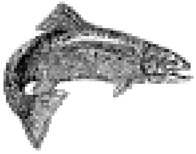
Chapter 9



Ecological Factors Affecting the Sustainability of Chinook and Coho Salmon Populations in the Great Lakes, Especially Lake Michigan

Michael J. Hansen and Mark E. Holey

Introduction

Pacific salmon are exotic species to the Great Lakes and their abundance has been largely driven by stocking, which leads to a different perspective on their ecology than is true elsewhere in their range (Kocik and Jones 1999). Further, salmon stocking programs have tended to focus on chinook salmon *Oncorhynchus tshawytscha* and coho salmon *Oncorhynchus kisutch*, which has led to fisheries largely dependent on these two species. Finally, salmon stocking in the Great Lakes was begun in Lake Michigan, and more salmon have been stocked in Lake Michigan than elsewhere in the Great Lakes basin. As a result, much of the study of salmon ecology has been pursued in Lake Michigan, and more of the salmon story has unfolded there than in the other lakes. For these reasons, we focus our description of salmon ecology (survival, growth and reproduction) on chinook and coho salmon in Lake Michigan, with comparisons to the other lakes where information is available. We believe that the ecology of chinook and coho salmon in Lake Michigan provides a reasonable example for the rest of the Great Lakes basin that nicely compliments the recent review by Kocik and Jones (1999).

History

The species composition of fish communities in the Great Lakes was relatively stable prior to the period of European settlement (Smith 1968). The native species complex of the Great Lakes was composed of top predators, lake trout *Salvelinus namaycush* and burbot *Lota lota*, and their prey, deepwater ciscos *Coregonus johannae*, which had evolved relatively quickly into morphologically diverse species flocks, following the Wisconsin glaciation (Smith 1968). Following settlement, until 1940, the native species complex was changed by the replacement of large, old individuals by small, young individuals of the same species (Smith 1968). Stream spawning runs of lake trout and most other species were likely eliminated prior to the period of fishery records (Smith 1968).

Native fish communities in the Great Lakes changed quickly and dramatically in the mid-1900s (Smith 1968). In response to excessive fishery exploitation, lake trout stocks collapsed sequentially during 1935–1947 in Lake Huron (a decade), 1943–1949 in Lake Michigan (a half decade), and 1950–1960 in Lake Superior (a decade) (Hansen 1999). The top predator in each of the upper Great Lakes had, therefore, been removed by the midpoint of the 20th century (Smith 1968). Sea lamprey *Petromyzon marinus*, which invaded the upper Great Lakes as lake trout stocks were collapsing, turned to large deepwater ciscos as their favored prey, which in turn enabled the smallest cisco, the bloater *Coregonus hoyi*, to increase in abundance (Smith 1968).

In the absence of top predators, alewife *Alosa pseudoharengus* invaded the upper Great Lakes, and in Lakes Michigan and Huron, exploded in abundance in only a few years, drastically altering the remaining native species complex (Smith 1970). Alewife, a schooling spring-spawning pelagic planktivore, dominated fish biomass and appeared able to suppress most native species, such as bloater and yellow perch *Perca flavescens*, through predation on pelagic larvae (Smith 1970; Crowder 1980; Jude and Tesar 1985; Eck and Wells 1987). Fish species in the Great Lakes had evolved in the absence of a schooling pelagic planktivore that spawned in spring, like the alewife, so they were ill equipped to survive in the face of such a species. Consequently, all remaining native species in Lakes Huron and Michigan declined to low levels by the 1960s. By 1967, alewife composed 90% of fish biomass in Lake Michigan (Brown 1972).

Part of the rationale for introducing coho salmon *Oncorhynchus kisutch* into the Great Lakes in the 1960s was to control abundant alewife (Tody and Tanner 1966; Tanner and Tody, this volume):

> "It can be speculated that the Great Lakes may offer a unique environment to the coho salmon. These lakes are sufficiently large to offer a sea to the anadromous fish except for the dissolved mineral content. The

> abundance of alewife, chubs, and smelt should offer the adult fish a sufficient food supply for rapid growth."

Though it has been mostly forgotten, one of the original goals stated by Tody and Tanner (1966; Tanner and Tody, this volume) was to establish Pacific salmon as self-sustaining species in the Great Lakes:

> "The coho may reproduce readily in fresh water. The lack of vertebrate predators in the Great Lakes as compared with the Pacific Ocean may lead to a relatively high rate of survival. Therefore, it is certainly possible that success may be achieved in establishing the coho with just the first life cycle."

Stocking

Though salmon had been stocked as early as the 1800s, survival of these early plantings was low and failed to sustain fisheries (Parsons 1973; Kocik and Jones 1999). In contrast, survival of stocked coho salmon and chinook salmon in the Great Lakes was very high in the 1960s, and fueled unprecedented growth of a sport fishery, especially in Lake Michigan (Kocik and Jones 1999). In 1972, Stanford Smith noted that ecosystem restoration must focus on improved land use, elimination of pollutants, and fish population restoration (Smith 1972):

> "Measures to reduce alewives should be intensified by introduction of greater numbers of large predators such as lake trout and salmon. The most critical requirement while alewife populations are being reduced is a concurrent restoration of the small native forage species. This transition will require several decades and will require careful measurement and close regulation of the kinds and amounts of fish introduced or removed from the lakes."

The Michigan Department of Natural Resources first introduced coho and chinook salmon into the Great Lakes Basin, in Lake Michigan, in 1966 and 1967, respectively (Keller et al. 1990). The first coho salmon were from fall runs in the lower Columbia and Cascade rivers, Oregon and the Toutle River, Washington, and the first chinook salmon were from fall runs in the lower Columbia River (Tule strain), Oregon and the Green River, Washington (Keller et al. 1990). Within three years, the Michigan Department of Natural Resources was supplying eggs of both coho and chinook salmon to other Great Lakes fishery management agencies, from which some developed their own stocking programs. Introductions of other strains of coho and chinook salmon have been attempted, but most hatchery production of both species in the Great Lakes basin stems from the original strains obtained by the State of Michigan.

Chinook salmon stocking has exceeded basin-wide stockings of all salmon since the 1960s. For example, chinook salmon stockings averaged 53% of all salmon stockings (chinook salmon; coho salmon; and steelhead *Oncorhynchus mykiss*) in all of the Great Lakes during 1983–1993 (Figure 1). Stocking programs in the Great Lakes quickly evolved to take advantage of the fact that chinook salmon smolt at a smaller size and younger age than coho salmon. Production systems could therefore produce many more chinook salmon than other species. Chinook salmon also reached larger sizes than other trout and salmon species, so anglers preferred them. Consequently, chinook salmon stocking grew steadily throughout the 1970s and 1980s, whereas coho salmon stocking was relatively stable after 1970.

Stocking of salmon has been substantially greater in Lake Michigan than in any other Great Lake since the 1960s. For example, average stockings of salmon in Lake Michigan during 1983–1993 (11 million) were 1.8–3.9 times greater than in any of the other Great Lakes (Figure 1). However, stocking rates of salmon per unit of surface area were greater in Lake

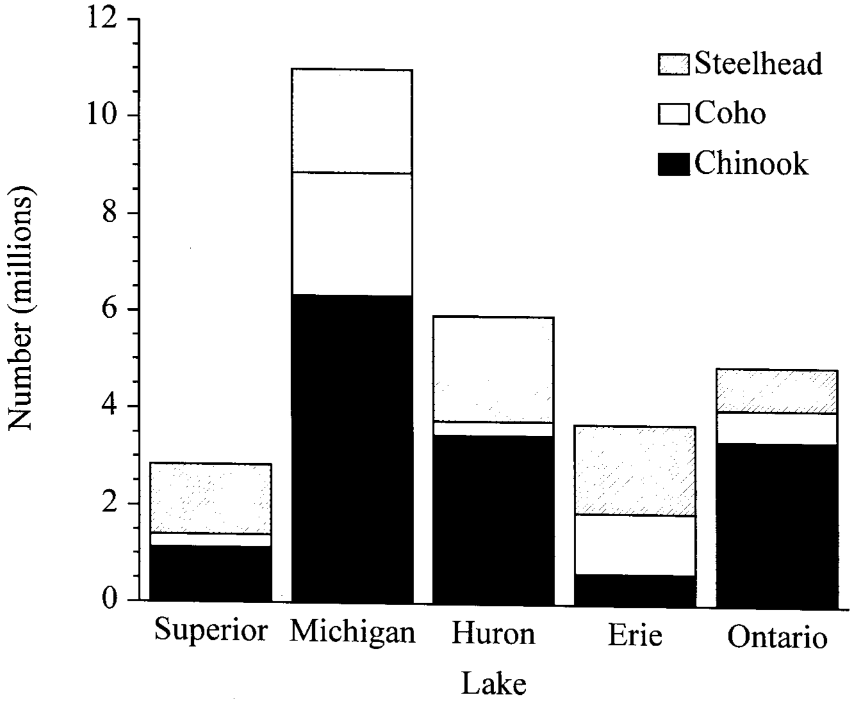


Figure 1. Average numbers of chinook salmon, coho salmon, and steelhead stocked in each Great Lake during 1983–1993 (data from Kocik and Jones 1999).

