

CISCO RECRUITMENT DYNAMICS IN LAKE SUPERIOR DURING 1978–2007

By

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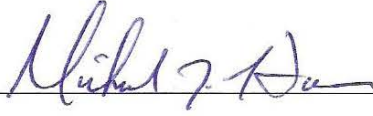
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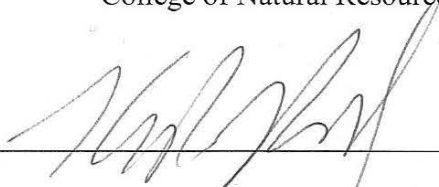
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## ABSTRACT

Historically, the cisco (*Coregonus artedii*) was the most abundant fish species in the Great Lakes, but by the mid-1900s, cisco populations were greatly reduced throughout the basin. Over-fishing, habitat degradation, and interactions with exotic species caused cisco yield to decline by 80–99% in each lake. Declining yields forced commercial fishers to target other species and brought about new regulations designed to prevent further losses, but except for a few strong year-classes in the 1990s, cisco stocks failed to recover in the lower Great Lakes. Reduced commercial fishing pressure enabled cisco to recover in portions of Lake Superior, but historic stock structure was altered, and abundance is now driven by highly erratic age-1 recruitment and few year-classes of adults. Management agencies have begun exploring the feasibility of restoring cisco stocks throughout Lake Superior and the entire Great Lakes basin, but limited understanding of factors that drive recruitment variation and the spatial scale at which these factors operate remain barriers to establishing self-sustaining populations. Identifying major density-independent and density-dependent factors that regulate age-1 cisco recruitment dynamics in Lake Superior, and the spatial scale at which these factors operate, would be invaluable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin.

In Chapter 1, I used a Ricker stock-recruitment model to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. I found that recruitment variation of cisco in Lake Superior was best described by an 8-parameter regional model with separate stock-recruitment relationships for western, southern, eastern, and northern stocks. The spatial scale for modeling was ~260

km (range = 230–290 km). I also found that the density-independent recruitment rate and the rate of compensatory density-dependence varied among regions at different rates. The density-independent recruitment rate varied 2-fold among regions (range = 2.4–4.9 age-1 recruits/spawner) and the rate of compensatory density-dependence varied 21-fold among regions (range = -0.2 to -3.4 spawners<sup>-1</sup>). Finally, I found that peak recruitment and the spawning stock size that produced peak recruitment varied among regions. Peak recruitment varied 10-fold among regions (range = 0.5–5.4 age-1 recruits/ha) and the spawning stock size that produced peak recruitment varied 21-fold among regions (range = 0.3–6.1 spawners/ha). My findings support the hypothesis that cisco recruitment is regulated within four different regions of Lake Superior, suggest that large-scale abiotic factors driving compensatory density-dependence are more important than small-scale biotic factors in regulating cisco recruitment in Lake Superior, and suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should address cisco restoration and management efforts on a regional scale in each lake.

In Chapter 2, I used a generalized version of the Ricker stock-recruitment model to identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics within four different regions of Lake Superior. I found that recruitment variation of cisco in Lake Superior was correlated to adult spawning stock size in all four regions, the density of juvenile cisco during the year prior to cisco hatching in three of four regions, average April air temperature during spring when ciscoes were 11–12 months of age in three of four regions, average April wind speed during spring when ciscoes were hatching in two of four regions, and the biomass of rainbow smelt during the year of cisco hatching in one of four regions. My findings support the hypothesis that

different biotic and abiotic factors regulate cisco recruitment within different regions of Lake Superior, suggest that air temperature during spring when ciscoes are 11–12 months of age drives recruitment variation on a lake-wide scale, whereas adult spawning stock size, intraspecific interactions with juvenile cisco, wind speed during spring when ciscoes are hatching, and interspecific interactions with rainbow smelt regulate recruitment variation on a regional scale in Lake Superior, and suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should evaluate the potential effects of similar biotic and abiotic factors on recruitment prior to addressing cisco restoration and management efforts in each lake.

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## INTRODUCTION

One of the most important but difficult problems in the assessment of fisheries is the relationship between spawning stock size and recruitment (Hilborn and Walters 1992). The stock-recruitment relationship quantifies the ability of a fish stock to replace itself over a range of spawning stock sizes (Koslow 1991; Hilborn and Walters 1992), and is essential to many models used to estimate optimal fishing strategies (Koslow 1991). However, the stock-recruitment relationship is often obscured by the effects of environmental variation, thereby causing recruitment to appear independent of spawning stock size (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). Recruitment can be indexed at any life stage, but for many fish stocks, recruitment is established within the first year of life, primarily during egg and larval stages (Ricker 1975). Spawning stock size and environmental variation collectively determine egg and larval survival through density-dependent and density-independent mechanisms (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). When annual variation in recruitment is driven by environmental variables, multi-factor stock-recruitment models can be used to quantify the separate effects of environmental variation and spawning stock size on recruitment (Ricker 1975; Walters et al. 1986; Madenjian et al. 1996; Hansen et al. 1998; Hoff 2004).

### ***Cisco in the Great Lakes***

Historically, the cisco (*Coregonus artedii*) was the most abundant, and most ecologically and economically important fish species in the Great Lakes (Smith 1995). Early observations and catch records indicate that cisco were plentiful throughout the basin (Dryer and Beil 1964; Smith 1995), and dominated total biomass of all Great Lakes fish communities (Berst and Spangler 1973; Hartman 1973; Lawrie and Rahrer 1973;

Wells and McLain 1973). Ecologically, cisco served as a key prey species in native food webs, where they acted as highly efficient trophic intermediaries and linked crustacean zooplankton production to commercially valuable piscivore stocks (Dryer and Beil 1964; Dryer et al. 1965; Berst and Spangler 1973; Conner et al. 1993; Smith 1995; Bronte et al. 2003; Hoff 2004; Fitzsimons and O’Gorman 2006). Economically, cisco contributed nearly 1.36-billion kg to commercial harvests (cumulative basin-wide yield based on lake-specific pre-decline averages) and predominated in fishery yields in each of the Great Lakes (Baldwin et al. 2006).

By the mid-1900s, a combination of over-fishing, habitat degradation, and interactions with exotic species led to severe declines in cisco abundance across the basin (Edsall and DeSorcie 2002; Fitzsimons and O’Gorman 2006). As cisco stocks collapsed, yield declined by 96% in Lake Ontario (1941–1953), 99% in Lake Erie (1946–1958), 95% in Lake Huron (1952–1957), 99% in Lake Michigan (1954–1963), and 80% in Lake Superior (1966–1976; Baldwin et al. 2006). Declining yields forced commercial fishers to target other species and brought about new regulations designed to prevent further losses, but except for a few strong year-classes in the 1990s, cisco stocks failed to recover in the lower Great Lakes (Fitzsimons and O’Gorman 2006). Annual yield has remained below 50,000 kg since 1953 in Lake Ontario, 1958 in Lake Erie, 1957 in Lake Huron, and 1963 in Lake Michigan (Baldwin et al. 2006). Reduced commercial fishing pressure enabled cisco to recover in portions of Lake Superior, but historic stock structure was altered (Goodyear et al. 1981; Selgeby 1982; Horns 2003), and abundance is now driven by highly erratic age-1 recruitment and few year-classes of adults (Bronte et al. 2003; Hoff 2004). Currently, Lake Superior sustains an average annual yield that is only 14.8%

(798,000 kg average annual yield during 1977–2000) of the average annual yield during the 50-year period prior to stock decline (5.4-million kg average annual yield during 1915–1965; Baldwin et al. 2006).

Cisco yield has always been variable in the Great Lakes (Wells and McLain 1973). In the 50-year period prior to stock declines, yield varied 10-fold in Lake Ontario (1890–1940), 588-fold in Lake Erie (1895–1945), 9-fold in Lake Huron (1901–1951), 20-fold in Lake Michigan (1903–1953), and 5-fold in Lake Superior (1915–1965; Baldwin et al. 2006). Variability in yield was influenced by changing market demand and weather conditions during peak commercial fishing seasons, but primarily by changes in cisco abundance as strong and weak year-classes moved through fisheries in each lake (Wells and McLain 1973). Some of the weakest year-classes were produced by large parental stocks, whereas some of the strongest year-classes were produced by small parental stocks. Early researchers believed that cisco recruitment was primarily established during the first year of life by density-independent environmental influences on egg and larval survival (Scott 1951; Powers et al. 1959). However, a lack of long-term data prevented stock-recruitment analysis to test such theories. Long-term data enabling stock-recruitment analysis are now available for Lake Superior (Hoff 2004).

The U.S. Geological Survey (USGS, Lake Superior Biological Station, Ashland, WI) has conducted spring bottom-trawl surveys of the near-shore fish community in U.S. waters of Lake Superior since 1978 and Canadian waters of Lake Superior since 1989. Bottom-trawl assessments have shown that cisco year-class strength and subsequent recruitment to the adult stage is primarily established prior to sampling age-1 fish in the spring of each year (Kinnunen 1997; Bronte et al. 2003; Hoff 2004; Ebener et al. 2008;

Stockwell et al. 2009). During 1978–2007, age-1 cisco recruitment varied 339-fold in U.S. waters (1978–2007) and 48-fold in Canadian waters (1989–2007; calculated from geometric mean spring bottom-trawl densities; USGS, Lake Superior Biological Station, Ashland, WI). Strong recruitment events were highly synchronous across the lake (Kinnunen 1997; Bronte et al. 2003; Ebener et al. 2008; Stockwell et al. 2009), and characterized by large regional differences in year-class strength (Ebener et al. 2008; Stockwell et al. 2009). Some of the weakest year-classes were produced by large parental stocks, whereas some of the strongest year-classes were produced by small parental stocks (Bronte et al. 2003; Horns 2003; Hoff 2004). These recruitment events suggest that density-independent and density-dependent factors may both be important regulators of age-1 cisco recruitment dynamics in Lake Superior (Ricker 1975; Hilborn and Walters 1992; Bronte et al. 2003; Hoff 2004). Similarity between current age-1 cisco recruitment variability in Lake Superior and historic variability in yield throughout the lower Great Lakes suggests that many of the same factors driving recruitment dynamics in Lake Superior may have been operating in the lower Great Lakes prior to cisco declines during the mid-1900s.

