacts on plankton size structure put some native species at a disadvantage. For example, bloaters feed on individual prey and are not able to filter-feed on smaller zooplankton, as alewives can (Crowder & Binkowski 1983). Juvenile bloaters also grow more slowly on small zooplankton than on large zooplankton, even when the total biomass of prey is the same (Miller *et al.* 1990).

Certainly alewives had competitive interactions with native planktivores, but in 1980 Larry Crowder made the case that predation on eggs and larvae, rather than competition,

Table 11.1 Most native Lake Michigan species with semi-pelagic eggs or larvae that overlapped spatially and temporally with alewife became rare or extinct after alewives became abundant, whereas native species with demersal eggs and larvae persisted after the alewife invasion (Crowder 1980).

Status after alewives became abundant	Eggs or larvae semi-pelagic and available to alewives?	
	Yes	No
Rare or Extinct	9	0
Persistent	1	11

Bloater was identified as the one species with semi-pelagic larvae (Figure 1.3b) that survived the invasion, but it also showed strong declines during periods of alewife abundance.

was the main mechanism by which alewives led to the decline or extinction of native species. He pointed out that all the native species that had become rare or extinct in Lake Michigan had eggs or larvae that were pelagic or semi-buoyant and co-occurred with alewives, while most of the remaining coexisting species had demersal eggs and larvae, and sometimes parental care (Table 11.1). Other researchers had suggested that alewives might prey upon fish eggs and larvae, and several observations of alewife cannibalism and predation on larval fishes had been reported in the early 1970s. Until Crowder's 1980 paper, however, the importance of alewife predation on fish early life stages had not been widely recognized.

In hindsight, Crowder's idea makes obvious sense. Fish eggs and larvae (ichthyoplankton) are larger than most other plankton species, and alewives, like most other planktivores, tend to consume the largest planktonic prey available (Brooks & Dodson 1965). Today, the importance of predation by alewives, and predation on larvae in general, is widely accepted. In fact, recent lab and field studies have shown that predation by alewives on lake trout fry may be inhibiting the recovery of lake trout populations (Krueger *et al.* 1995).

Empirical evidence of predation in the field is rare because larvae are digested so quickly. Doran Mason and Stephen Brandt, however, were able to document that alewife predation was a major source of mortality for newly hatched yellow perch (*Perca flavescens*, Figure 1.3j) in Lake Ontario embayments when the onshore spawning migration of alewives coincided with yellow perch hatching (see Box 8.2 and Section 8.5.2). Thus, it seems plausible that predation by alewives on larval yellow perch may be an important factor underlying the generally inverse relationship observed between yellow perch year-class strength and alewife abundance over the last half century.

Predation plays an important role, but it is not the whole story. The alewife–yellow perch interaction is a classic example of the importance of understanding how ontogenetic niche shifts (Chapter 7) influence the outcome of interactions between species. While alewives shift from being a competitor to a predator of young yellow perch as they grow, perch also change roles. Small yellow perch feed primarily on zooplankton, but become more piscivorous as they grow, including both alewife eggs and young-of-the-year alewives in their diet. Indeed, yellow perch predation on alewife eggs has been implicated as a factor in the decline of alewives in Lake Michigan during the 1980s (Hansson *et al.* 1997). Thus, as these ontogenetic shifts occur, the nature of competitive and predatory interactions between species often completely reverses. Similar dynamics underlie the Lake Erie yellow perch–walleye (*Stizostedion vitreum*) oscillation, where these species are competitors as juveniles, as well as both predator and prey for each other at other life stages. Perhaps one of the most enduring lessons of the alewife invasion of the Great Lakes will be the awareness that fully understanding the interactions between species requires that we take into account the dynamics occurring at all ontogenetic stages.

11.11 Bloater recruitment and the characteristics of survivors approach

Throughout the 1970s there was a growing awareness of the importance of events occurring early in life for determining survival and year-class strength of fishes. Researchers, however, were often frustrated in their efforts to pinpoint the mechanisms governing annual recruitment variation. What were the most important factors? Starvation? Predation? Environmental effects? Despite our growing knowledge of fish early life dynamics, the list was getting longer, rather than shorter. Simultaneously collecting information on all the potentially important factors affecting recruitment of a particular species was virtually impossible.