Ontario (250/km^2) than in Lake Michigan (190/km^2) during 1983–1993 (Kocik and Jones 1999). Stocking of salmon has been greatest in Lake Michigan, Lake Huron, and Lake Ontario, largely because of the predominance of alewife as a pelagic prey species (O'Gorman and Stewart 1999) and because nearby human population centers fueled recreational fishing effort (Bence and Smith 1999). Lake Superior was generally too cold to support high densities of alewife (O'Gorman and Stewart 1999) and Lake Erie already supported a highly productive coolwater fishery for walleye *Stizostedion vitreum* and yellow perch (Koonce et al. 1999).

Numbers of chinook salmon stocked in Lake Michigan greatly exceeded total numbers of coho salmon and steelhead stocked since 1969 because a sport fishery for chinook salmon quickly developed to utilize this species. For example, in the Wisconsin waters of Lake Michigan, harvest and stocking of chinook salmon exceeded harvest and stocking of both coho salmon and steelhead during 1980–1987 (Figure 2). Further, the ratio of annual harvest to the number stocked was much higher for chinook salmon than for either coho salmon or steelhead. The fishery quickly became known for the quality of chinook salmon fishing. Many factors were likely involved in the strength of interest in chinook salmon fishing, but the fighting ability and larger average size of chinook salmon, compared with the other species, were undoubtedly among the most important qualities that gained angler interest.

Abundance

Harvest rates of chinook salmon in Lake Michigan grew in concert with angling effort throughout the 1970s and early 1980s, while harvest rates of coho salmon varied, without trend, during the same period. For example, in Wisconsin waters of Lake Michigan, chinook salmon harvest rates increased directly with angling effort, while coho salmon harvest rates failed to increase (Figure 3). This suggests that angling effort in Lake Michigan increased with salmon abundance, which was being driven largely by chinook salmon stocking, rather than coho salmon stocking. As a result, harvest rates of chinook salmon in Lake Michigan were generally higher than for other species of trout and salmon by the mid-1970s, which suggests that chinook salmon density was higher than other species of trout and salmon at that time.

By 1985, the harvest of chinook salmon from Wisconsin's waters of Lake Michigan exceeded that from any of the other Great Lakes (Figure 4). Further, the magnitude of the chinook salmon harvest in Lake Michigan was beyond anything produced in the lake's recorded history (Figure 5). The exceptional production of chinook salmon in the 1980s seemed to indicate that this species had fulfilled the role that had been predicted by

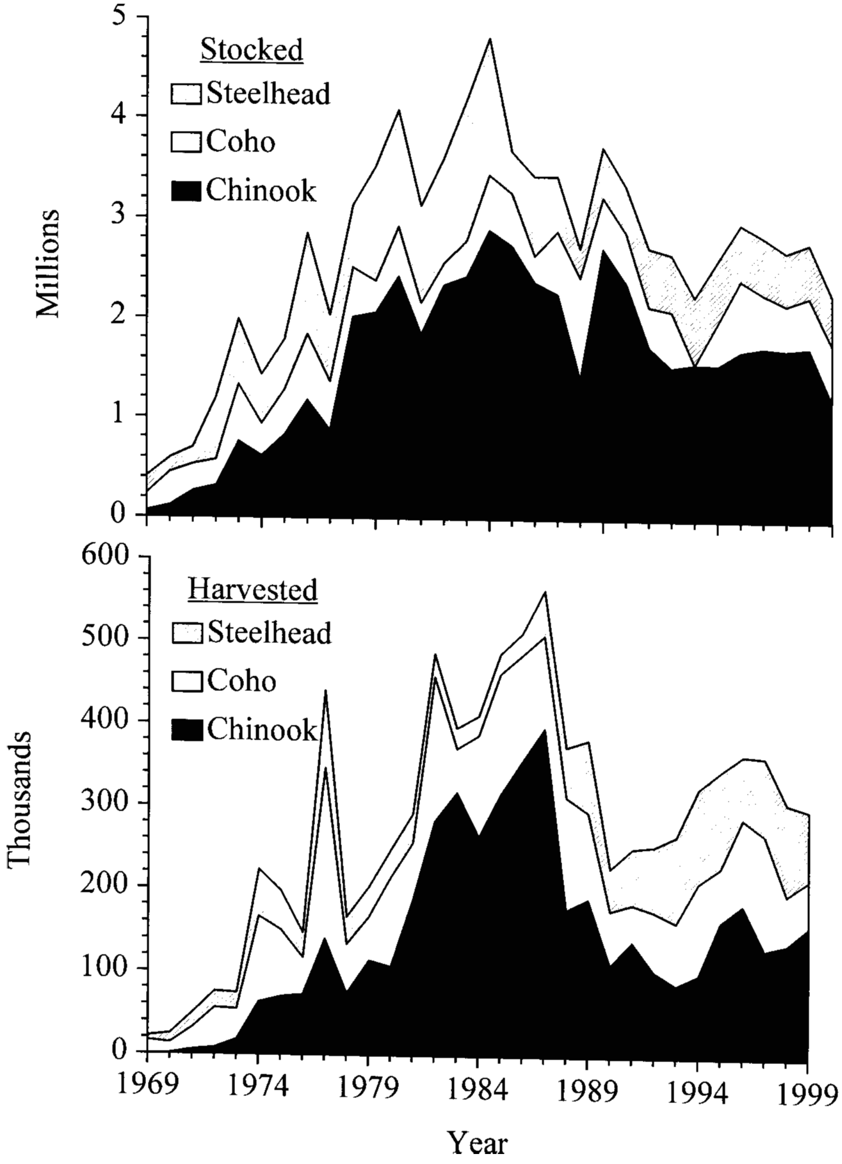


Figure 2. Numbers of chinook salmon, coho salmon, and other salmonines stocked (upper panel) and harvested (lower panel) in the Wisconsin waters of Lake Michigan during 1969–1999 (updated from Hansen et al. 1990, 1991).

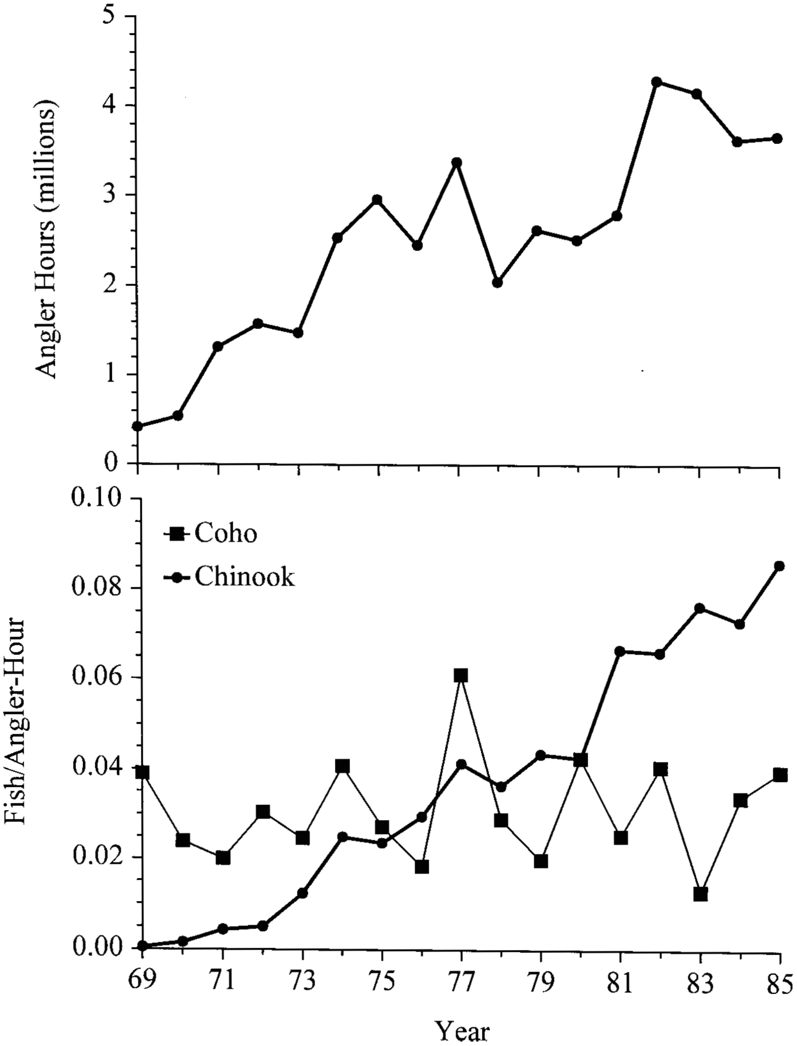


Figure 3. Angler hours (upper panel) and harvest rates (lower panel) for chinook and coho salmon in the Wisconsin waters of Lake Michigan during 1969–1985 (from Hansen et al. 1990, 1991).