The fish-community objective for prey species in Lake Superior calls for rehabilitation of cisco stocks to historic levels of abundance to provide a forage base for lake trout (*Salvelinus namaycush*) and to support a commercial fishery (Busiahn 1990). Fishery management plans for the lower Great Lakes recognize the cisco as an important member of the native fish community and call for reestablishment of self-sustaining populations throughout the species historic range (Edsall and DeSorcie 2002). Management agencies have begun exploring the feasibility of restoring cisco stocks



throughout Lake Superior and the entire Great Lakes basin, but limited understanding of factors that drive recruitment variation and the spatial scale at which these factors operate remain barriers to establishing self-sustaining populations (Hoff 2004; Fitzsimons and O’Gorman 2006). Identifying major density-independent and density-dependent factors that regulate age-1 cisco recruitment dynamics in Lake Superior, and the spatial scale at which these factors operate, would be invaluable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin.

### ***Cisco Distribution and Life History***

The cisco is endemic to North America and is widely distributed throughout the northern portion of the continent (Figure 1; Scott and Crossman 1973; Lee et al. 1980; Becker 1983; Latta 1995). Native and introduced populations inhabit water bodies from the Great Lakes and upper Mississippi River drainage throughout eastern and central Canada (Lee et al. 1980; Becker 1983; Fisher and Fielder 1998). Near the northern limit of the species range, individuals inhabit large rivers, ponds, and coastal waters of Hudson Bay (Scott and Crossman 1973; Lee et al. 1980; Becker 1983). In the Great Lakes region, the cisco is primarily a lake species that is limited to deep, glaciated, oligotrophic lakes (Dorr and Eschman 1970; Scott and Crossman 1973; Latta 1995; Edsall and DeSorcie 2002).

Because of the cisco’s wide geographic distribution and wide variety of habitats, individuals exhibit a high degree of phenotypic plasticity (Scott and Crossman 1973; Lee et al. 1980; Becker 1983; Hubbs and Lagler 2004). The species has been divided into as many as 24 different subspecies (Koelz 1931), but the cisco is presently considered a species complex (McPhail and Lindsey 1970). A member of the family Salmonidae and

the subfamily Coregoninae, typical individuals are elongate and silver, with a black, blue-green, gray, or tan back (Figure 2; Scott and Crossman 1973; Becker 1983). The cisco can be distinguished from other related species by internal characteristics, the presence of large cycloid scales, a count of 38–64 gill-rakers, and a terminal mouth with the lower jaw protruding slightly beyond the upper lip (Scott and Crossman 1973; Becker 1983; Hubbs and Lagler 2004). The species averages 203–305 mm total length (TL; Scott and Crossman 1973) and 75–285 g weight (Scott and Crossman 1973; Fisher and Fielder 1998). The largest cisco ever recorded was a 3,629 g female taken from central Lake Erie in 1949 (Scott and Crossman 1973).

In the Great Lakes, adult ciscoes are pelagic and form schools in mid-water, where they feed primarily on large crustacean zooplankton (Dryer and Beil 1964; Scott and Crossman 1973; Becker 1983). Ciscoes are usually found where water temperatures are less than 17–18°C and dissolved oxygen concentrations are greater than 3–4 mg/L (Hile 1936; McLain and Magnuson 1988). The upper lethal temperature for adult cisco is about 20°C (Frey 1955; Colby and Brooke 1969) and the lower lethal temperature is near 0°C (Frey 1955).

In spring and early summer, adult ciscoes occupy near-shore surface waters. As surface waters warm, individuals move offshore, where they maintain a wide vertical distribution in the water column (Selgeby and Hoff 1996). In autumn, adult ciscoes return to near-shore surface waters, where they remain until spawning (Dryer and Beil 1964; Scott and Crossman 1973; Becker 1983; Selgeby and Hoff 1996). Despite large seasonal variation in lateral distribution, most ciscoes do not travel great distances (Scott and Crossman 1973). A 3-year tagging study in Lake Michigan reported an average

movement distance of 16.5 km and a maximum movement distance of 88.5 km (Smith and Van Oosten 1940).

Ciscoes mature at 3–4 years of age (Scott and Crossman 1973; Becker 1983) and may live 20 years or more (Ebener et al. 2008; Stockwell et al. 2009). Spawning is from late November to early December when water temperature reaches 2.8–4.4°C (Scott and Crossman 1973; Becker 1983). Adult ciscoes form large schools and spawn pelagically in near-shore waters (Dryer and Beil 1964; Scott and Crossman 1973; Becker 1983). Spawning occurs over a variety of substrates in depths ranging 3–64 m (Smith 1956; Dryer and Beil 1964; Scott and Crossman 1973). In Lake Superior, most commercial fishers target adult females prior to spawning, which may limit recruitment by reducing egg deposition (Yule et al. 2006a).

During spawning, cisco eggs are fertilized in the water column and drift to the bottom, where they remain until hatching in late April to early May (Pritchard 1930; John and Hasler 1956; Oyadomari 2005). A single individual may spawn multiple times during its life (Scott and Crossman 1973). The number of eggs deposited by each female is correlated to body size, and fecundity varies among populations (Anderson and Smith 1971; Scott and Crossman 1973; Becker 1983). In the Apostle Islands region of Lake Superior, cisco fecundity was linearly related to female body size ( $R^2 = 0.88$ ;  $n = 22$  females;  $P < 0.0001$ ; range = 127–568 g; Yule et al. 2006b):

$$\text{Fecundity}(\text{number of eggs}) = -86.5 + 46.5 \times \text{Female Mass (g)}$$

Incubation lasts about 43 days at 10.0°C (Hinrichs and Brooke 1975), 92 days at 5.6°C, 106 days at 5.0°C, and 236 days at 0.5°C (Colby and Brooke 1970). The optimum temperature for incubation is 2–8°C (Colby and Brooke 1970). Laboratory tests indicate

that hatching date may be independent of spawning date, synchronous across lakes, and determined by local spring thermal and light regimes (John and Hasler 1956). Following severe winters, hatching date may be delayed by a dormancy mechanism related to spring ice cover (John and Hasler 1956). Under laboratory conditions, longer incubation periods result in larger post-hatch larvae than shorter incubation periods, and stable incubation temperatures result in greater hatching success than unstable incubation temperatures (Colby and Brooke 1970). Extended spring ice cover may increase recruitment by delaying hatching, thereby producing larger post-hatch larvae that are more likely to avoid size-dependent predation, and stabilizing temperatures during incubation, thereby increasing hatching success (Colby and Brooke 1970; Kinnunen 1997). In shallow waters, extended spring ice cover may also protect incubating eggs from late-winter storms (Kinnunen 1997). During spawning, recruitment may be limited by egg predation from other cisco age-classes (Dryer and Beil 1964; Anderson and Smith 1971; Becker 1983). During incubation, recruitment may be limited by egg predation from slimy sculpin (*Cottus cognatus*; Anderson and Smith 1971; Hoff 2004).

Upon hatching in late April to early May, age-0 cisco live in near-shore surface waters, where they feed on immature copepod zooplankton for 3–4 weeks until they move into deeper waters (Anderson and Smith 1971; Scott and Crossman 1973; Becker 1983; Selgeby et al. 1994). Age-0 ciscoes are about 10 mm TL at hatching and take 1–2 days to reach the swim-up stage (John and Hasler 1956; Hinrichs and Brooke 1975; Hatch and Underhill 1988). Exogenous feeding requires light, overlaps endogenous feeding, and starts on the day of hatching (John and Hasler 1956; Colby and Brooke 1970; Selgeby et al. 1994). Under laboratory conditions, age-0 cisco can survive without

food for about 20 days after hatching at normal spring temperatures (4–11°C) and up to 30 days at lower temperatures (3–4°C; John and Hasler 1956). The yolk sac is completely absorbed at 13 mm TL, 25–30 days after hatching (Oyadomari 2005). By the end of June, age-0 ciscoes are 15–20 mm TL, and move into deeper waters (Pritchard 1930; Hatch and Underhill 1988; Oyadomari and Auer 2004). Upon hatching, recruitment may be limited by predation and competition from other cisco age-classes (Pritchard 1931; Anderson and Smith 1971; Becker 1983; Jensen 1996; Hoff et al. 1997; Bronte et al. 2003; Hoff 2004), rainbow smelt (*Osmerus mordax*; Anderson and Smith 1971; Walter and Hoagman 1975; Selgeby et al. 1978; Hrabik et al. 1998; Cox and Kitchell 2004), and bloater (*Coregonus hoyi*; Anderson and Smith 1971; Davis and Todd 1992). Strong winds during hatching may disperse patches of newly hatched larvae, thereby limiting age-0 predation (Hoff 2004). Upon moving into deeper waters, age-0 ciscoes are an important food for lake trout (Edsall and DeSorcie 2002).

Age-0 ciscoes actively seek optimal temperatures for growth and development (Edsall and DeSorcie 2002). The upper lethal temperature for age-0 cisco is about 26°C and the lower lethal temperature is near 0°C (Edsall and Colby 1970). Under laboratory conditions, temperatures of 13–18°C were ideal for sustained growth (McCormick et al. 1971). In the Keweenaw Peninsula region of Lake Superior, ciscoes in near-shore waters were more abundant and larger than ciscoes in offshore waters (Oyadomari and Auer 2004). Differences in size were likely because near-shore ciscoes were older and grew faster in warmer near-shore waters than ciscoes in colder offshore waters (Oyadomari and Auer 2004). Sub-optimal temperatures during age-0 development may magnify the effects of predation and competition (Kinnunen 1997; Pangle et al. 2004) or prevent

individuals from reaching adequate size for over-winter survival (Edsall and DeSorcie 2002; Pangle et al. 2004). Wind-driven currents may mediate age-0 survival through transport to optimal or sub-optimal waters for growth and development (Oyadomari and Auer 2004). Sub-optimal temperatures during spring when ciscoes are 11–12 months of age may place additional stress on new recruits following severe winters (Kinnunen 1997; Hoff 2004; Pangle et al. 2004).

### ***Study Area***

Lake Superior is located near the head of the St. Lawrence River drainage, and is bordered by one Canadian province to the north (Ontario) and three U.S. states to the south (Michigan, Wisconsin, and Minnesota). A surface area of 8.24-million ha and a volume of 12,233 km<sup>3</sup> make Lake Superior the largest of the Great Lakes (Lawrie and Rahrer 1973). Lake Superior has the lowest annual average temperature (3.6°C) of any of the Great Lakes and the longest spring convective period (Bennett 1978; Hoff 2004). The interaction of cold temperature, extended convective period, and large fetch result in strong wind-driven currents (Hoff 2004). Persistent thermal stratification is usually present by mid-July in near-shore waters, but stratification is often well developed during extended calm periods in more exposed waters, only to be disrupted by strong winds (Lawrie and Rahrer 1973). Lake Superior does not freeze over, but substantial ice cover is present during winter months (Marshall 1967).