Two developments converged to allow a radical change in our approach to understanding recruitment variability. The first was Gregor Pannella's (1971) discovery of daily growth increments in the otoliths of larval fishes, which allowed us to collect detailed information on the history of individual fish (Chapter 2). The second was the development of techniques for rearing larvae in the lab, which was an essential prerequisite for conducting process-oriented experiments on the factors affecting larval fish growth and survival. These tools allowed us to shift our focus from the vast majority of larvae, which die, to the small fraction of larvae that survive. Rather than trying to account for all the factors determining mortality, we could instead ask, "What is unique about survivors?" and use the answer to help us identify what is important in determining survival and recruitment. This concept, pioneered by Richard Methot (1983), has since been dubbed the "characteristics of survivors" approach (Chapter 4).

In the early 1980s, Larry Crowder, Fred Binkowski and I applied the characteristics of survivors approach to try to decipher the mechanisms underlying the poor recruitment of Lake Michigan bloaters in the 1970s. Binkowski had developed techniques to reliably rear bloater larvae (and subsequently alewife and yellow perch larvae) in the lab, which allowed us to conduct experiments to determine what information we could get from their otoliths (Rice *et al.* 1985). We found that bloaters begin depositing growth increments at first feeding (about 3 days after hatching), and we could determine the date of first feeding within 6 days for bloaters up to 5 months old (Figure 11.15). Using this age estimate we could also determine their growth rate. Lastly, we found that periods of low ration would leave noticeable stress marks on the otolith (Figure 11.16).

We applied this ability to interpret bloater otoliths to larvae that were collected from the field in 1982 and 1983. Bloaters spawn on the bottom in deep water, where the eggs incubate for several months (Wells 1966). Larvae spend 1–10 days in the hypolimnion before moving to the surface (Wells 1966, Crowder & Crawford 1984). We used data on bloater

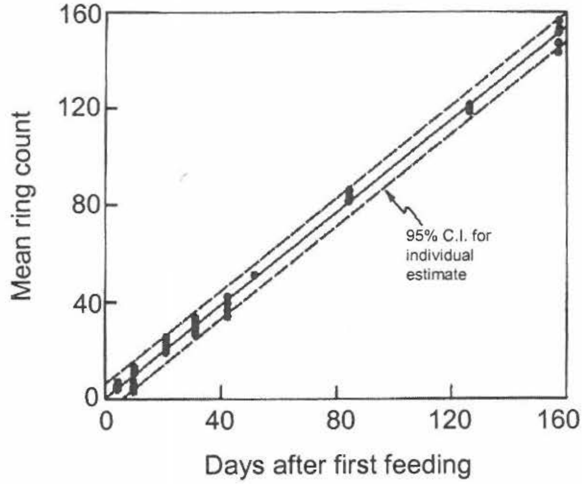

Figure 11.15 Relationship between the number of rings (increments) on the otolith and the number of days after first feeding for lab-reared bloater larvae. The regression line and 95% confidence interval are shown. The regression equation is: Ring Count = 0.331 + 0.961 × days ($R^2 = 0.99$).

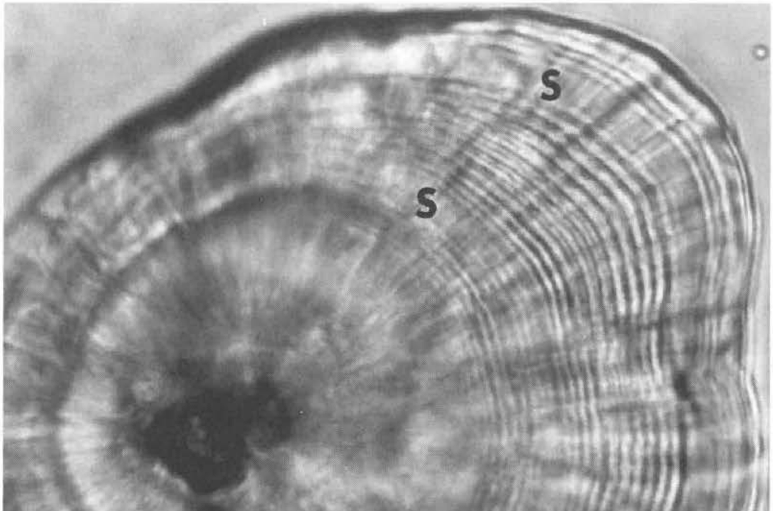

Figure 11.16 Otolith of a 13.1-mm lab-reared bloater larva 35 days after first feeding, showing evidence of stress resulting from two 5-day periods of low ration (indicated by S). Scale bar represents 20 μm. (From Rice *et al.* 1985.)