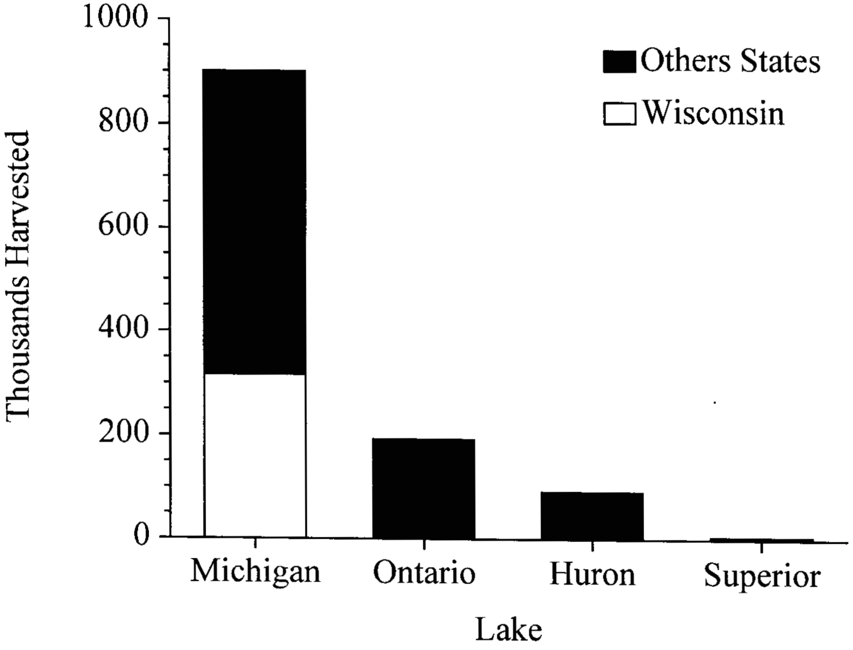


Figure 4. Numbers of chinook salmon harvested from Lakes Michigan, Ontario, Huron, and Superior in 1985 (from Hansen et al. 1991).

Tody and Tanner (1966). Chinook salmon seemed ideally suited to the environment of Lake Michigan that existed after the collapse of the native species, rich with an ideal prey source and free from predators (other than humans). Fishery managers basked in one of the greatest fishery management success stories, but they were ill prepared for the sequence of events that would soon play out.

In 1988, catch rates of chinook salmon in Lake Michigan declined sharply, particularly in Michigan waters (Figure 6). In Michigan waters, chinook salmon catch rates declined 50% from 1987 to 1989 and 85% by 1993. In Wisconsin waters, chinook salmon catch rates declined one year later than in Michigan, and they remained higher than in Michigan. Declining catch rates of chinook salmon in Lake Michigan, in conjunction with reduced effort caused by declining catch rates, were largely responsible for an 80% decline in yield from 1986 to 1990 (Benjamin 1998; Holey et al. 1998; Bence and Smith 1999; Benjamin and Bence, in press a). The decline of chinook salmon stocks in Lake Michigan was nearly as dramatic as the collapse of lake trout stocks 40 years earlier (Figure 5).

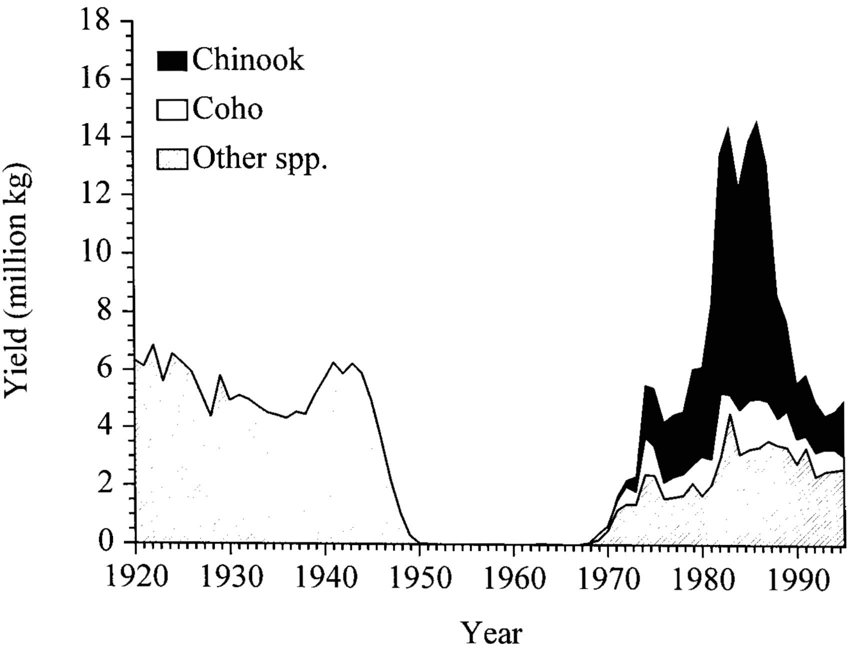


Figure 5. Harvest of chinook salmon, coho salmon, and other salmonines from Lake Michigan during 1920–1995 (from Holey et al. 1998). All harvest prior to 1950 was lake trout.

Survival

Survival of chinook salmon from stocking to harvest was extraordinarily high and independent of stocking density in Lake Michigan during the 1970s and 1980s. For example, in Wisconsin's waters of Lake Michigan, the harvest during 1969–1985 was directly proportional to the number previously stocked (Figure 7), which suggested survival was density independent and averaged 12–13% from stocking to harvest (Hansen 1989; Hansen et al. 1990; 1991). In contrast, survival of chinook salmon from stocking to harvest in most West Coast fisheries was 1% or less (Hansen 1989). The harvest of chinook salmon from Lake Michigan in 1985 reflected this extraordinary survival; more than 900,000 were harvested from 6.0 million stocked three years earlier, a 15% return to the creel (Hansen 1989)!

By the late 1980s, survival changed dramatically, as dead adult chinook salmon appeared along Lake Michigan beaches (Johnson and Hnath 1991),

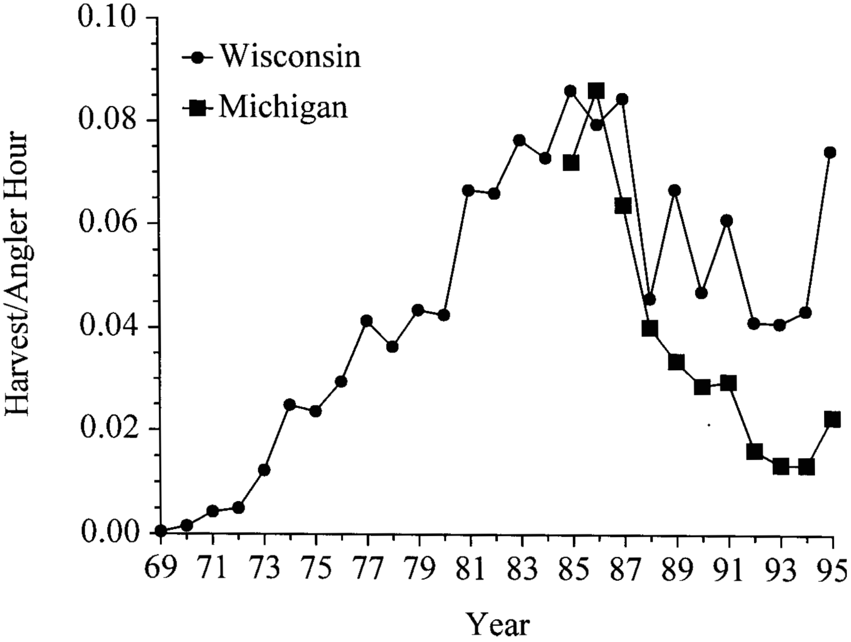


Figure 6. Numbers of chinook salmon harvested per angler-hour from the Michigan and Wisconsin waters of Lake Michigan during 1969–1995 (from Hansen et al. 1990, 1991; Holey et al. 1998).

and the fishery collapsed (Figure 5). After 1985, numbers of chinook salmon caught by angling, in relation to numbers previously stocked in Wisconsin's waters of Lake Michigan, was lower and more variable than before 1985 (Figure 7). Over the entire period 1969–1995, this suggests that survival of chinook salmon was regulated by density-dependent processes in Lake Michigan. Also, changes in survival after 1985 may have been confounded with changes in movement among areas of Lake Michigan, combined with changes in stocking by jurisdictions (Benjamin 1998).