Lake Superior is highly oligotrophic (Hansen 1990). Transparency is usually 10 m or more (Hansen 1990) and dissolved oxygen concentration is above 100% saturation for all months except November (Weiler 1978). Primary production is near the low end of the range for freshwater lakes, so commercial fish production per unit of surface area

is lower than in all other Great Lakes (Table 1; Hansen 1990; Horns 2003). Total lake-wide commercial production peaked at 11.6-million kg (1941; Lawrie and Rahrer 1973) and currently sustains yields around 2.6-million kg (average annual yield during 1985–2000; Baldwin et al. 2006). The native fish community of Lake Superior included 73 species in 18 families (Lawrie 1978), but biomass was dominated by lake trout, lake whitefish (*Coregonus clupeaformis*), cisco, and several species of related deepwater chubs (*Coregonus* spp.; Hansen 1990).

Despite decades of growth throughout the lower Great Lakes basin, human population density has remained relatively low (less than 20 people per km<sup>2</sup>) in the Lake Superior basin (Lee and Beaulieu 1971). A large amount of the basin remains forested, with little agricultural or urban development (Lawrie and Rahrer 1973). Lake Superior has been little affected by industrial pollution or run-off from agricultural and residential sources. The greatest influences from human development have been over-fishing and introductions of exotic species (Lawrie and Rahrer 1973).

Cisco recruitment is not limited by habitat at any historic spawning sites in Lake Superior (Figure 3; Horns 2003). Over-fishing of discrete stocks (Selgeby 1982; Bronte et al. 2003) and interactions with rainbow smelt (Anderson and Smith 1971; Selgeby et al. 1978; Cox and Kitchell 2004) are generally considered the two most likely factors contributing to cisco declines during the mid-1900s. Many studies have attempted to identify factors driving contemporary age-1 cisco recruitment dynamics in Lake Superior, but most have provided inconclusive or conflicting results. Factors that may regulate contemporary age-1 cisco recruitment include adult spawning stock size (Bronte et al. 2003; Horns 2003; Hoff 2004), commercial fishing mortality (Selgeby 1982),

intraspecific and interspecific interactions (Dryer and Beil 1964; Dryer et al. 1965; Anderson and Smith 1971; Berst and Spangler 1973; Selgeby et al. 1978; Jensen 1996; Bronte et al. 2003; Horns 2003; Cox and Kitchell 2004; Hoff 2004), and environmental variation (Kinnunen 1997; Bronte et al. 2003; Hoff 2004). Highly synchronous, lake-wide recruitment events suggest that large-scale abiotic factors drive recruitment variation on a lake-wide scale, whereas small-scale biotic factors regulate recruitment variation on a regional scale in Lake Superior (Kinnunen 1997; Bronte et al. 2003; Stockwell et al. 2009).

## **OBJECTIVES**

My first objective was to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. In Chapter 1, I used a Ricker stock-recruitment model (Ricker 1975) to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. I expected to find that multiple cisco stocks within geographic regions of Lake Superior could be modeled using a single set of stock-recruitment parameters, because large-scale abiotic factors are generally considered more important than small-scale biotic factors in regulating age-1 cisco recruitment in Lake Superior (Kinnunen 1997; Bronte et al. 2003; Hoff 2004; Stockwell et al. 2009). I also expected to find compensatory density-dependence for regional stock-recruitment models, because a previous stock-recruitment study (Hoff 2004) found significant compensatory density-dependence in Wisconsin waters of Lake Superior. Finally, I expected to find different rates of compensatory density-dependence among regional stock-recruitment models, because age-1 cisco



recruitment has previously been observed to vary regionally in Lake Superior (Ebener et al. 2008; Stockwell et al. 2009).

My second objective was to identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics in Lake Superior at spatial scales identified in Chapter 1. In Chapter 2, I used a generalized version of the Ricker stock-recruitment model (Ricker 1975; Hilborn and Walters 1992) to identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics within four different regions of Lake Superior. I expected to find a significant positive effect on age-1 cisco recruitment from wind speed during spring when ciscoes were hatching, and air temperature during spring when ciscoes were 11–12 months of age, because a previous study (Hoff 2004) showed that these factors were correlated to age-1 cisco recruitment in Lake Superior. I also expected to find a significant negative effect on age-1 cisco recruitment from slimy sculpin biomass during the year prior to cisco hatching, and lake trout biomass during the year of cisco hatching, because a previous study (Hoff 2004) showed that these factors were correlated to age-1 cisco recruitment in Lake Superior. Additionally, I expected to find significant negative effects on age-1 cisco recruitment from juvenile cisco density and rainbow smelt biomass during the year of cisco hatching, because intraspecific interactions with other cisco age-classes and interspecific interactions with rainbow smelt are generally considered to limit age-1 cisco recruitment in Lake Superior (Anderson and Smith 1971; Selgeby et al. 1978; Jensen 1996; Bronte et al. 2003; Horns 2003; Cox and Kitchell 2004; Hoff 2004; Ebener et al. 2008; Stockwell et al. 2009). Finally, I expected to find that different variables explained variation in

recruitment within different regions, because age-1 cisco recruitment has previously been observed to vary regionally in Lake Superior (Ebener et al. 2008; Stockwell et al. 2009).

Table 1. Primary production and average annual commercial fish yield in each of the Great Lakes during 15-year periods of maximum commercial harvest (Horns 2003).

<b>Lake</b>	<b>Primary Production (g/m<sup>2</sup>/yr)</b>	<b>Fish Yield (kg/ha)</b>
Erie	240–250	9.71
Ontario	180–190	1.24
Michigan	140–150	2.23
Huron	80–90	2.09
Superior	40–50	1.19



Figure 1. Cisco distribution in North America (Lee et al. 1980; Becker 1983; Fisher and Fielder 1998).

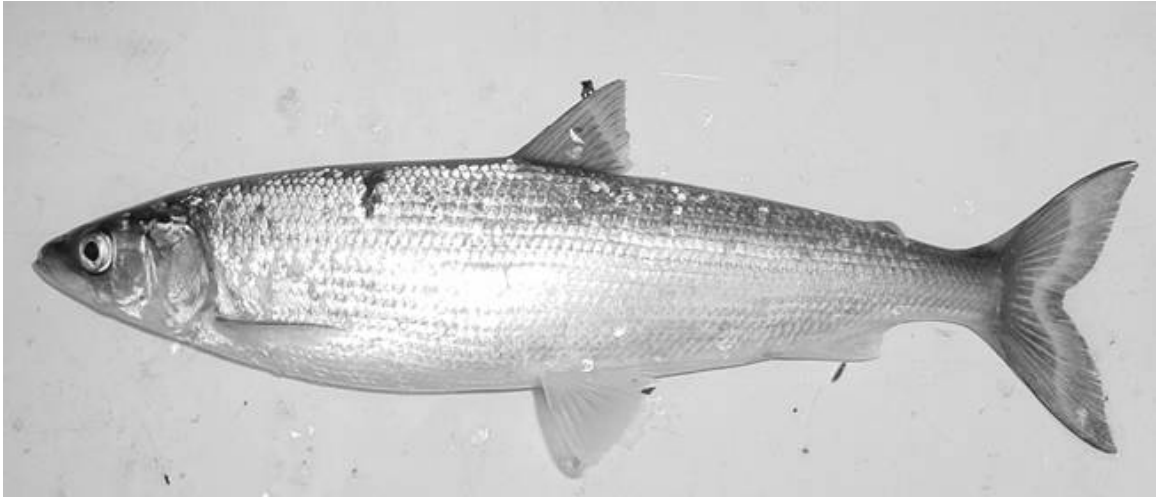
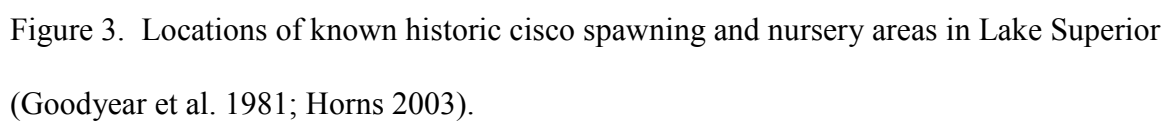


Figure 2. Adult cisco taken from southern Lake Superior in June 2006 (USGS, Lake Superior Biological Station, Ashland, WI).



## Chapter 1:

### The Spatial Scale for Cisco Recruitment Dynamics in Lake Superior during 1978–2007

**Abstract** – The cisco (*Coregonus artedii*) was once the most abundant fish species in the Great Lakes, but currently, cisco populations are greatly reduced, and management agencies are attempting to restore the species throughout the basin. To increase understanding of the spatial scale at which density-independent and density-dependent factors regulate cisco recruitment dynamics in the Great Lakes, I used a Ricker stock-recruitment model to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. I found that recruitment variation of cisco in Lake Superior was best described by an 8-parameter regional model with separate stock-recruitment relationships for western, southern, eastern, and northern stocks. The spatial scale for modeling was ~260 km (range = 230–290 km). I also found that the density-independent recruitment rate and the rate of compensatory density-dependence varied among regions at different rates. The density-independent recruitment rate varied 2-fold among regions (range = 2.4–4.9 age-1 recruits/spawner) and the rate of compensatory density-dependence varied 21-fold among regions (range = -0.2 to -3.4 spawners<sup>-1</sup>). Finally, I found that peak recruitment and the spawning stock size that produced peak recruitment varied among regions. Peak recruitment varied 10-fold among regions (range = 0.5–5.4 age-1 recruits/ha) and the spawning stock size that produced peak recruitment varied 21-fold among regions (range = 0.3–6.1 spawners/ha). My findings support the hypothesis that cisco recruitment is regulated within four

different regions of Lake Superior, suggest that large-scale abiotic factors driving compensatory density-dependence are more important than small-scale biotic factors in regulating cisco recruitment in Lake Superior, and suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should address cisco restoration and management efforts on a regional scale in each lake.



## INTRODUCTION

Historically, the cisco (*Coregonus artedii*) was the most abundant fish species in the Great Lakes (Smith 1995), but by the mid-1900s, cisco populations were greatly reduced throughout the basin (Fitzsimons and O’Gorman 2006). Over-fishing, habitat degradation, and interactions with exotic species caused cisco yield to decline by 80–99% in each lake (Edsall and DeSorcie 2002; Baldwin et al. 2006; Fitzsimons and O’Gorman 2006). Declining yields forced commercial fishers to target other species and brought about new regulations designed to prevent further losses, but except for a few strong year-classes in the 1990s, cisco stocks failed to recover in the lower Great Lakes (Fitzsimons and O’Gorman 2006). Reduced commercial fishing pressure enabled cisco to recover in portions of Lake Superior, but historic stock structure was altered (Goodyear et al. 1981; Selgeby 1982; Horns 2003), and abundance is now driven by highly erratic age-1 recruitment and few year-classes of adults (Bronte et al. 2003; Hoff 2004). Management agencies have begun exploring the feasibility of restoring cisco stocks throughout Lake Superior and the entire Great Lakes basin, but limited understanding of factors that drive recruitment variation and the spatial scale at which these factors operate remain barriers to establishing self-sustaining populations (Hoff 2004; Fitzsimons and O’Gorman 2006). Identifying major density-independent and density-dependent factors that regulate age-1 cisco recruitment dynamics in Lake Superior, and the spatial scale at which these factors operate, would be invaluable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin. A comprehensive analysis of cisco stock-recruitment in Lake Superior can provide a framework for addressing these questions.