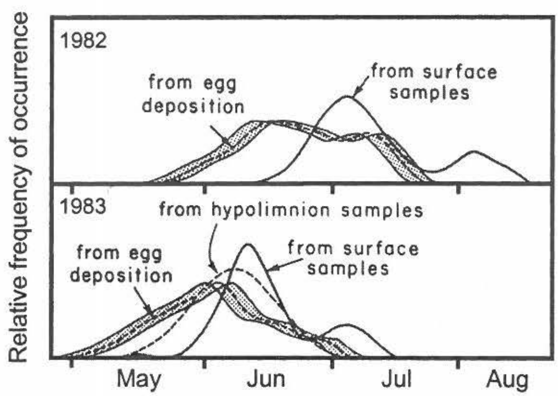

Figure 11.17 Expected first-feeding date distributions estimated from egg deposition, and observed first-feeding date distributions observed for bloater larvae collected in the hypolimnion shortly after hatching or at the surface about 1 month after hatching. Shading around the expected distributions reflects uncertainty in the position of these curves on the X-axis due to possible variation in when ripe females deposited their eggs. Hypolimnetic samples were not collected in 1982. (After Rice *et al.* 1987a.)

egg deposition and a temperature-dependent egg-incubation model to estimate the temporal pattern of bloater hatching dates. Otolith analysis of bloater larvae collected in the hypolimnion provided the first-feeding date distribution of newly hatched bloaters, and otolith analysis of bloaters collected at the surface provided the first-feeding date distribution of larvae about one to two months old. We compared the characteristics of older larvae (first-feeding date distributions, growth rates, stress-mark patterns) with larvae collected at earlier stages to determine how survivors differed from the average individual (Rice *et al.* 1987a).

Our results suggested that events during egg incubation and the first month after hatching strongly influenced patterns of bloater survival. Larvae with early hatching dates were much less common in hypolimnion samples of recently hatched larvae than we expected based on the distribution predicted from observed egg deposition (Figure 11.17). Early-spawned eggs likely experienced higher total mortality because cooler temperatures early in the incubation period extended their incubation period by about two and a half weeks, prolonging their exposure to sources of egg mortality. Because environmental conditions in the hypolimnion of Lake Michigan are very stable during the winter, egg mortality was likely due to biotic factors such as predation, rather than abiotic stressors.

Similarly, larvae that hatched early were less common among older larvae collected in surface samples than expected from the distribution of first-feeding dates for younger larvae collected in the hypolimnion, while larvae hatched later were over-represented among these older survivors (Figure 11.17). Growth rates of larvae collected in the field were generally as high or higher than growth rates of larvae reared in the lab on *ad libitum* rations. Larvae that hatched early, however, grew less than half as fast during the first 3 weeks of life as larvae that hatched later in the season. Furthermore, larvae hatched early were significantly more likely to show evidence of brief stress periods on their otoliths; 43% of larvae with stress marks first fed early in the season when survival was less than expected,

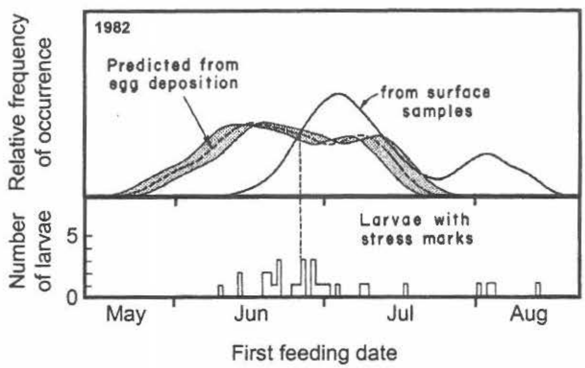

Figure 11.18 First-feeding date distributions of bloater larvae in 1982 estimated from egg deposition and observed for larvae collected at the surface about 1 month after hatching (top panel), compared to the first-feeding dates for larvae in surface samples that had stress marks on their otoliths. While only 13% of all surviving larvae fed first early in the season when survival was less than expected (to the left of the vertical dashed line), 43% of larvae with stress marks fed first during this period. (From Rice *et al.* 1987a.)

while only 13% of all larvae first fed during this period (Figure 11.18). Stress marks all occurred at a common point in ontogeny, 5–10 days after first feeding, rather than on common dates, suggesting the stress was associated with migration from the hypolimnion to the surface rather than with temporal phenomena, such as storms.