The cause of this change in survival of chinook salmon in Lake Michigan is uncertain but may relate to a change in body condition of adult fish that began in the late 1970s. For example, body condition of chinook salmon in the Wisconsin sport fishery returning to the Strawberry Creek weir declined steadily during the 1970s, then fluctuated erratically during the 1980s and early 1990s (Figure 8). The reduced body condition of adult chinook salmon in Lake Michigan may have made them susceptible to bacterial kidney disease (BKD), which first appeared in spawning adults in 1986 and became prevalent thereafter. The incidence of BKD in chinook salmon

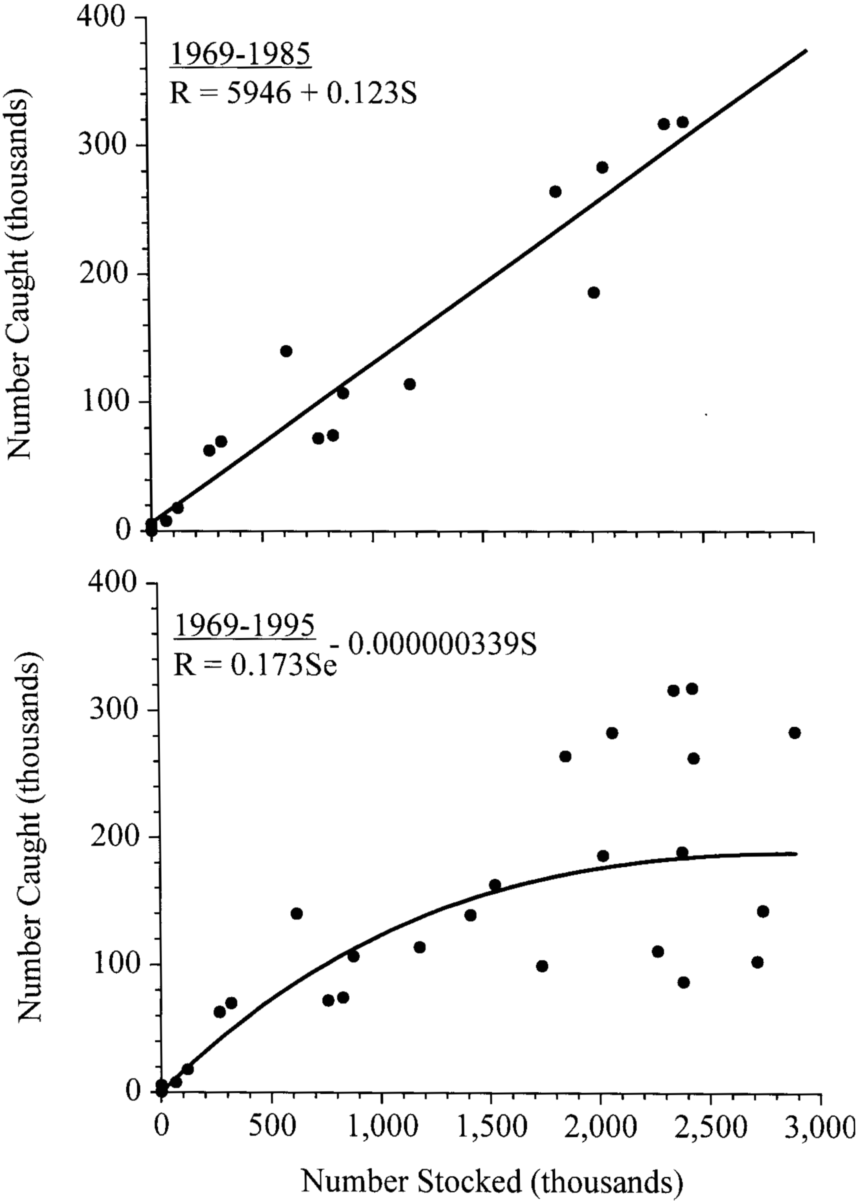


Figure 7. Number of chinook salmon caught versus the number previously stocked in the Wisconsin waters of Lake Michigan during 1969–1985 (upper panel; from Hansen 1989) and 1969–1995 (lower panel).

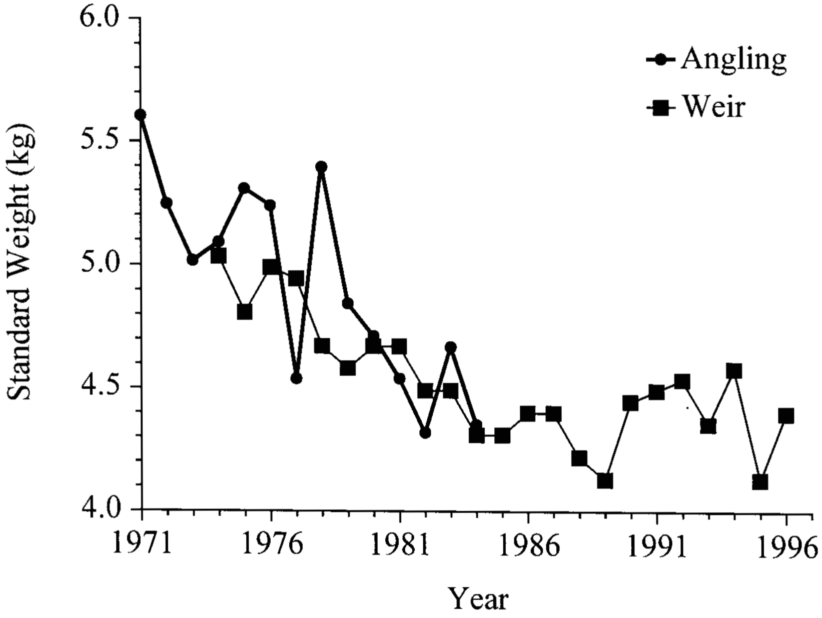


Figure 8. Predicted weight of an average length (762-mm TL) chinook salmon (standard weight) caught by anglers and returning to the Strawberry Creek weir in the Wisconsin waters of Lake Michigan during 1971–1997 (from Hansen 1986; Peeters and Royseck 1997).

returning to the Strawberry Creek weir in Wisconsin increased from 0% before 1986 to 67% in 1988, then ranged between 10% and 28% during 1989–1992 (Holey et al. 1998). In Michigan, the incidence of BKD in chinook salmon returning to the Little Manistee River weir was even higher, ranging between 53% and 100% during 1986–1991 (Holey et al. 1998). As a consequence, the rate of natural mortality increased for chinook salmon of ages 2-5 in Lake Michigan, based on statistical catch-at-age analysis (Benjamin and Bence, in press b).

The predominant age of chinook salmon returning to spawn shifted from age 3 prior to 1990 to age 2 after 1990 in Lake Michigan (Benjamin and Bence, in press b). Total annual mortality of age 2-3 chinook salmon increased sharply during 1986–1991, largely through an increase in natural mortality, then remained high through 1995 (Benjamin and Bence, in press b). During the same period, returns of age-2 chinook salmon to the Strawberry Creek weir in Wisconsin increased after 1988 to levels more typical of age-3 chinook salmon in previous years (Figure 9). By 1991, returns of age-1 chinook salmon increased to levels more typical of age-2 chinook salmon