The stock-recruitment relationship quantifies the ability of a fish stock to replace itself over a range of spawning stock sizes (Koslow 1991; Hilborn and Walters 1992), and is essential to many models used to estimate optimal fishing strategies (Koslow 1991). However, the stock-recruitment relationship is often obscured by the effects of environmental variation, thereby causing recruitment to appear independent of spawning stock size (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). Recruitment can be indexed at any life stage, but for many fish stocks, recruitment is established within the first year of life, primarily during egg and larval stages (Ricker 1975). Spawning stock size and environmental variation collectively determine egg and larval survival through density-dependent and density-independent mechanisms (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). When annual variation in recruitment is driven by environmental variables, multi-factor stock-recruitment models can be used to quantify the separate effects of environmental variation and spawning stock size on recruitment (Ricker 1975; Walters et al. 1986; Madenjian et al. 1996; Hansen et al. 1998; Hoff 2004). Identifying the appropriate spatial scale for modeling the stock-recruitment relationship is an important preliminary step in any multi-factor stock-recruitment analysis.

The U.S. Geological Survey (USGS, Lake Superior Biological Station, Ashland, WI) has conducted spring bottom-trawl surveys of the near-shore fish community in U.S. waters of Lake Superior since 1978 and Canadian waters of Lake Superior since 1989. During 1978–2007, age-1 cisco recruitment varied 339-fold in U.S. waters (1978–2007) and 48-fold in Canadian waters (1989–2007; calculated from geometric mean spring bottom-trawl densities; USGS, Lake Superior Biological Station, Ashland, WI). Strong recruitment events were highly synchronous across the lake (Kinnunen 1997; Bronte et

al. 2003; Ebener et al. 2008; Stockwell et al. 2009), and characterized by large regional differences in year-class strength (Ebener et al. 2008; Stockwell et al. 2009). Lake-wide recruitment events occurred in 1984, 1988–1990, 1998, and 2003 (Ebener et al. 2008; Stockwell et al. 2009). Additional localized large year-classes were established in Minnesota waters in 1978 and eastern Michigan waters in 1983 (Stockwell et al. 2009). In 1984, the large year-class in Minnesota waters was smaller than in other U.S. waters (Stockwell et al. 2009). In 1998, the large year-class in eastern Michigan and eastern Ontario waters was smaller than in other U.S. and Canadian waters (Ebener et al. 2008; Stockwell et al. 2009). Large regional differences in age-1 cisco year-class strength and regional deviations from normal patterns of recruitment synchrony suggest that separate stock-recruitment models should be developed for western, southern, eastern, and northern regions of Lake Superior.

My objective was to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. I used a Ricker stock-recruitment model (Ricker 1975) to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. I expected to find that multiple cisco stocks within geographic regions of Lake Superior could be modeled using a single set of stock-recruitment parameters, because large-scale abiotic factors are generally considered more important than small-scale biotic factors in regulating age-1 cisco recruitment in Lake Superior (Kinnunen 1997; Bronte et al. 2003; Hoff 2004; Stockwell et al. 2009). I also expected to find compensatory density-dependence for regional stock-recruitment models, because a previous stock-recruitment study (Hoff 2004) found significant compensatory density-dependence in Wisconsin waters of Lake

Superior. Finally, I expected to find different rates of compensatory density-dependence among regional stock-recruitment models, because age-1 cisco recruitment has previously been observed to vary regionally in Lake Superior (Ebener et al. 2008; Stockwell et al. 2009).

## METHODS

### *Study Area*

Lake Superior is located near the head of the St. Lawrence River drainage, and is bordered by one Canadian province to the north (Ontario) and three U.S. states to the south (Michigan, Wisconsin, and Minnesota). A surface area of 8.24-million ha and a volume of 12,233 km<sup>3</sup> make Lake Superior the largest of the Great Lakes (Lawrie and Rahrer 1973). Lake Superior is highly oligotrophic (Hansen 1990). Primary production is near the low end of the range for freshwater lakes, so commercial fish production per unit of surface area is lower than in all other Great Lakes (Hansen 1990; Horns 2003). The native fish community of Lake Superior included 73 species in 18 families (Lawrie 1978), but biomass was dominated by lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), cisco, and several species of related deepwater chubs (*Coregonus* spp.; Hansen 1990). Lake Superior has been little affected by point or non-point source pollution. The greatest influences from human development have been over-fishing and introductions of exotic species (Lawrie and Rahrer 1973).

### *Cisco Sampling*

Cisco recruitment was indexed using catch rates of age-1 cisco in spring bottom-trawl surveys when fish were 13–14 months of age and  $\leq 140$  mm total length (TL; Hoff

2004). Large cisco year-classes typically include a significant number of individuals >140 mm TL (USGS, Lake Superior Biological Station, Ashland, WI), so length-frequency distributions were examined and the TL cut-off was adjusted to include all age-1 individuals. Spring bottom-trawl surveys of the Lake Superior near-shore fish community included an average of 49 sites (range = 32–53) in U.S. waters since 1978 and an average of 30 sites (range = 18–34) in Canadian waters since 1989 (Figure 1).

Yankee bottom-trawls with an 11.9-m head-rope and 12-mm mesh cod end were towed at a speed of 3.5 km per hour across contours at fixed sampling stations spaced every ~24 km along the U.S. and Canadian shorelines. Trawling began at a depth of 10–15 m and progressed in an offshore direction until 60 min elapsed or the trawl reached the maximum depth that would be attained at the end of 60 min. Trawling targeted all fish species during daylight hours. Catches from each trawl tow were grouped by species and measured in total length (mm) and weight (kg). Density (number/ha) and biomass (kg/ha) were computed from the total number and weight of fish caught and the area swept by each trawl tow. Data were summarized for each trawl tow (USGS, Lake Superior Biological Station, Ashland, WI).

Cisco spawning stock size was indexed using catch rates of adult cisco in bottom-trawls in U.S. and Canadian waters (methods described above), fishery-independent gill-net surveys in U.S. waters, and targeted commercial fisheries in Canadian waters. Most agencies with jurisdiction in Lake Superior conducted fishery-independent summer lake trout surveys with graded-mesh bottom-set gill-nets placed at fixed sampling stations throughout lake trout management units (Figure 2). Although most surveys did not target cisco, the species was collected as by-catch (Ebener et al. 2008). Summer surveys were

conducted in all Wisconsin lake trout management units since 1970 and all Minnesota and most Michigan lake trout management units since the mid-1980s. The average depth of summer survey nets was 34 m in Wisconsin (range = 18–61 m), 45 m in Minnesota (range = 36–57 m), and 46 m in Michigan (range = 15–105 m; Ebener et al. 2008). Soak times typically ranged 1–4 nights. Catch/effort (CPUE; number/km) was computed from the number of fish caught and net length. Data were summarized by mesh size and species for each gill-net gang. Prior to analysis, data were standardized to a soak time of one night by dividing by total number of nights. Fishery-independent gill-net surveys were not available for Canadian lake trout management units in Lake Superior (Ebener et al. 2008), so CPUE in targeted commercial fisheries was used to index cisco spawning stock size. In Ontario, the commercial cisco fishery was primarily a roe fishery and relied on floating gill-nets targeting adults during autumn spawning (Yule et al. 2006a). Commercial operators reported daily total biomass (kg) of cisco harvested, effort (km), and locations of harvest. Catch/effort (kg/km) was computed from biomass caught and net length for each gill-net gang in each lake trout management unit (Yule et al. 2006a).

In Lake Superior, most ciscoes mature at 200 mm TL in spring (Hoff 2004) and 250 mm TL in autumn (Dryer and Beil 1964; Yule et al. 2006a). Therefore, cisco spawning stock size was indexed as the density of fish  $\geq 200$  mm TL in spring bottom-trawl surveys, CPUE of fish  $\geq 225$  mm TL in summer lake trout surveys, and CPUE of fish  $\geq 250$  mm TL in autumn targeted commercial fisheries. Total length cut-offs were applied to density distribution data from spring bottom-trawl surveys to calculate the density of fish  $\geq 200$  mm TL. Mesh sizes used in summer lake trout surveys varied among agencies, so only mesh sizes from 2.0 to 2.5-inch stretch-measure were used to

index cisco spawning stock CPUE. Based on a preliminary analysis of length-frequency distributions for various mesh sizes, this mesh-size range likely excludes smaller and larger adult cisco, but is the most appropriate standardized index of cisco spawning stock size ( $\geq 225$  mm TL) in summer. Mesh sizes used in the Ontario commercial fishery were not available, but the fishery targeted spawning fish (Yule et al. 2006a), so I assumed that commercial CPUE appropriately indexed cisco spawning stock size ( $\geq 250$  mm TL) in autumn.

### ***Spatial Summarization***

I defined 11 spatial units in U.S. and Canadian waters of Lake Superior (Figure 3), and calculated summary statistics for each index of recruitment and spawning stock size in each spatial unit. Spatial units were required to account for different spatial scales used for data collection and reporting, and were based on regional combinations of whole (U.S. and Canadian waters) and partial (Canadian waters) lake trout management units (described above) that loosely corresponded to U.S. Geological Survey Eco-Regions (Figure 4). For bottom-trawl density and fishery-independent gill-net CPUE, individual observations were treated as replicate samples and used to calculate summary statistics for each spatial unit. For targeted commercial fishery CPUE, individual observations were treated as replicate samples and used to calculate summary statistics for each whole and partial lake trout management unit. Weighted averages for whole and partial lake trout management units were then used to calculate summary statistics for each spatial unit. Weights were based on the area of each whole and partial lake trout management unit. In two Canadian lake trout management units, targeted commercial fishery CPUE was sporadic, but was strongly and linearly related to the CPUE from a neighboring unit.

Therefore, prior to calculating summary statistics for each spatial unit, linear regression (Zar 1999) was used to predict CPUE for lake trout management units in which targeted commercial fishery CPUE was not available (Figure 5).