Taken together, these patterns suggest that mechanisms operating during the first month or so after hatching have an important effect on bloater survival and recruitment. The relatively high growth rates of all larvae, including those with stress marks, suggested that starvation was not an important factor affecting bloater survival. Subsequent lab experiments lend support to this conclusion; starved bloater larvae took 25 days to reach 50% mortality (Rice *et al.* 1987b)! There was also no evidence to suggest that short term environmental variability, such as storms, played a significant role in determining bloater recruitment. Rather, the patterns we observed implicated sources of mortality that were size- or growth-rate dependent, particularly during the first few weeks of life. We hypothesized that predation was the most likely mechanism; predation is typically size-dependent, and variations in growth rate would determine how long larvae remain susceptible to gape-limited predators.

The characteristics of survivors approach allowed us to eliminate some hypotheses and narrow the scope of our research to the most likely mechanisms. In subsequent research we evaluated the impact of potential predators on bloater eggs and larvae (Luecke *et al.* 1990). Potential hypolimnetic predators included deepwater sculpins (*Myoxocephalus thompsoni*) and slimy sculpins (*Cottus cognatus*), adult alewives, and adult bloaters. Of these, only sculpins proved to be significant predators on bloater eggs and yolk-sac larvae under hypolimnetic conditions (darkness and low temperature). Rainbow smelt (*Osmerus mordax*), yearling alewives, and yearling bloaters overlap with bloater larvae once they move to the surface. All three of these predators consumed bloater larvae under epilimnetic conditions, in a strongly size-dependent manner, with capture success falling from about 85% on 13.2-mm larvae to about 5% on 31.5-mm larvae (Figure 11.19). The presence of zooplankton as alternative prey substantially reduced the predation rate of smelt and yearling bloaters on bloater larvae, but the feeding rate of alewives did not change. Rather, as the density of bloater larvae increased, alewives ate more larvae and fewer zooplankton, suggesting that they have a preference for fish larvae.

Of the potential predators on bloater eggs and larvae, sculpins in the hypolimnion and alewives in the epilimnion appear to be most important to bloater recruitment. The negative relationship between alewife and bloater abundance is likely driven by direct effects of alewife predation, as well as indirect effects of competition, which reduces growth rate of bloater larvae and thus increases the time they are vulnerable to predation. As alewife abundance declined somewhat in the 1980s, bloater populations rebounded dramatically and once again became a major component of total fish biomass.

The characteristics of survivors approach proved to be a powerful tool in our effort to decipher the mechanisms governing bloater survival. It not only helped us understand the dynamics of bloater recruitment, but suggested broader generalities that might be applicable to other species as well.

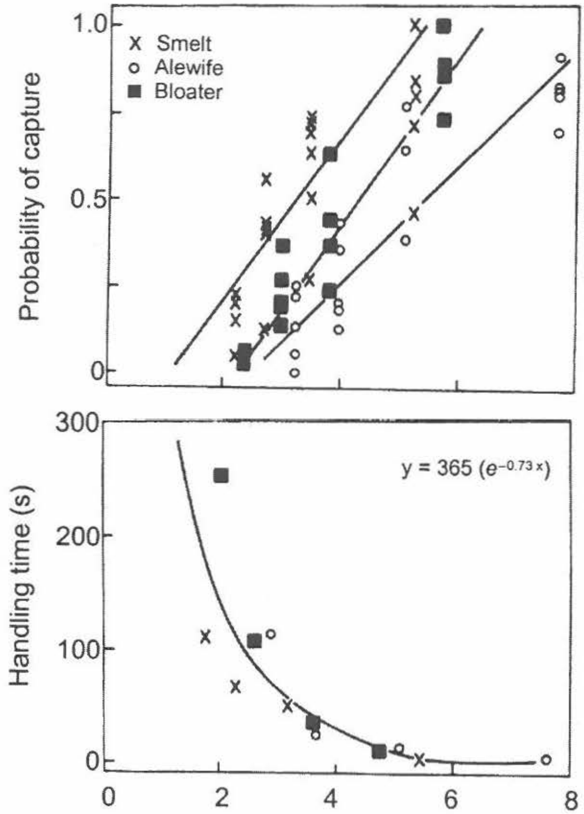

Figure 11.19 Size-dependent capture success (top) and handling time (bottom) of yearling rainbow smelt, alewife, and bloater preying upon bloater larvae. (Reproduced from Luecke *et al.* 1990 with permission of NRC Research Press.)