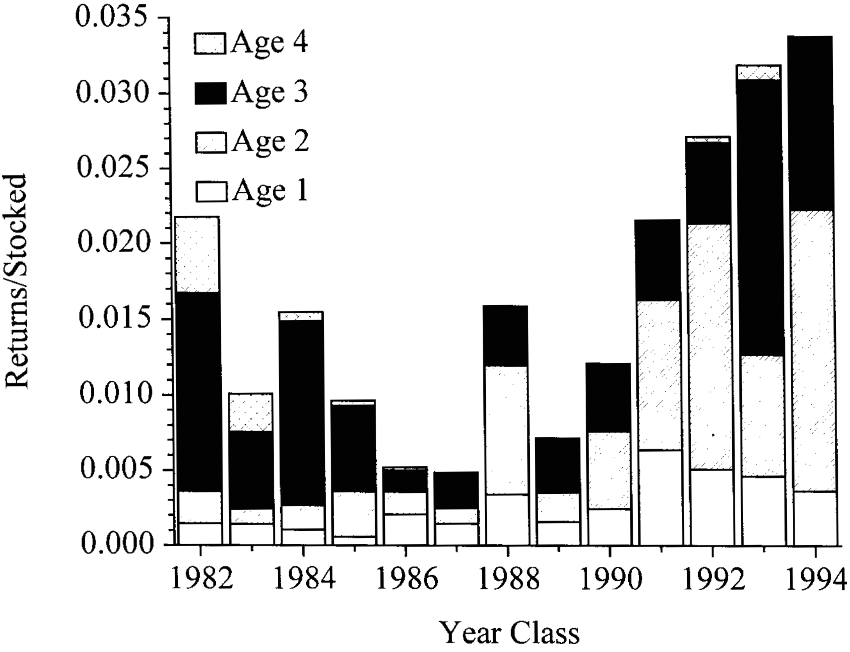


Figure 9. Rate of return of the 1982–1994 year classes of coded-wire-tagged chinook salmon stocked in and returned to the Strawberry Creek weir in the Wisconsin waters of Lake Michigan (from Peeters and Royseck 1997).

in previous years. By the time the 1991 year-class returned at age 1 in 1992, age 2 in 1993, and age 3 in 1994, the age structure of the spawning run had shifted sharply downward. Total returns of the 1991 year-class were 50% higher than the 1984 year-class, the last year-class to be fully recruited prior to the 1988 die-off of adults.

Growth and Diet

Size at age of chinook salmon fluctuated inversely with population density during the 1980s and 1990s in Lake Michigan (Clark 1996). For example, mean length and weight of age-2 and age-3 male chinook salmon returning to spawn in Strawberry Creek, Wisconsin, increased during 1983–1997, as catch rates in the sport fishery were declining, while age-1 fish did not increase in either mean length or weight (Figure 10). Similarly, in Michigan waters of Lake Michigan, mean length and weight of age 2-4 chinook salmon increased from 1983 to 1986 (before BKD) to 1990–1993 (after

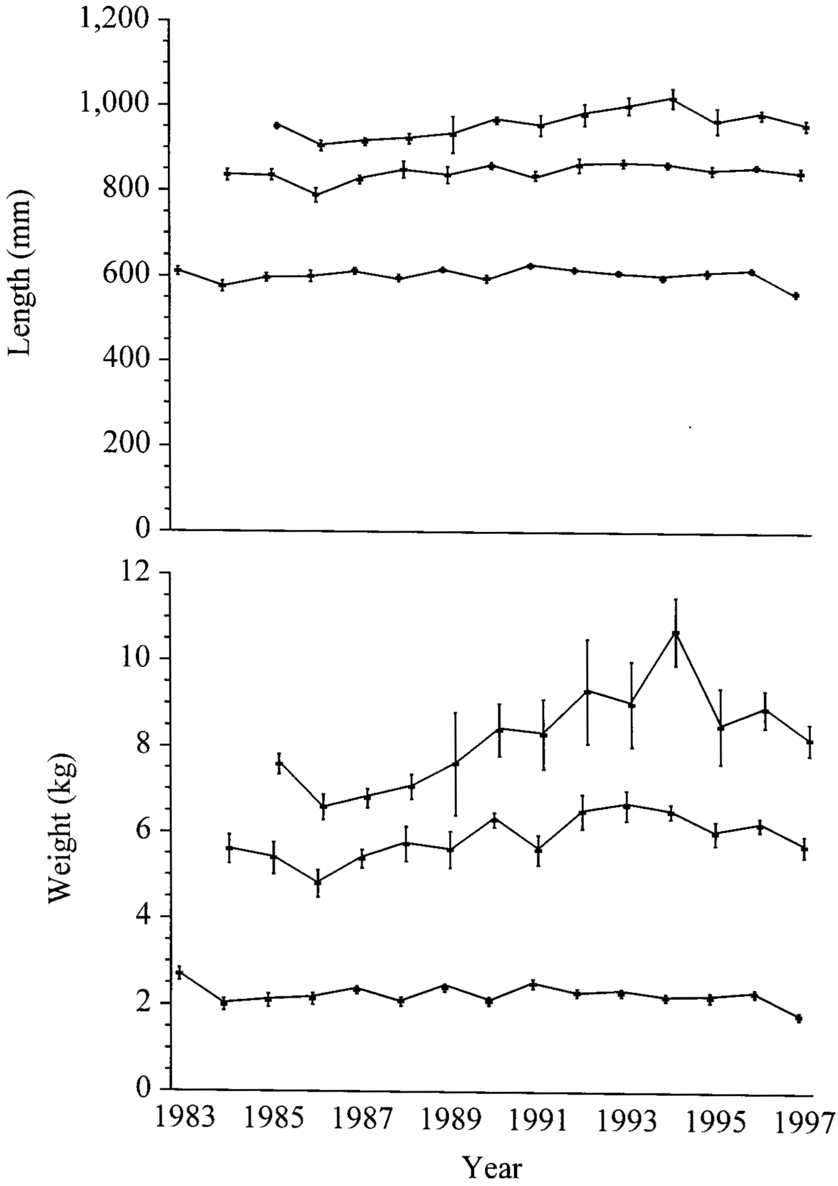


Figure 10. Mean length (upper panel) and weight (lower panel) of coded-wire-tagged male chinook salmon stocked in and returned to the Strawberry Creek weir in the Wisconsin waters of Lake Michigan during 1984–1997 (from Peeters and Royseck 1997). Error bars depict two standard errors of the mean, above and below the mean length and weight.

BKD), whereas mean length and weight of age-1 chinook salmon did not change significantly between the same periods (Wesley 1996). These patterns in size at age suggest that growth of chinook salmon in Lake Michigan was strongly density dependent; adult chinook salmon were more abundant and grew slower before BKD than after BKD (Clark 1996).

Chinook salmon consume primarily adult alewife in the Great Lakes, even though other prey species have been more abundant during some periods. For example, in Lake Michigan, adult chinook salmon consumed primarily adult alewife during 1986–1995 (Elliott 1993; Rybicki and Clapp 1996; Holey et al. 1998). However, age 2-3 chinook salmon consumed dramatically fewer alewife per predator in 1986, just before the BKD mortality, than during 1994–1995, several years after the BKD mortality (Figure 11). In contrast, bloaters were a significant portion of the diets of only age-2 chinook salmon during 1986 (Figure 11) and salmon 38–57 cm in 1991–1993 (Rybicki and Clapp 1996), even though bloaters were 5–15 times more abundant than alewives at that time (Fleischer et al. 2000).

The relatively low occurrence of bloater in chinook salmon diet, espe-

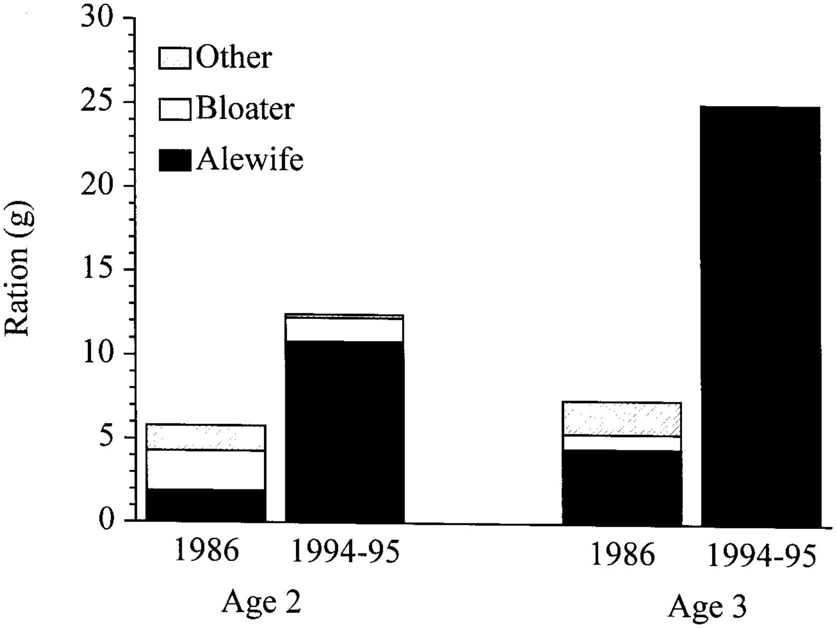


Figure 11. Index of ration of alewife and other prey types (average weight per stomach) for age-2 and age-3 chinook salmon caught by Michigan anglers in southeastern Lake Michigan in 1986 and 1994–1995 (from Holey et al. 1998).

cially large salmon, in relation to bloater abundance, suggests limited habitat overlap between salmon and bloater, especially adult bloater. Bloaters were a significant diet item for chinook salmon in Lake Michigan primarily when juvenile bloaters were available during the mid-1980s and early 1990s, even though chinook salmon are large enough to eat adult bloaters and adult bloaters were abundant throughout the 1980s and 1990s. Juvenile bloaters were sparse during the mid-1990s because of a decrease in recruitment (Fleischer et al. 2000). Juvenile bloaters are pelagic whereas adult bloaters are benthic (Wells 1966; 1968; Crowder and Crawford 1984), which favors overlap between juvenile bloaters and chinook salmon but not between adult bloaters and chinook salmon. Consequently, the high biomass of adult bloaters in Lake Michigan is largely unavailable to chinook salmon.