I calculated the geometric mean, coefficient of variation, and relative standard error for each index of recruitment and spawning stock size in each spatial unit. First, to account for zero catches, a value equal to  $\frac{1}{2}$  the minimum observed density (0.145 fish/ha) was added to each observation of bottom-trawl density and a value of 1.0 was added to each observation of fishery-independent gill-net or targeted commercial fishery CPUE. The resulting values were then  $\log_e$ -transformed and used to calculate an arithmetic average and 95% confidence limits for each spatial unit. The arithmetic average and 95% confidence limits of the  $\log_e$ -transformed values were then back-transformed to obtain the geometric mean and back-transformed 95% confidence limits. The geometric mean ( $\mu$ ), sample size ( $n$ ), and back-transformed upper and lower 95% confidence limits ( $U95$  and  $L95$ ) were then used to calculate the coefficient of variation ( $CV$ ) and relative standard error ( $RSE$ ; Zar 1999):

$$CV = \left( \frac{\left( \frac{U95 - L95}{3.92} \right) \times \sqrt{n}}{\mu} \right); RSE = \left( \frac{(U95 - L95)/3.92}{\mu} \right)$$

### ***Prediction of Missing Values***

In several spatial units, the number of years with CPUE from fishery-independent gill-net surveys or targeted commercial fisheries was much less than the number of years with density from bottom-trawling. Missing values were for years in which assessment gill-net fishing (U.S. waters) or commercial fishing (Canadian waters) did not occur.



Therefore, a measurement-error model (Fuller 1987) was applied to  $\log_e$ -transformed relationships between adult cisco density in bottom-trawls and adult cisco CPUE in fishery-independent gill-net surveys or targeted commercial fisheries to predict missing gill-net CPUE. A measurement-error model was required for predicting missing gill-net CPUE, because cisco spawning stock size indexed as density in bottom-trawls and CPUE in fishery-independent gill-net surveys or targeted commercial fisheries were each measured with error, thereby making ordinary least-squares regression parameter estimates biased (Fuller 1987). The measurement-error model was:

$$\hat{b}_1 = \frac{m_{YY} - \delta m_{XX} + \sqrt{(m_{YY} - \delta m_{XX})^2 + 4\delta m_{XY}^2}}{2m_{XY}}$$

$$b_0 = \bar{Y} - \hat{b}_1 \bar{X}$$

Where  $\hat{b}_1$  is the bias-corrected slope,  $m_{YY}$  is the variance of fishery-independent gill-net or targeted commercial fishery CPUE,  $m_{XX}$  is the variance of bottom-trawl density,  $m_{XY}$  is the covariance between gill-net CPUE and bottom-trawl density,  $\delta$  is the measurement-error ratio,  $b_0$  is the bias-corrected intercept,  $\bar{Y}$  is the mean of the fishery-independent gill-net or targeted commercial fishery CPUE, and  $\bar{X}$  is the mean of the bottom-trawl density (Fuller 1987). The measurement-error ratio is calculated from the equation:

$$\delta = \frac{CV_{gill-net}}{CV_{trawl}}$$

Where  $CV_{gill-net}$  is the average  $CV$  of fishery-independent gill-net or targeted commercial fishery CPUE and  $CV_{trawl}$  is the average  $CV$  of bottom-trawl density (Fuller 1987). Bias

corrected slopes and intercepts were tested for significance ( $P \leq 0.05$ ) against null hypotheses of  $\hat{b}_1 = 0.0$  and  $b_0 = 0.0$  using  $t$ -tests (Zar 1999):

$$t = \frac{\hat{b}_1}{SE(\hat{b}_1)}; t = \frac{b_0}{SE(b_0)}$$

Where bias-corrected parameters are as defined above and standard errors ( $SE$ ) are as defined by Fuller (1987). Measurement-error models were only used to predict gill-net CPUE when the model slope and intercept were both significantly larger than zero ( $P \leq 0.05$ ). Years in which bottom-trawl density was zero were not used to estimate parameters of the measurement-error model. This method was used to predict gill-net CPUE for three spatial units (Figure 6).

### ***Combined Index of Spawning Stock Size***

To index cisco spawning stock size, the geometric mean density of adult cisco in bottom-trawls was combined with the geometric mean CPUE of adult cisco in fishery-independent gill-net surveys or targeted commercial fisheries. First, mean density and CPUE estimates were  $\log_e$ -transformed to meet assumptions of normality (Zar 1999), and spatial unit averages and standard deviations were calculated from pooled means. All mean density and CPUE estimates were assumed to be drawn from a standard normal distribution with average and standard deviation identical to those calculated from pooled means. Mean density and CPUE estimates were then converted to  $Z$ -scores (Zar 1999):

$$Z = \frac{X - \mu}{\sigma}$$

Where  $Z$  is the standardized value calculated for each mean density or CPUE estimate,  $X$  is the mean density or CPUE estimate,  $\mu$  is the average of pooled means for each spatial unit, and  $\sigma$  is the standard deviation of pooled means for each spatial unit (Zar 1999). The  $Z$ -scores for each index of cisco spawning stock size were then averaged across capture methods and back-transformed into units of bottom-trawl density (fish/ha) using the average and standard deviation calculated from pooled means. In some cases, back-transformation resulted in estimates of cisco spawning stock size  $<0.145$  fish/ha, so  $\frac{1}{2}$  the minimum observed bottom-trawl density (0.145 fish/ha) was used to replace each estimate  $<0.145$  fish/ha. This situation was due to small indices of cisco spawning stock size in both bottom-trawls and fishery-independent gill-net surveys or targeted commercial fisheries.

### ***Model Description, Selection, and Validation***

To identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior, estimates of spawner density were paired with estimates of recruit density two years later, and a sequence of Ricker stock-recruitment models (Ricker 1975) were fitted to describe varying spatial scales for age-1 cisco recruitment dynamics in Lake Superior. The Ricker stock-recruitment model describes recruitment of the  $i^{\text{th}}$  year-class ( $R_i$ ) as a function of spawning stock size ( $S_i$ ; Ricker 1975):

$$R_i = \alpha S_i e^{-\beta S_i} e^{\epsilon}$$

Where  $\alpha$  is the number of recruits produced per spawner at low spawning stock size,  $\beta$  is the rate at which the logarithm of recruits per spawner declines with spawning stock size,

and  $e^\varepsilon$  = multiplicative process error (Ricker 1975). An insignificant  $\beta$  -coefficient indicates a density-independent recruitment rate, a negative  $\beta$  -coefficient indicates a compensatory density-dependent recruitment rate, and a positive  $\beta$  -coefficient indicates a depensatory density-dependent recruitment rate (Hilborn and Walters 1992). Stock-recruitment errors are usually lognormal (Peterman 1981), so parameters ( $\alpha$  and  $\beta$ ) were estimated using linear regression (Zar 1999) and the additive-error  $\log_e$ -transformed model:

$$\log_e(R_i / S_i) = \log_e(\alpha) - \beta S_i + \varepsilon$$

Stock-recruit density estimates were used to fit stock-recruitment curves at five different spatial scales in Lake Superior. Spatial models included: (1) a 22-parameter global model (Model 1) where a separate stock-recruitment curve was fit to density estimates for each of 11 putative stocks; (2) a 2-parameter reduced model (Model 2) where one stock-recruitment curve was fit to density estimates for the entire lake; (3) a 6-parameter regional model (Model 3) where separate stock-recruitment curves were fit to density estimates for western, eastern, and northern stocks; (4) an 8-parameter regional model (Model 4) where separate stock-recruitment curves were fit to density estimates for western, southern, eastern, and northern stocks; and (5) an 8-parameter regional model (Model 5) where separate stock-recruitment curves were fit to density estimates for a different grouping of western, southern, eastern, and northern stocks (Figure 7).

The most parsimonious model describing age-1 cisco recruitment dynamics in Lake Superior was selected from the set of candidate models using Akaike's Information

Criterion (  $AIC$  ) and likelihood statistics (Anderson et al. 2000; Burnham and Anderson 2002):

$$AIC = n \log_e \left( \frac{RSS}{n} \right) + 2K$$

Where  $n$  = sample size,  $RSS$  = residual sum of squares for each model, and  $K$  = number of parameters estimated for each model (Burnham and Anderson 2002). Because the number of data points used in model construction was small compared to the number of model parameters ( $n / K < 40$ ) for most (3 of 5) models, a second-order modification of the  $AIC$  statistic (  $AIC_c$  ) was used for model ranking (Burnham and Anderson 2002):

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$$

All models were ranked relative to the most parsimonious model (lowest  $AIC_c$  value) based on scaled  $AIC_c$  values (  $\Delta AIC_c$  ), which were calculated as the difference between the lowest  $AIC_c$  value (  $AIC_{c\min}$  ) and  $AIC_c$  values of other models. Primary inferences were drawn from models within 4–7  $\Delta AIC_c$  units of  $AIC_{c\min}$  (Burnham and Anderson 2002). Akaike weights (  $w_i$  ) were calculated to determine the weight of evidence in favor of each model (Burnham and Anderson 2002).

For the most parsimonious model describing age-1 cisco recruitment dynamics in Lake Superior, peak recruitment (  $R_{\max}$  ) and the spawning stock size that produced peak recruitment (  $S_{\max}$  ) were estimated for each region to show how cisco recruitment differed among regions. Peak recruitment was estimated as:

$$R_{\max} = \frac{\alpha}{\beta e}$$

Where  $\alpha$  and  $\beta$  are parameters estimated from the Ricker stock-recruitment model (Ricker 1975; Hilborn and Walters 1992). The spawning stock size that produced peak recruitment was estimated as:

$$S_{\max} = \frac{1}{\beta}$$

Where  $\beta$  is the density-dependent parameter estimated from the Ricker stock-recruitment model (Ricker 1975; Hilborn and Walters 1992).

## RESULTS

### *Spawner and Recruit Density*

In years used for model construction, estimates of recruit density varied 102-fold in Minnesota, 197-fold in WI-1, 2,975-fold in WI-2, 158-fold in Western Keweenaw, 1,424-fold in MI-4, 435-fold in Michigan South Shore, 10-fold in Whitefish Bay, 104-fold in Eastern Canada, 71-fold in Nipigon Bay, 48-fold in Black Bay, and 276-fold in Thunder Bay. Average recruit density was greatest in WI-2 (38.1 fish/ha), followed by MI-4 (11.9 fish/ha), WI-1 (11.2 fish/ha), Michigan South Shore (4.8 fish/ha), Thunder Bay (4.6 fish/ha), Western Keweenaw (3.1 fish/ha), Nipigon Bay (2.1 fish/ha), Eastern Canada (1.6 fish/ha), Black Bay (1.4 fish/ha), Minnesota (1.1 fish/ha), and Whitefish Bay (0.4 fish/ha; Table 1). Based on available density estimates (1978–2007 in U.S. waters and 1989–2007 in Canadian waters), lake-wide recruitment events occurred in 1984,

1988–1990, 1998, and 2003. However, relative year-class strength during lake-wide recruitment events was highly variable among regions (Figures 8–11).