11.12 All larvae are small (but some are smaller than others!)

At the time we began our work on bloater recruitment, there was no unifying conceptual framework that reconciled conflicting information among species about which factors, such as starvation, predation, or abiotic conditions, played the key role in governing survival. In fact, Reuben Lasker, one of the most prominent scientists working on the early life stages of fishes, stated in his plenary address to the 1986 Larval Fish Conference that recruitment "depends on a species' behavioral and physiological response to the biotic and abiotic environment and that generalities with respect to recruitment mechanisms cannot be made."

Our experience with bloater larvae suggested that body size might provide such a unifying framework. We realized that while bloater larvae seemed quite small to us (having worked mostly with adult fishes), they are quite big in comparison to other species (Figure 11.20). We had been surprised to find that 50% of newly hatched bloater larvae survived 25 days without food – very different from results with anchovies and sardines, which are much smaller at hatching! In fact, about 90% of all fish species hatch at a length less than 9.8 mm, the size of bloaters at hatching (Chapter 1). Our subsequent analysis of the available published data (Miller *et al.* 1988) indicated that fishes from diverse taxa and habitats share common size-dependent relationships, suggesting that body size does indeed provide a good starting point for understanding survival and recruitment mechanisms of larval fishes. As we saw in Chapter 1, such scaling relationships can be further refined by accounting for differences among species in their size at comparable stages of development.

The accumulating studies on early life stages of Great Lakes fishes created an ideal opportunity to test the relative importance of species vs. body size. Thomas Miller chose three species from different families with very different morphologies and hatching sizes (alewife, 3.8 mm; yellow perch, 5.5 mm; bloater, 9.8 mm). He conducted a series of experiments with all three species at several common sizes ranging from 10 to 40 mm, evaluating the effects of size and species on foraging ability, including prey detection, pursuit, attack, and capture. For most of these traits, body size accounted for much more of the variation than did species differences. Size explained 71–91% of the variation in parameters of the Holling Type II

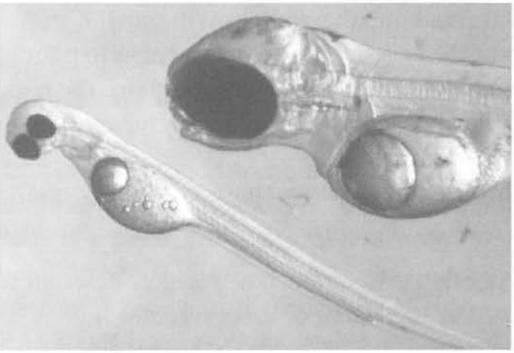

Figure 11.20 A newly hatched bloater larva (9.8 mm in length) in comparison to a newly hatched rainbow smelt larva (4.4 mm in length). The differences in size and development are pronounced, even though smelt are even larger at hatching than about half of all fishes.

functional response relationship (attack constant and handling time), whereas the effect of species was not significant (Miller *et al.* 1992). Similarly, body size explained 72–78% of the variation in measures of visual ability critical for foraging (histological acuity, reactive distance, visual angle), while species did not have a significant effect (Miller *et al.* 1993).

In contrast, both size and species significantly affected swimming speed and the distance from which larvae initiated attacks on prey. Capture success was not closely related to absolute size, but was more dependent on the predator–prey size ratio. In longer term experiments with these same three species, Benjamin Letcher and colleagues (1997) noted that species had a significant effect on ingestion and growth rates, especially as larva size increased and morphologies diverged.

While species effects were evident in some of these traits, and would surely be more important in some other species, these experiments confirmed the general importance of body size in governing the dynamics of fish early life history across species. These results from early life-history studies on Great Lakes fishes have provided an enduring framework for current and future investigations of larval fish ecology and population dynamics.

11.13 Environment matters too

Most of the examples presented so far have focused on the importance of biotic interactions, but environmental conditions also play an important role in determining recruitment for many Great Lakes species. Unlike bloaters, which deposit their eggs in relatively stable hypolimnetic conditions, many species spawn in shallower nearshore or riverine environments that are much more susceptible to changes in physical conditions.