Chinook salmon consume more alewife per individual during their lifetime, especially adult alewife, than other trout or salmon species (Figure 12). Chinook salmon exert greater lifetime predation pressure per individual than coho salmon because chinook salmon spend one more year in the lake than coho salmon (Stewart et al. 1981). In contrast, the lifetime predation pressure exerted by chinook salmon is greater than lake trout

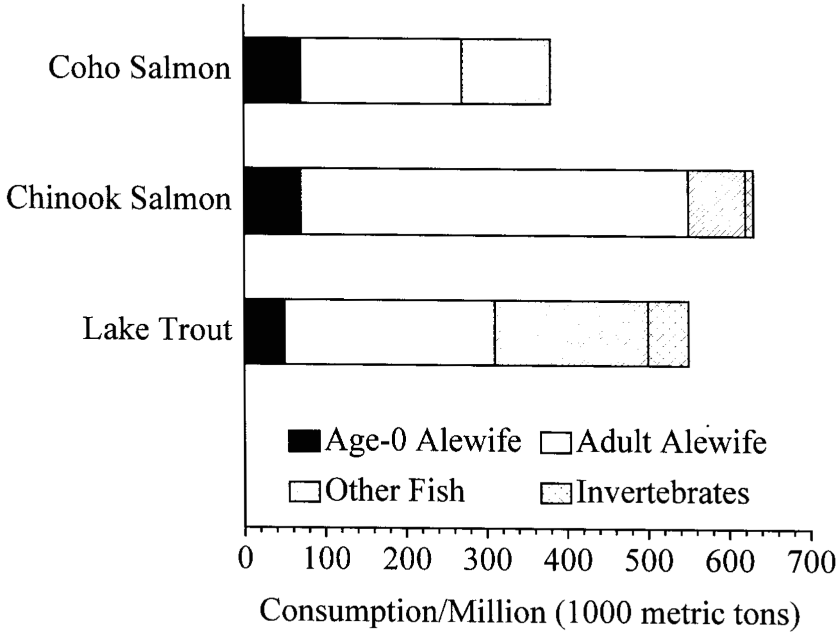


Figure 12. Estimated total consumption of various prey items (per million fish stocked) by coho salmon, chinook salmon, and lake trout in Lake Michigan (from Stewart et al. 1981).

because chinook salmon achieve adult size (8–10 kg) in only four years, whereas lake trout achieve a similar adult size in six to eight years (Stewart et al. 1981). Because chinook salmon require more alewives per individual than other species of trout and salmon, chinook salmon condition and growth is more responsive than other trout and salmon species to short-term changes in alewife abundance (Stewart and Ibarra 1991).

Predation by trout and salmon, in conjunction with severe winters in 1976–1982, suppressed alewife populations in Lake Michigan to low levels by the early 1980s (Figure 13; Stewart et al. 1981; Eck and Brown 1985; Kitchell and Crowder 1986; Eck and Wells 1987; Stewart and Ibarra 1991). After alewife declined in abundance, bloaters rapidly increased in abundance and were predominant by 1983. Abundance of age-0 bloater was inversely related to abundance of age-4-and-older alewife (Figure 14), perhaps through predation on larval bloater by adult alewife (Eck and Wells 1987). By 1987, salmonine predation and commercial fisheries harvested 60% of the available alewife production in Lake Michigan and, consequently,

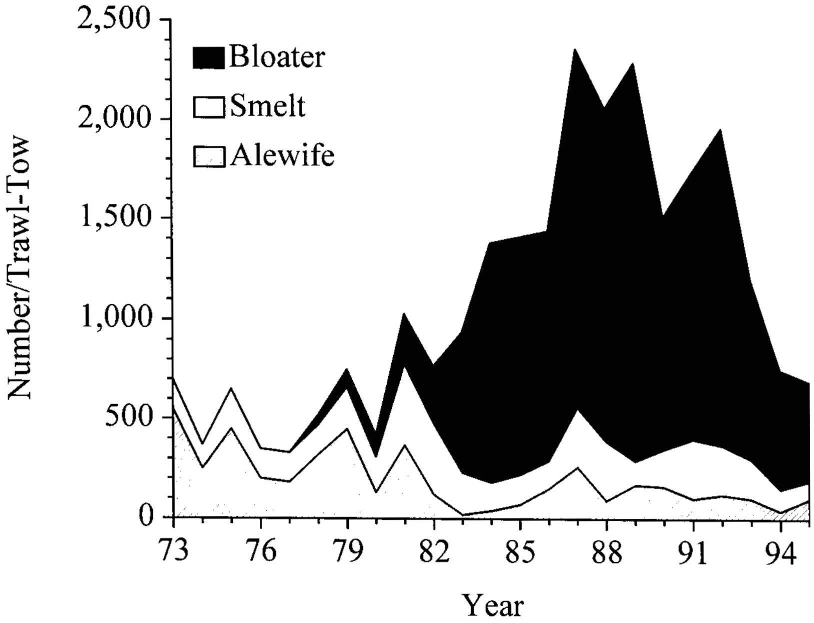


Figure 13. Number of adult alewife, rainbow smelt, and bloater per trawl tow in Lake Michigan during 1973–1995 (from Fleischer et al. 2000).

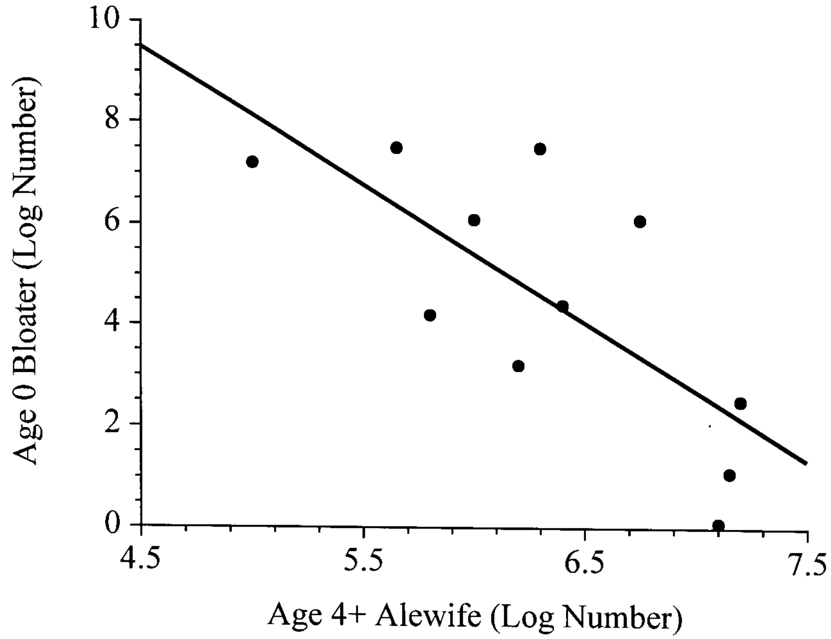


Figure 14. Estimated numbers of age-0 bloater versus estimated number of age-4-and-older alewife in Lake Michigan during 1974–1983 (from Eck and Wells 1987).

may now regulate the alewife population at low, relatively stable levels (Stewart and Ibarra 1991).