In years used for model construction, estimates of spawner density varied 1.2-fold in Minnesota, 120-fold in WI-1, 51-fold in WI-2, 19-fold in Western Keweenaw, 94-fold in MI-4, 6-fold in Michigan South Shore, 8-fold in Whitefish Bay, 5-fold in Eastern Canada, 7-fold in Nipigon Bay, 17-fold in Black Bay, and 28-fold in Thunder Bay. Average spawner density was greatest in WI-1 (8.6 fish/ha), followed by MI-4 (3.4 fish/ha), WI-2 (1.9 fish/ha), Thunder Bay (1.2 fish/ha), Black Bay (1.2 fish/ha), Nipigon Bay (0.5 fish/ha), Western Keweenaw (0.5 fish/ha), Whitefish Bay (0.5 fish/ha), Eastern Canada (0.4 fish/ha), Michigan South Shore (0.4 fish/ha), and Minnesota (0.2 fish/ha; Table 2). Based on available density estimates (1978–2007 in U.S. waters and 1989–2007 in Canadian waters), spawner densities were generally low prior to 1988, increased during 1988–1997, and decreased after 1997 (Figures 12–22).

### ***Spatial Scale***

Recruitment variation of cisco in Lake Superior was best described by an 8-parameter regional model (Model 4) with separate stock-recruitment relationships for western, southern, eastern, and northern stocks (Table 3). Regional stocks included: (1) Minnesota and WI-1 (Region 1), (2) WI-2, Western Keweenaw, and MI-4 (Region 2), (3) Michigan South Shore, Whitefish Bay, and Eastern Canada (Region 3), and (4) Nipigon Bay, Black Bay, and Thunder Bay (Region 4; Figure 7). The 4-stock regional model had a 96% likelihood of being the correct model of all models considered, was 28-fold more likely than the second-ranked model, and was 27-fold more likely than all other models combined. The spatial scale for modeling was ~260 km (range = 230–290 km).

### ***Model Parameters and Fit***

Estimates of the density-independent recruitment rate ( $\alpha$ ) and the rate of compensatory density-dependence ( $\beta$ ) varied among regions at different rates. The density-independent recruitment rate varied 2-fold among regions and the rate of compensatory density-dependence varied 21-fold among regions, and were greatest in Region 3 ( $\alpha = 4.9$  age-1 recruits/spawner and  $\beta = -3.4$  spawners<sup>-1</sup>), followed by Region 4 ( $\alpha = 4.8$  age-1 recruits/spawner and  $\beta = -1.3$  spawners<sup>-1</sup>), Region 2 ( $\alpha = 3.8$  age-1 recruits/spawner and  $\beta = -0.5$  spawners<sup>-1</sup>), and Region 1 ( $\alpha = 2.4$  age-1 recruits/spawner and  $\beta = -0.2$  spawners<sup>-1</sup>; Table 4). Standard errors were relatively large for estimates of  $\alpha$  and small for estimates of  $\beta$ .

Estimates of peak recruitment ( $R_{\max}$ ) and the spawning stock size that produced peak recruitment ( $S_{\max}$ ) varied among regions. Peak recruitment varied 10-fold among regions and the spawning stock size that produced peak recruitment varied 21-fold among regions, and were greatest in Region 1 ( $R_{\max} = 5.4$  age-1 recruits/ha and  $S_{\max} = 6.1$  spawners/ha), followed by Region 2 ( $R_{\max} = 3.1$  age-1 recruits/ha and  $S_{\max} = 2.2$  spawners/ha), Region 4 ( $R_{\max} = 1.3$  age-1 recruits/ha and  $S_{\max} = 0.8$  spawners/ha), and Region 3 ( $R_{\max} = 0.5$  age-1 recruits/ha and  $S_{\max} = 0.3$  spawners/ha; Table 4; Figure 23). Adjusted  $R^2$  values were low for both linear and non-linear models for all four regions.

## **DISCUSSION**

My findings are consistent with previously observed regional differences in age-1 cisco year-class strength and regional deviations from normal patterns of recruitment



synchrony (Ebener et al. 2008; Stockwell et al. 2009), and support the hypothesis that cisco recruitment is regulated within four different regions of Lake Superior. Previously, commercial fishery records were used to identify six major cisco spawning stocks (Selgeby 1982) and eight discrete cisco spawning stocks (Goodyear et al. 1981) in Wisconsin waters of Lake Superior. More recently, genetically discrete cisco spawning stocks were identified in Black Bay and Thunder Bay (K. T. Scribner, Michigan State University, *Personal Communication*). Therefore, regions identified in my study may contain multiple discrete cisco spawning stocks.

The spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior was 16-fold larger than the average movement distance (16.5 km) and 3-fold larger than the maximum movement distance (88.5 km) reported for cisco in Lake Michigan (Smith and Van Oosten 1940), and suggests that large-scale abiotic factors are more important than small-scale biotic factors in regulating cisco recruitment in Lake Superior. Compared to the spatial scale of recruitment correlations for other fish species, the spatial scale for modeling was larger than for other freshwater species (<50 km), smaller than for marine species (~500 km), and similar to anadromous species and species with estuarine nursery regions (50–500 km; Myers et al. 1995; Myers et al. 1997; Myers 2001), which suggests that the effects of large-scale abiotic factors on cisco recruitment in Lake Superior are less important for other freshwater species, more important for marine species, and similarly important for anadromous species and species with estuarine nursery regions. Differences between the spatial scale for modeling and the spatial scale of recruitment correlations for other freshwater species may be related to the size of Lake Superior (Lawrie and Rahrer 1973), which is larger than most freshwater lakes, or the

early life-history characteristics of cisco in Lake Superior (Anderson and Smith 1971; Scott and Crossman 1973; Becker 1983; Selgeby et al. 1994; Oyadomari and Auer 2004), which are similar to marine species with planktonic larvae and species with estuarine nursery regions.

Density-independent recruitment rates estimated in my study were similar to a previous estimate for cisco in Lake Superior in all four regions, intermediate compared to estimates for other Great Lakes fish species in all four regions, and relatively constant among regions. Previously, a density-independent recruitment rate of 5.4 age-1 recruits per spawner was reported for cisco in Wisconsin waters of Lake Superior (Hoff 2004). The previously reported rate was greater than rates in my study, but within the range of estimation errors, which suggests that parameter estimates in my study did not differ substantially from the previous study. Density-independent recruitment rates for all four regions in my study were intermediate compared to previously reported rates for alewives (*Alosa pseudoharengus*) in Lake Ontario (0.7 age-1 recruits/spawner; O’Gorman et al. 2004) and Lake Michigan (0.5 age-3 recruits/spawner; Madenjian et al. 2005), walleye (*Sander vitreus*) in Lake Erie (8.4 age-2 recruits/spawner; Madenjian et al. 1996), and lake trout in Lake Superior (range = 0.1–3.6 age-7 recruits/spawner; Richards et al. 2004; Corradin et al. 2008), which suggests that the ability of cisco stocks in Lake Superior to reproduce at low spawning stock size is intermediate compared to other Great Lakes species. Relatively constant density-independent recruitment rates among regions in my study are consistent with previous studies (Myers et al. 1996; Myers et al. 1999) that found relatively constant within species maximum annual reproductive rates for multiple freshwater and marine fish stocks, and suggest that the ability to reproduce at low

spawning stock size may be genetically pre-determined and similar for cisco stocks throughout Lake Superior.

Rates of compensatory density-dependence estimated in my study were similar to a previous estimate for cisco in Lake Superior in two of four regions, differed from estimates for other Great Lakes fish species in three of four regions, and were highly variable among regions. Previously, a rate of compensatory density-dependence of  $-0.3 \text{ spawners}^{-1}$  was reported for cisco in Wisconsin waters of Lake Superior (Hoff 2004). In western and southern stocks, the previously reported rate was intermediate compared to rates in my study and within the range of estimation errors, which suggests that parameter estimates in my study did not differ substantially from the previous study. In eastern and northern stocks, the previously reported rate was lower than rates in my study and outside the range of estimation errors, which suggests that differences in parameter estimates between my study and the previous study were related to regional differences in compensatory density-dependence. Rates of compensatory density-dependence for most (3 of 4) regions in my study were greater than previously reported rates for alewives in Lake Ontario and Lake Michigan, walleye in Lake Erie, and lake trout in Lake Superior (range =  $-0.001$  to  $-0.250 \text{ spawners}^{-1}$ ; Madenjian et al. 1996; O’Gorman et al. 2004; Richards et al. 2004; Madenjian et al. 2005; Corradin et al. 2008), which suggests that compensatory density-dependence is more important in regulating cisco recruitment in Lake Superior than for other Great Lakes species. Highly variable rates of compensatory density-dependence among regions in my study suggest that large-scale abiotic factors drive regional differences in age-1 cisco year-class strength and regional deviations from normal patterns of recruitment synchrony in Lake Superior (Ebener et al. 2008; Stockwell

et al. 2009) through regional differences in compensatory density-dependence, such as egg predation (Dryer and Beil 1964; Anderson and Smith 1971; Becker 1983), larval predation (Pritchard 1931; Becker 1983; Hoff et al. 1997), or competition during the first year of life (Selgeby et al. 1978; Rudstam et al. 1993; Link et al. 1995; Jensen 1996; Kinnunen 1997; Pangle et al. 2004).

Estimates of peak recruitment and the spawning stock size that produced peak recruitment in my study were consistently lower than previous estimates for cisco in Lake Superior, varied among regions, and were greatest for the most productive (western and southern) and lowest for the least productive (eastern and northern) regions. Peak recruitment was lower than a previous estimate for cisco in Wisconsin waters of Lake Superior (8.0 age-1 recruits/ha; Hoff 2004) in all four regions, varied 10-fold among regions, and was 5-fold greater for western and southern stocks than eastern and northern stocks. The spawning stock size that produced peak recruitment was lower than a previous estimate for cisco in Wisconsin waters of Lake Superior (4.0 spawners/ha; Hoff 2004) in most (3 of 4) regions, varied 21-fold among regions, and was 8-fold greater for western and southern stocks than eastern and northern stocks. Consistently lower estimates of peak recruitment and the spawning stock size that produced peak recruitment in my study suggest that differences between my study and the previous study may be related to both spatial and temporal differences in the data used for analysis. Regional differences in peak recruitment and the spawning stock size that produced peak recruitment in my study suggest that carrying capacity may be an important underlying factor driving regional differences in rates of compensatory density-dependence for cisco stocks in Lake Superior.