In the early 1980s, William Taylor published several studies with his students and colleagues (for example, Taylor *et al.* 1987, Freeberg *et al.* 1990, Brown *et al.* 1993) that explored how the highly variable recruitment of lake whitefish is affected by the characteristics of the adult stock (mainly spawning biomass) as well as events during egg incubation and larva development. Lake whitefish spawn in late November, depositing most of their eggs in shallow water (<3 m deep), where they incubate for about 4 months. Taylor's group found that egg survival was nine times higher during harsh winters when the spawning grounds were covered by ice, than in warmer, ice-free years when the eggs were exposed to wind and wave action throughout the winter. Without the protection of the ice cover, mechanical destruction of the eggs and movement of eggs to poor incubation habitat (sand and muck) resulted in higher mortality. Following hatching, the importance of biotic factors increased. Larval survival was strongly dependent on the availability of intermediate sized copepods during the first 6 weeks of life.

Thus, final recruitment strength of lake whitefish depended on the integrated outcome of three main processes:

(1) the magnitude of egg deposition, which was largely determined by spawning biomass;
(2) egg survival, dictated by the extent of ice cover; and
(3) larval survival, which varied with the ratio of zooplankton densities to larval densities.

Recruitment models incorporating both abiotic and biotic factors explained about 60% of the variation in lake whitefish recruitment, compared to only about 10–35% for traditional stock–recruitment relationships. Although physical factors such as climatic conditions cannot be controlled, their impacts on year-class strength can be predicted, and used in making stock and harvest management decisions.

Joseph Mion and colleagues (1998) used the characteristics of survivors approach to evaluate the importance of river discharge in driving the recruitment variability of Lake Erie walleye. They hypothesized that high discharge in the rivers where walleye spawn would result in strong recruitment by reducing the residence time of larvae in the food-poor riverine environment and transporting them quickly to more productive nursery areas in the lake. They sampled newly hatched larvae at upstream sites to estimate daily larval production, and compared the temporal pattern of hatching to the hatching dates of surviving larvae (determined from otoliths) collected at mid- and downstream sites. The hatching-date distributions of surviving walleye larvae were markedly different from the temporal patterns of larval production; 75–84% of all survivors came from brief, discrete periods (4–7 days) of high survival during the hatching season. Contrary to their initial hypothesis, Mion and his colleagues found a dramatic and unexpected negative relationship between larval survival and river discharge. They attributed this negative effect to increased suspended sediment loads during high, turbulent discharge, which can suffocate and physically damage fragile, newly hatched larvae. Indeed, torn and abraded larvae were common in their upstream samples during high flows.

Low flow is necessary, but not sufficient, for larval walleye survival. The rate of seasonal warming and variable patterns of zooplankton availability combine to determine whether larvae starve or grow, and other fishes moving into the river to spawn create a predatory gauntlet for late hatching larvae. Thus, the timing of storms (high discharge events), water temperature changes, zooplankton blooms, and periods of high predation risk all interact to determine periods of high and low larval survival (Figure 11.21). Interestingly, the same suite of factors, including physical damage from wave action during storms, appears to govern survival of walleye spawned on open lake reefs, resulting in similar patterns of survival for river-spawned and lake-spawned walleye (Roseman *et al.* 1996). These results suggest that the increased storm frequency and intensity, an expected consequence of global warming, may cause a general decline in Lake Erie walleye recruitment. However, improving land use practices to reduce water runoff rates and sediment input can improve conditions for larval walleye survival (Mion *et al.* 1998).

Just as deforestation, dams, and other historical changes in the Great Lakes watershed had major abiotic impacts on spawning habitats in the lakes and their tributaries, current efforts to improve watersheds are having important effects on recruitment of fishes in the Great Lakes. For example, increasing numbers of young lake sturgeon (*Acipenser fulvescens*) are being observed in the Manistee and Muskegon Rivers in Michigan, after changes were implemented to stabilize flows on those rivers.