Reproduction

Pacific salmon have reproduced in the Great Lakes wherever streams provide suitable spawning and rearing habitat (Kocik and Jones 1999). In Lake Superior, 50–90% of chinook salmon (Peck et al. 1999) and 94% of coho salmon are produced naturally (Peck 1992). In Lake Michigan, wild chinook salmon composed 13% of the total number stocked in 1972 (Carl 1982). In the early 1990s, wild fish composed 27–37% of all chinook salmon caught by anglers in the southeast basin and 45–66% in the northeast basin of Lake Michigan (Hesse 1994; Elliott 1994). The contribution of the 1992–1995 year classes of wild chinook salmon to assessment catches, when all stocked salmon of the same age were marked, ranged from 27.8% to 53.4% at age 2 (Clapp 1998). During 1996–1997, 76–82% of returning adult chinook salmon in the Manistee and Muskegon Rivers were of wild origin (Rutherford et al. 1999). Increased proportions of wild chinook salmon in fisheries and spawning runs is partly caused by increased spawning success and by decreased survival of hatchery-reared fish. Reproduction by coho salmon in the same streams has been measurable (Seelbach 1985) but contributes an unknown fraction to the Lake Michigan fishery. In the other lakes, reproduction by chinook and coho salmon occurs but has not been quantified. Production of wild chinook and coho salmon could be greatly increased from current levels if prime tributary nursery habitats above dams were made accessible to adult salmon via fish ladders or dam removal.

Survival of feral salmon eggs reared in hatcheries under experimental conditions, especially of coho salmon, declined in the 1990s. From the mid-1980s to the mid-1990s, egg mortality during hatchery incubation increased from 20% to 70% for coho salmon and from 10% to 60% for chinook salmon (Marcquenski and Brown 1997; Honeyfield et al. 1998a,b). Egg survival was so poor for coho salmon in Lake Michigan that fishery managers feared there would be too few adult coho salmon returning to spawning weirs to sustain the stocking program. Consequently, management agencies adopted emergency lakewide harvest regulations in 1994 to ensure that enough adult coho salmon returned to spawning weirs.

Low survival of salmon eggs, known as Early Mortality Syndrome (EMS), is related to low concentration of thiamine in the egg, which may be related to thiaminase concentration in predominant prey species eaten by adult salmon during egg development (Honeyfield et al. 1998b). Immersion of coho salmon eggs and fry in thiamine water baths has increased egg and fry survival to preEMS levels (Hornung et al. 1998), and it is now a standard practice in hatcheries that obtain eggs from feral adult salmon in Lake Michigan (Honeyfield et al. 1998b). Low thiamine levels that trigger the onset of EMS may be related to the percentage of alewife and rainbow smelt *Osmerus mordax* in the diet (Honeyfield et al. 1998b). Both alewife and rainbow smelt posses the thiamine-degrading enzyme, thiaminase (Anglesea and Jackson 1985; Ji and Adelman 1998). Alewife have been a major prey of coho and chinook salmon since their successful introduction into Lake Michigan (Elliott 1993; Stewart et al. 1981; Stewart and Ibarra 1991). The increase in EMS in Lake Michigan trout and salmon is more likely the result of a larger ecosystem change in the basin that has changed the nutritional value of alewife. Though the cause of EMS has yet to be described, its occurrence will either prevent further development of wild year classes or add increased variation in salmon spawning success in Lake Michigan and the other Great Lakes.

The Future

Chinook and coho salmon may now be functioning as important members of the fish communities in all five Great Lakes. Both species played major roles as predators in reducing the abundance of alewife in Lake Michigan, which facilitated recovery of native prey species. Sport and commercial fisheries that developed for chinook and coho salmon are popular and in high demand by the public throughout the Great Lakes basin. The ability of chinook and coho salmon to reproduce in many areas of the Great Lakes has led fishery managers to develop management goals that are intended to decrease dependence on hatchery-reared fish in the future. Fish community objectives for Lake Michigan now recognize chinook and coho salmon as naturalized members of the trout and salmon species assemblage and recommend that natural reproduction of all species be enhanced (Eshenroder et al. 1995). Subsequently, stocking objectives for chinook and coho salmon in Lake Michigan have been adopted to reduce salmon biomass, minimize BKD mortality, and promote sustainability of the fishery (Clark 1996).

Chinook and coho salmon survived best in the Great Lakes when alewife were the predominant prey fish, and they became established members of the fish community, but the future of both species is uncertain. During the 1990s in Lake Michigan, chinook salmon suffered high mortality and high prevalence of BKD when alewife no longer predominated in the prey fish community. Chinook salmon are susceptible to BKD (Starliper et al. 1997), which makes them susceptible to high mortality during low prey abundance. In Lakes Huron and Ontario, reduced chinook salmon growth recently occurred in conjunction with reduced alewife abundance, and fishery managers fear a large-scale die-off in the near future in both lakes (Brandt et al. 1996; Johnson et al. 1999). EMS also threatens the sustainability of wild coho salmon in the Great Lakes because coho salmon are susceptible to EMS (Marcquenski and Brown 1997; Honeyfield et al. 1998a,b) and suffer near 100% mortality of their eggs if not treated with thiamine, thereby limiting the ability of coho salmon to establish self-sustaining populations in the Great Lakes.

Despite the uncertainty of the future for chinook and coho salmon in the Great Lakes, we believe both species will continue to contribute to the restoration and stability of Great Lakes fish communities in the foreseeable future, in contrast with conventional wisdom that suggests introduced species do not usually fill valuable roles in ecosystem restoration and stability. Though not native to the Great Lakes, chinook and coho salmon are better adapted to controlling alewives than native Great Lakes predators, which enhances the ecological value of chinook and coho salmon in Great Lakes ecosystems. Stocking chinook and coho salmon has been one of the most effective fishery management tools for controlling alewife abundance, and it also facilitates native species restoration and the development of sustainable predator populations. However, a return to the "good old days" of high chinook and coho salmon abundance is unlikely, even with further increases in chinook and coho salmon stocking and recruitment, because chinook salmon are so vulnerable to low alewife abundance. Species such as rainbow trout and lake trout may be needed to exert a larger portion of the predation pressure in the future should forage populations less dominated by alewife continue to develop in each of the Great Lakes. Research is needed to determine appropriate levels of chinook and coho salmon stocking for maintaining alewife populations at levels that will least affect the development of sustainable predator stocks and native species restoration. In the meantime, chinook and coho salmon will likely sustain sizeable wild populations that are supplemented by stocking, because of their ecological value as biological controllers of alewives and their economic value as a sport fish.

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References

Anglesea, J. D., and A. J. Jackson. 1985. Thiaminase activity in fish silage and moist fish feed. Animal Feed Science and Technology 13:39–46.

Bence, J. R., and K. D. Smith. 1999. An overview of recreational fisheries in the Great Lakes. Pages 259–306 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing.

Benjamin, D. M. 1998. Chinook salmon (*Oncorhynchus tshawytscha*) population dynamics in Lake Michigan, 1985-1996. Master's thesis. Michigan State University, East Lansing.

Benjamin, D. M., and J. R. Bence. In press. a. Spatial, and temporal changes in the Lake Michigan chinook salmon fishery, 1985-1996. Michigan Department of Natural Resources, Fisheries Research Report, Ann Arbor, Michigan.

Benjamin, D. M., and J. R. Bence. In press. b. Statistical catch-at-age analysis of chinook salmon in Lake Michigan, 1985-1996. Michigan Department of Natural Resources, Fisheries Research Report, Ann Arbor, Michigan.

Brandt, S., J. DePinto, M. Hansen, K. Hartman, E. Mills, R. O'Gorman, P. Rand, H. Riessen, L. Rudstam, R Snyder, and D. Stewart. 1996. A review of the current status of Lake Ontario's pelagic fish community: report of the 1996 Lake Ontario technical panel. Great Lakes Research Reviews 2:4–10.

Brown, E. H., Jr. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949-1970. Journal of the Fisheries Research Board of Canada 29:477–500.

Carl, L. M. 1982. Natural reproduction of coho salmon and chinook salmon in some Michigan streams. North American Journal of Fisheries Management 2:375–380.

Clapp, D. F. 1998. Chinook salmon population dynamics in Michigan's waters of the Great Lakes. Michigan Department of Natural Resources, Federal Aid in Sport Fish Restoration Completion Report, Project F-53-R-14-471, Lansing, Michigan.

Clark, R. D., Jr. 1996. Status of chinook salmon in the upper Great Lakes, 1995. Michigan Department of Natural Resources, Fisheries Division, Administrative Report, Lansing, Michigan.

Crowder, L. B., and H. L. Crawford. 1984. Ecological shifts in resources use by bloaters in Lake Michigan. Transactions of the American Fisheries Society 113:694–700.

Crowder, L. B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environmental Biology of Fishes 5:225–233.

Eck, G. W., and E. H. Brown, Jr. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. Canadian Journal of Fisheries and Aquatic Sciences 42:449–454.

Eck, G. W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement 2):53–60.

Elliott, R. F. 1993. Feeding habits of chinook salmon in eastern Lake Michigan. Master's thesis. Michigan State University, East Lansing.