I used single-factor stock-recruitment models to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior, but low adjusted  $R^2$  values for both linear and non-linear models for all four regions in my study suggest that one or more important variables may be missing from each regional model. Therefore, future studies of cisco stock-recruitment in Lake Superior should focus on developing multi-factor stock-recruitment models for regions identified in my study. Adding multiple biotic and abiotic factors to stock-recruitment models developed for regions identified in my study may help researchers identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics in Lake Superior, generate hypotheses that can be tested in future laboratory and field studies, and substantially improve model fit. Candidate variables for multi-factor models should include variables previously correlated to age-1 cisco recruitment or generally considered to regulate age-1 cisco recruitment in Lake Superior, such as wind speed, air temperature, slimy sculpin (*Cottus cognatus*) biomass, lake trout abundance (Hoff 2004), rainbow smelt (*Osmerus mordax*) abundance (Anderson and Smith 1971; Walter and Hoagman 1975; Selgeby et al. 1978; Hrabik et al. 1998; Cox and Kitchell 2004), bloater (*Coregonus hoyi*) abundance (Anderson and Smith 1971; Davis and Todd 1992), and the abundance of other cisco age-classes (Jensen 1996; Bronte et al. 2003; Hoff 2004), and variables previously correlated to recruitment of other coregonid species in the Great Lakes, such as ice cover (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993).

## **MANAGEMENT IMPLICATIONS**

The fish-community objective for prey species in Lake Superior calls for rehabilitation of cisco stocks to historic levels of abundance to provide a forage base for

lake trout and to support a commercial fishery (Busiahn 1990). Fishery management plans for the lower Great Lakes recognize the cisco as an important member of the native fish community and call for reestablishment of self-sustaining populations throughout the species historic range (Edsall and DeSorcie 2002). Previously, studies of cisco stock-recruitment in the Great Lakes were limited to one study of cisco stock-recruitment in Wisconsin waters of Lake Superior (Hoff 2004). The previous study identified and quantified the effects of multiple biotic and abiotic factors correlated to age-1 cisco recruitment, but failed to identify or quantify the spatial scale for cisco recruitment dynamics, and management parameters estimated for cisco stocks in Wisconsin waters of Lake Superior were not broadly applicable to cisco stocks in other regions of Lake Superior or the lower Great Lakes. Therefore, fishery managers were forced to carry out cisco restoration and management efforts without reliable estimates of the spatial scale for cisco recruitment dynamics and basic management parameters. My findings provide the first estimate of the spatial scale for cisco recruitment dynamics and the first comprehensive estimates of basic management parameters for cisco stocks in Lake Superior, and are broadly applicable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin.

My findings suggest that cisco spawning stock size should be maintained near densities of 6.1 spawners/ha in western stocks, 2.2 spawners/ha in southern stocks, 0.3 spawners/ha in eastern stocks, and 0.8 spawners/ha in northern stocks to produce peak recruitment of age-1 cisco in Lake Superior. Regional differences in the spawning stock size required to produce peak recruitment of age-1 cisco in Lake Superior suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should

address cisco restoration and management efforts on a regional scale in each lake. The spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior suggests that regions targeted for cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin should range from 200–300 km.

Estimates of the spawning stock size that produced peak recruitment of age-1 cisco in Lake Superior can be used as targets for the restoration of remnant cisco populations throughout the lower Great Lakes, but because the productivity and fish-community structure of Lake Superior differs from many of the lower Great Lakes, fishery managers should exercise caution when applying management parameters estimated in my study to the lower Great Lakes. Because of Lake Superior's low productivity (Hansen 1990; Horns 2003), fishery managers should consider regional estimates of the spawning stock size that produced peak recruitment of age-1 cisco in Lake Superior as minimum targets for the restoration of cisco populations throughout the lower Great Lakes. Therefore, the spawning stock size that produced peak recruitment of age-1 cisco in western stocks may be an appropriate minimum target for the restoration of cisco populations in Lake Ontario, Lake Erie, Lake Huron, and Lake Michigan. Because the fish-community structure of the lower Great Lakes is dominated by invasive species, such as the alewife (Fitzsimons and O'Gorman 2006; Stockwell et al. 2009), fishery managers throughout the lower Great Lakes should also evaluate the potential effects of increased interspecific predation and competition on cisco populations prior to addressing cisco restoration and management efforts in each lake.

Table 1. Summary statistics for estimated recruit densities used in model construction.

Number of years used in model construction ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) recruit density, average coefficient of variation (Avg.  $CV$ ), and average relative standard error (Avg.  $RSE$ ) are provided for each spatial unit.

Spatial Unit	Recruit Density Bottom-Trawls (fish/ha)					
	$n$	Avg.	Min.	Max.	Avg. $CV$	Avg. $RSE$
MINN	22	1.1	0.2	14.8	2.67	0.89
WI-1	14	11.2	0.2	45.9	110.31	62.24
WI-2	28	38.1	0.2	431.3	3.07	0.94
WKEW	16	3.1	0.2	22.9	5.29	2.63
MI-4	26	11.9	0.2	206.5	8.73	4.07
MISS	20	4.8	0.2	63.1	5.79	2.44
WFBY	11	0.4	0.2	1.5	1.65	0.75
ECAN	12	1.6	0.2	15.1	1.43	0.47
NIPB	17	2.1	0.2	10.2	5.68	2.15
BLKB	17	1.4	0.2	7.0	42.49	21.25
THBY	17	4.6	0.2	40.0	15.40	6.93



Table 2. Summary statistics for estimated spawner densities used in model construction. Number of years used in model construction ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) spawner density, average coefficient of variation (Avg. *CV* Trawls) and relative standard error (Avg. *RSE* Trawls) for bottom-trawl density, and average coefficient of variation (Avg. *CV* Gill-Nets) and relative standard error (Avg. *RSE* Gill-Nets) for gill-net CPUE are provided for each spatial unit.

Spatial Unit	Spawner Density (fish/ha)							
	$n$	Avg.	Min.	Max.	Avg. <i>CV</i> Trawls	Avg. <i>RSE</i> Trawls	Avg. <i>CV</i> Gill-Nets	Avg. <i>RSE</i> Gill-Nets
MINN	22	0.2	0.2	0.2	0.36	0.13	1.24	0.36
WI-1	14	8.6	0.3	36.2	19.59	10.43	2.42	0.49
WI-2	28	1.9	0.2	8.1	4.30	1.31	1.86	0.27
WKEW	16	0.5	0.2	2.7	2.39	0.96	1.94	0.56
MI-4	26	3.4	0.2	13.7	13.00	5.05	2.14	0.76
MISS	20	0.4	0.2	0.9	6.64	2.71	2.36	0.83
WFBY	11	0.5	0.2	1.2	2.50	0.84	77.28	54.17
ECAN	12	0.4	0.2	0.7	3.16	0.99	111.76	78.68
NIPB	17	0.5	0.2	1.2	4.30	1.68	4.68	2.99
BLKB	17	1.2	0.2	3.8	9.31	4.66	1.20	0.15
THBY	17	1.2	0.2	4.0	11.97	5.42	0.82	0.14

Table 3. Comparison of Ricker stock-recruitment models describing age-1 cisco recruitment dynamics in Lake Superior. Models are ranked in order of scaled second-order Akaike Information Criterion ( $AIC_c$ ) values. Akaike weights ( $w_i$ ) can be interpreted as the probability that a given model is the correct model of all models considered. The top-ranked model (Model 4) had a 96% likelihood of being the correct model of all models considered, was 28-fold more likely than the second-ranked model, and was 27-fold more likely than all other models combined.

<b>Model</b>	<b><math>n</math></b>	<b>Parameters</b>	<b><math>RSS</math></b>	<b><math>AIC</math></b>	<b><math>AIC_c</math></b>	<b>Scaled <math>AIC_c</math></b>	<b><math>w_i</math></b>
4	200	8	550.02	218.33	219.08	0.00	0.96
5	200	8	568.75	225.02	225.78	6.70	0.03
3	200	6	600.69	231.95	232.39	13.31	0.00
1	200	22	517.71	234.22	239.94	20.85	0.00
2	200	2	672.64	246.58	246.64	27.56	0.00

Table 4. Comparison of regional stock-recruitment curves based on the top-ranked model describing age-1 cisco recruitment dynamics in Lake Superior. Estimated parameters ( $\alpha$  and  $\beta$ ) and standard errors ( $SE$ ) are provided, along with peak recruitment ( $R_{\max}$ ), the spawning stock size that produced peak recruitment ( $S_{\max}$ ), and adjusted  $R^2$  values for both linear and non-linear versions of the Ricker stock-recruitment model. Differences among regional models were primarily driven by different levels of compensatory density-dependence in each region.

<b>Region</b>	<b><math>\alpha</math></b>	<b><math>SE</math></b>	<b><math>\beta</math></b>	<b><math>SE</math></b>	<b><math>R_{\max}</math></b>	<b><math>S_{\max}</math></b>	<b>Adjusted <math>R^2</math> Linear Model</b>	<b>Adjusted <math>R^2</math> Non-Linear Model</b>
MINN								
WI-1	2.4	0.78	-0.2	0.04	5.4	6.1	0.32	0.09
WI-2								
WKEW								
MI-4	3.8	1.20	-0.5	0.08	3.1	2.2	0.29	0.06
MISS								
WFBY								
ECAN	4.9	2.44	-3.4	0.93	0.5	0.3	0.23	0.03
NIPB								
BLKB								
THBY	4.8	1.60	-1.3	0.24	1.3	0.8	0.38	0.05

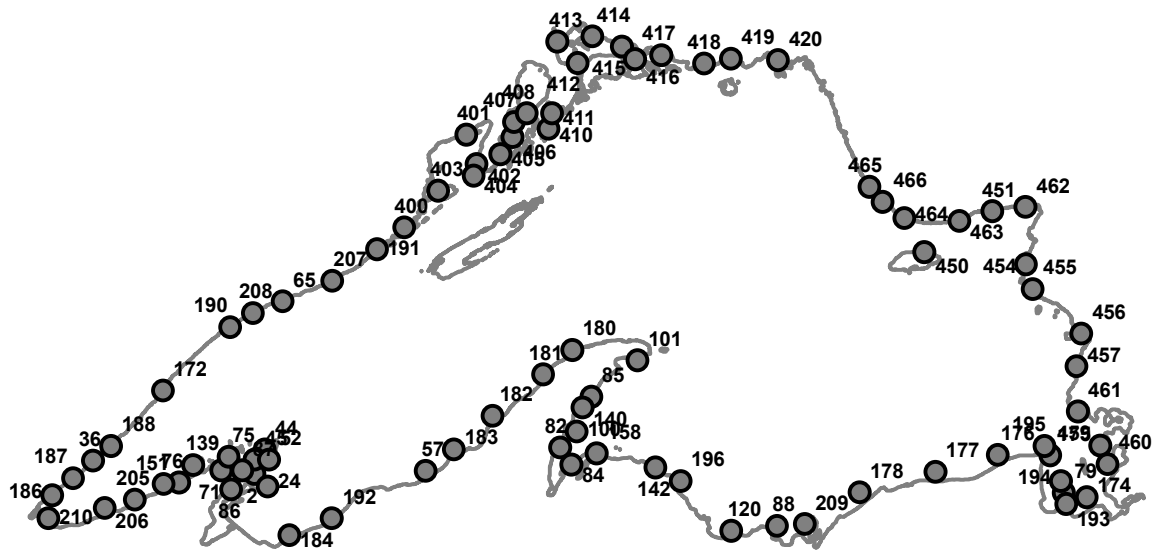


Figure 1. Locations of spring bottom-trawl survey stations in Lake Superior. Individual survey stations are denoted by a unique numeric code. Survey stations in U.S. waters are numbered  $<300$  and survey stations in Canadian waters are numbered  $\geq 400$  (USGS, Lake Superior Biological Station, Ashland, WI).