The effects of such changes are not always anticipated, however. Improvements in water quality due to better pollution controls, and reduced stream temperatures resulting from reforestation of riparian zones, have had the unintended consequence of turning many streams that had been unsuitable into excellent spawning habitat for lampreys. Due to the increase in the number of lamprey spawning streams, and the fact that some of them are too large to treat effectively with TFM, the job of lamprey control has become increasingly difficult. Similarly, stream improvements are making many Great Lakes tributaries suitable

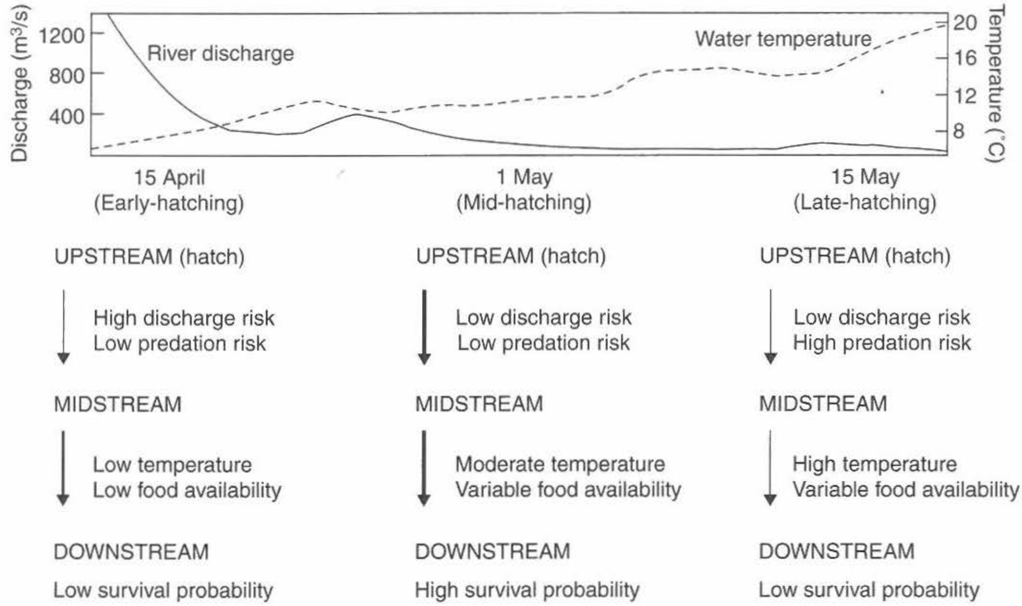

Figure 11.21 Conceptual model of generalized trends in river discharge and water temperature (plot shows data from the Maumee River, 1995) during the larval walleye hatch, coupled with the spatio-temporal influence of river discharge, predation, water temperature, and zooplankton density on survival of larval walleye during river out-migration. Interactions between time of hatching (early-, mid-, and late-hatching) and river location (up-, mid-, and downstream) largely determine which mechanisms are most important for determining larval survival. Arrows indicate movement between sites of larvae hatched during different periods (thicker arrows indicate greater relative probability of larval survival). Factors influencing larval survival at that location are listed next to each arrow. (From Mion *et al.* 1998.)

spawning habitat for the exotic salmonids that were stocked to control alewife populations. Initially, these predator populations were maintained exclusively by stocking. As flows have been stabilized at hydropower dams on many streams, particularly in Michigan, natural reproduction by chinook salmon has increased to the point that natural spawning accounts for more than 30% of the smolts entering the lake. While this change may substantially reduce hatchery costs, it is also greatly reducing the extent to which fishery managers can regulate salmonid populations. When reproduction was controlled artificially, managers could manipulate predator populations in response to changes in the prey base or the multi-billion-dollar sport fishery. This flexibility is being lost. Landscape-scale changes will continue to affect the Great Lakes fisheries and how they must be managed, and many of those effects will be mediated by dynamics that occur during the early life of fishes.

11.14 Summary

The biological communities of the Laurentian Great Lakes have undergone frequent and dramatic changes over the last 200 years, largely due to past and ongoing human impacts.

Over the last several decades, our knowledge of early life processes has become increasingly important to understanding and managing fish populations in these dynamic systems. Efforts to restore Great Lakes fisheries depended initially on finding a way to reduce the abundance of exotic sea lampreys. Knowledge of sea lamprey early life history allowed biologists to identify a vulnerable stage in their ontogeny and develop a chemical control method that eventually brought the lamprey population under control. Despite lamprey reductions and an aggressive stocking program, natural reproduction of lake trout remains very limited. This failure may be due to EMS, a vitamin deficiency that results in high larval mortality because of a lack of thiamine in alewives, the primary prey of lake trout. Other factors during early life stages, such as predation on eggs and larvae, may also be important.