Elliott, R. F. 1994. Early life history of chinook salmon in Lake Michigan. Michigan Department of Natural Resources, Federal Aid in Sport Fish Restoration Completion Report, Project F-53-R-472, Lansing, Michigan.

Eshenroder, R. L., M. E. Holey, T. K. Gorenflo, and R. D. Clark, Jr. 1995. Fish community objectives for Lake Michigan. Great Lakes Fishery Commission, Special Publication 95-3, Ann Arbor, Michigan.

Fleischer, G. W., C. P. Madenjian, T. J. DeSorcie, and J. D. Holuszko. 2000. Status of trends of prey fish populations in Lake Michigan. 1999. Great Lakes Fishery Commission, Minutes of the Annual Meeting of the Lake Michigan Committee, Ann Arbor, Michigan.

Hansen, M. J. 1986. Size and condition of trout and salmon from the Wisconsin waters of Lake Michigan, 1969-84. Wisconsin Department of Natural Resources, Fisheries Management Report 126, Madison, Wisconsin.

Hansen, M. J. 1989. Chinook salmon and Wisconsin's Lake Michigan sport fishery 1969-1985. Pages 8–17 *in* B. G. Shepherd, editor. Proceedings of the 1988 Northeast Pacific chinook and coho salmon workshop. American Fisheries Society, Northeast Pacific International Chapter, Penticton, British Columbia.

Hansen, M. J. 1999. Lake trout in the Great Lakes: basin-wide stock collapse and binational restoration. Pages 417–453 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing.

Hansen, M. J., P. T. Schultz, and B. A. Lasee. 1990. Changes in Wisconsin's Lake

Michigan salmonid sport fishery, 1969-1985. North American Journal of Fisheries Management 10:442–457.

Hansen, M. J., P. T. Schultz, and B. A. Lasee. 1991. Wisconsin's Lake Michigan salmonid sport fishery, 1969-85. Wisconsin Department of Natural Resources, Fisheries Management Report 145, Madison, Wisconsin.

Hesse, J. A. 1994. Contribution of hatchery and natural chinook salmon to the Eastern Lake Michigan fishery, 1992-1993. Master's thesis. Michigan State University, East Lansing.

Holey, M. E., R. F. Elliott, S. V. Marcquenski, J. G. Hnath, and K. D. Smith. 1998. Chinook salmon epizootics in Lake Michigan: possible contributing factors and management implications. Journal of Aquatic Animal Health 10:202–210.

Honeyfield, D. C., J. D. Fitzsimons, S. B. Brown, S. V. Marcquenski, G. McDonald. 1998a. Introduction and overview of early life stage mortality. Pages 1–7 *in* G. McDonald, J. D. Fitzsimons, and D. C. Honeyfield, editors. Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea. American Fisheries Society, Symposium 21, Bethesda, Maryland.

Honeyfield, D. C., J. G. Hnath, J. Copeland, K. Dabrowski, and J. H. Blom. 1998.b. Correlation of nutrients and environmental contaminants in Lake Michigan coho salmon with incidence of early mortality syndrome. Pages 135–145 *in* G. McDonald, J. D. Fitzsimons, and D. C. Honeyfield, editors. Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea. American Fisheries Society, Symposium 21, Bethesda, Maryland.

Hornung, M. W., L. Miller, R. E. Peterson, R. E. Peterson, S. Marcquenski, and S. B. Brown. 1998. Efficacy of thiamine, astaxanthin, b-carotene, and thyroxine treatments in reducing early mortality syndrome in Lake Michigan salmonid embryos. Pages 124–134 *in* G. McDonald, J. D. Fitzsimons, and D. C. Honeyfield, editors. Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea. American Fisheries Society, Symposium 21, Bethesda, Maryland.

Ji, Y. Q., and I. R. Adelman. 1998. Thiaminase activity in alewives and smelt in Lakes Huron, Michigan, and Superior. Pages 154–159 *in* G. McDonald, J. D. Fitzsimons, and D. C. Honeyfield, editors. Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea. American Fisheries Society, Symposium 21, Bethesda, Maryland.

Johnson, D. C., and J. G. Hnath. 1991. Lake Michigan chinook salmon mortality - 1988. Michigan Department of Natural Resources, Fisheries Division Technical Report 91-4, Lansing, Michigan.

Johnson, J., A. Woldt, and G. Wright. 1999. Trends in chinook salmon growth in north-central Lake Huron. Great Lakes Fishery Commission, Minutes of the Annual Meeting of the Lake Huron Committee, Ann Arbor, Michigan.

Jude, D. J., and F. J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 42:1154–1157.

Keller, M., K. D. Smith, and R. W. Rybicki, editors. 1990. Review of salmon and trout management in Lake Michigan. Michigan Department of Natural Resources, Fisheries Division Special Report 14, Lansing, Michigan.

Kitchell, J. F., and L. B. Crowder. 1986. Predator-prey interactions in Lake Michigan: model predictions and recent dynamics. Environmental Biology of Fishes 16:205–211.

Kocik, J. F., and M. L. Jones. 1999. Pacific salmonines in the Great Lakes basin. Pages 455–488 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing.

Koonce, J. F., A. B. Locci, and R. L. Knight. 1999. Contribution of fishery management in walleye and yellow perch populations of Lake Erie. Pages 397–416 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing.

Marcquenski, S. V., and S. B. Brown. 1997. Early mortality syndrome in the Great Lakes. Pages 135–152 *in* R. M. Rolland, M. Gilbertson, and R. E. Peterson, editors. Chemically induced alterations in functional development and reproduction in fishes. SETAC (Society of Environmental Toxicology and Chemistry), Pensacola, Florida.

O'Gorman, R., and T. J. Stewart. 1999. Ascent, dominance, and decline of the alewife in the Great Lakes: food web interactions and management strategies. Pages 489–513 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing.

Parsons, J. W. 1973. History of salmon in the Great Lakes, 1850-1970. U.S. Fish and Wildlife Service, Technical Paper 68, Washington, D.C.

Peck, J. W. 1992. The sport fishery and contribution of hatchery trout and salmon in Lake Superior and tributaries at Marquette, Michigan, 1984-1987. Michigan Department of Natural Resources, Fisheries Research Report 1975, Ann Arbor, Michigan.

Peck, J. W., T. S. Jones, W. R. MacCallum, and S. T. Schram. 1999. Contribution of hatchery-reared fish to chinook salmon populations and sport fisheries in Lake Superior. North American Journal of Fisheries Management 19:155–164.

Peeters, P., and K. Royseck. 1997. Harvest, age, and size at age of chinook and coho salmon at Strawberry Creek weir and Besadny anadromous fisheries facility. Wisconsin Department of Natural Resources, Sturgeon Bay, Wisconsin.

Rutherford, E., S. T. Horrold, A. Woldt, D. Swank, and N. Golby. 1999. Abundance, production and harvest of anadromous salmonids in the Manistee, Muskegon, and Au Sable Rivers. Report to the Michigan Department of Natural Resources, Contract #231663, Lansing, Michigan.

Rybicki, R. W., and D. F. Clapp. 1996. Diet of chinook salmon in eastern Lake Michigan, 1991-1993. Michigan Department of Natural Resources, Research Report 2027, Lansing, Michigan.

Seelbach, P. W. 1985. Smolt migration of wild and hatchery-raised coho and chinook salmon in a tributary of northern Lake Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1935, Lansing, Michigan.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. Journal of the Fisheries Research Board of Canada 25:667–693.

Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Transactions of the American Fisheries Society 99:754–765.

Smith, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. Journal of the Fisheries Research Board of Canada 29:717–730.

Starliper, C. E., D. R. Smith, and T. Shatzer. 1997. Virulence of *Renibacterium salmoninarum* to salmonids. Journal of Aquatic Animal Health 9:1–7.

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

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

Tody, W. H., and H. A. Tanner. 1966. Coho salmon for the Great Lakes. Michigan Department of Natural Resources, Fish Management Report 1, Lansing, Michigan.

Tanner, H. A, and W. H. Tody. 2001. History of the Great Lakes salmon fishery: A Michigan perspective. Pages XXX–XXX *in* Lynch, K. D., M. L. Jones, and W. W. Taylor, editors. Sustaining North American salmon: perspectives across regions and disciplines. American Fisheries Society, Bethesda, Maryland.

Wells, L. 1966. Seasonal and depth distribution of larval bloaters (*Coregonus hoyi*) in southeastern Lake Michigan. Transactions of the American Fisheries Society 95:388–396.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Service Fisheries Bulletin 67(1):1–15.

Wesley, J. K. 1996. Age and growth of chinook salmon in Lake Michigan: verification, current analysis and past trends. Master's thesis. University of Michigan, Ann Arbor.