The proliferation of alewives following the decimation of piscivore populations resulted in the dramatic decline and even extinction of several native planktivore species. Initially these impacts were attributed to competitive interactions with alewives, but later research revealed that alewife predation on pelagic eggs and larvae was also a major factor. Because the way species interact (through competition and predation) can change markedly as they grow, events occurring at all ontogenetic stages must be considered in order to fully understand population dynamics.

The discovery of daily growth increments in the otoliths of larval fishes made possible development of the characteristics of survivors approach, which uses the unique characteristics of surviving larvae to suggest which of many potential mechanisms are important in determining survival. Application of this approach to the decline of Lake Michigan bloaters in the 1970s suggested that size-dependent predation by alewives during the first few weeks of life was controlling bloater recruitment, and subsequent lab experiments supported this conclusion.

Our experience studying bloater recruitment dynamics suggested that body size might provide a general explanation for some of the differences among species in the mechanisms controlling survival of larval fishes. A review of published data supported this notion, and lab experiments with three Great Lakes species (bloater, alewife and yellow perch) demonstrated that, at least for these three species, body size explained much more variation in the outcome of most (but not all) processes affecting survival than did species.

While biotic interactions likely influence survival of most larval fishes, some species are strongly influenced by abiotic conditions. Recruitment of Great Lakes fishes that spawn in shallow, nearshore areas, such as lake whitefish, or in tributary streams, such as walleye, can be strongly affected by physical factors such as ice cover, frequency of storms, water temperatures, and suspended sediment, as well as by biological factors such as food availability and predation. Physical conditions in the Great Lakes and their tributaries are being modified by land use in the watershed, with substantial and often unanticipated consequences for fish populations. For every species, multiple mechanisms interact to determine survival and recruitment, and must be considered together, rather than in isolation, to understand and manage fish populations.

As the examples presented here illustrate, early life-history studies have become a prominent part of Great Lakes fishery research and management in recent decades. Fishery scientists have recognized that the dynamics of adult populations and communities are determined in large part by events and interactions that occur early in ontogeny.

This change in perspective is shaping Great Lakes management decisions from lamprey control to habitat and harvest management. At the same time, studies in the Great Lakes have contributed substantially to our understanding of the important processes affecting survival of fish early life stages in general.

Understanding Conservation Issues of the Danube River

Hubert Keckeis and Fritz Schiemer

11.15 The river and its fish fauna

11.15.1 Geomorphology and longitudinal zonation of the Danube River

The Danube River is the second largest river in Europe, with a drainage area of 805 000 km^2, a length of approximately 2850 km, and a discharge of 6450 m^3 s^{-1} at its mouth. From its source in Germany to its mouth in the Black Sea in Romania, it crosses nine countries (Germany, Austria, Slovakia, Hungary, Croatia, Serbia, Bulgaria, Romania, and Ukraine), representing a large variety of landscapes and climates.

Geomorphological conditions define three distinct sections of the river. The upper section (river 2850–1750 km) ranges from Germany to the border of Austria and Slovakia and has an average slope of 40 cm km^{-1}, with a high bedload-transport capacity. Before regulation, the morphology of the river in this section alternated between canyons with narrow riparian zones – where the river breaks through massive rocky layers – and braided alluvial sections with many side arms and backwaters in large floodplain areas. This was especially true in the plains in the eastern part of Austria. The middle section is characterized by a drastic reduction in the slope (6 cm km^{-1}) and lower bedload-transport capacity. This section is separated from the lower section (river 940–0 km) by a 100-km-long cataract (the "Iron Gate"), where the river cuts through the Carpathian Mountains. In the lower Danube River, the average slope is 3.9 cm km^{-1} and the deposition of suspended solids increases significantly.

11.15.2 Biogeographical aspects

The fish fauna of the Danube River is the richest of any European river, with more than 100 species from 23 families (Busnita 1967, Bacalbaşa-Dobrovici 1989). The fish fauna is dominated by Cyprinidae (39 species), followed by Percidae (11), Gobiidae (11), Cobitidae (8), Salmonidae (7) and Acipenseridae (6). There is a clear succession of species associations along the longitudinal course of the river (Bacalbaşa-Dobrovici 1989). The species richness is due to the unique direction of flow of the Danube River. It flows from west to east, which leads to a significant role for it as a biocorridor, connecting the Ponto-Caspic and Central Asian areas in the east with the high mountain alpine regions in the west. The aquatic fauna is sharply delimited against that of Siberia and tropical Africa,