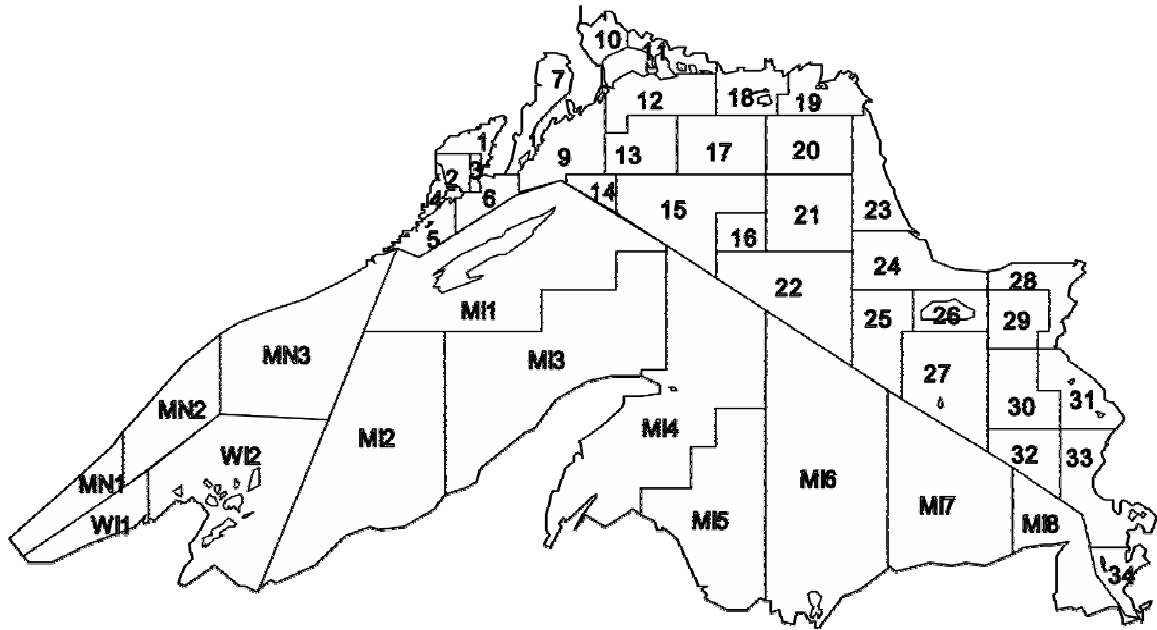


Figure 2. Locations of lake trout management units in Lake Superior. Jurisdictions in U.S. waters are denoted by a unique alpha-numeric code (MI = Michigan, WI = Wisconsin, and MN = Minnesota) and jurisdictions in Canadian waters are denoted by a unique numeric code (Hansen 1996). In Canadian waters, partial unit boundaries were added from the northern point of MI-8 east to the Canadian shoreline (unit 33), the western point of unit 14 northwest to the Canadian shoreline (unit 9), and the tip of the peninsula between Black Bay and Thunder Bay south to the boundary of MI-1 (unit 6). Partial unit boundaries were added to loosely correspond to the boundaries of U.S. Geological Survey Eco-Regions (described below), and were needed for weighting targeted commercial fishery CPUE used to index cisco spawning stock size.

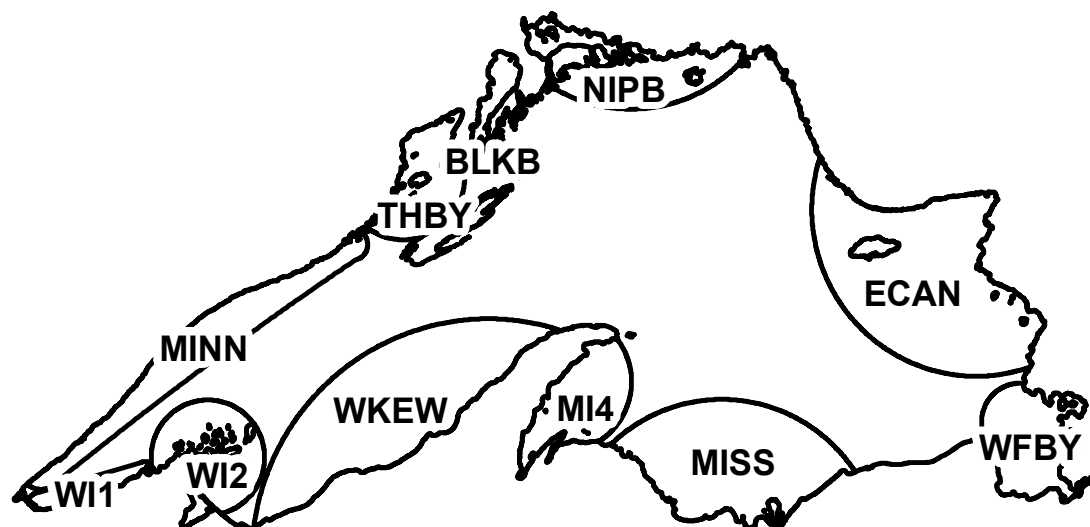


Figure 3. Spatial units used for stock-recruitment analysis (Minnesota-MINN corresponds to a combination of lake trout management units MN-1, MN-2, and MN-3; WI-1 corresponds to lake trout management unit WI-1; WI-2 corresponds to lake trout management unit WI-2; Western Keweenaw-WKEW corresponds to a combination of lake trout management units MI-2 and MI-3; MI-4 corresponds to lake trout management unit MI-4; Michigan South Shore-MISS corresponds to a combination of lake trout management units MI-5 and MI-6; Whitefish Bay-WFBY corresponds to a combination of lake trout management units MI-8, 34, and the southern 63.5% of unit 33; Eastern Canada-ECAN corresponds to a combination of lake trout management units 23, 24, 26, 28, 29, 31, and the northern 36.5% of unit 33; Nipigon Bay-NIPB corresponds to a combination of lake trout management units 10, 11, 12, 18, and 19; Black Bay-BLKB corresponds to a combination of lake trout management unit 7, the eastern 41.2% of unit 6, and the western 28.8% of unit 9; Thunder Bay-THBY corresponds to a combination of lake trout management units 1, 2, 3, 4, 5, and the western 58.8% of unit 6).

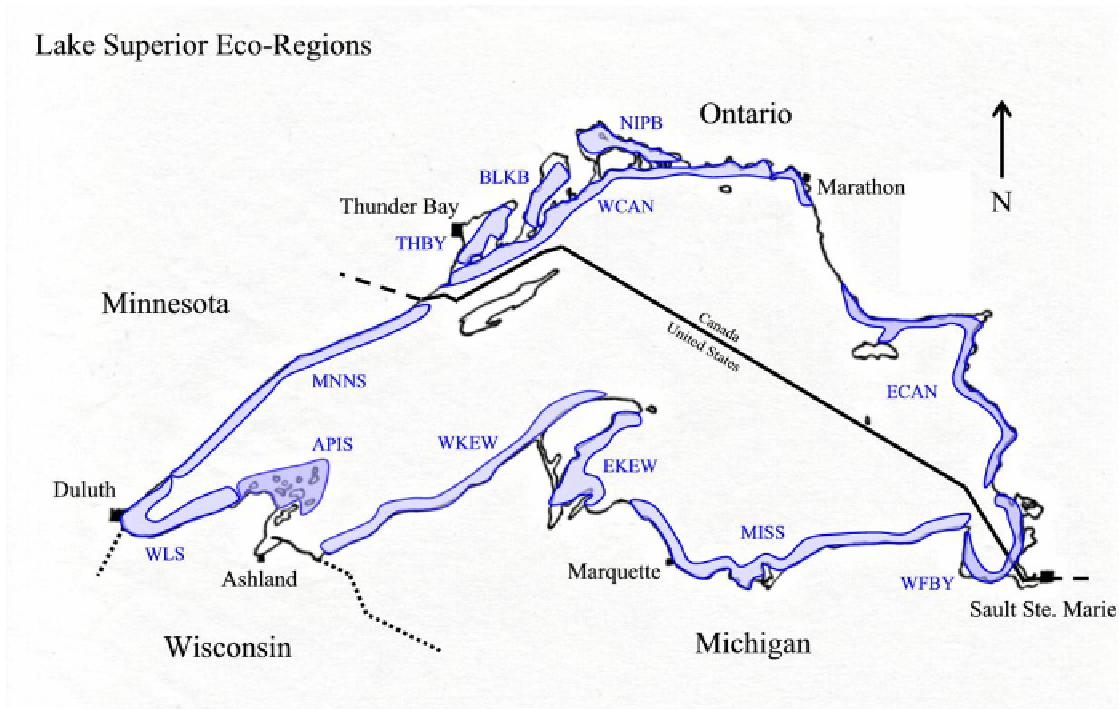


Figure 4. Locations of U.S. Geological Survey (USGS) Eco-Regions in Lake Superior. Eco-Regions were developed to summarize spring bottom-trawl data based on observed changes in habitat and fish-community structure (MNNS = Minnesota North Shore; WLS = Western Lake Superior; APIS = Apostle Islands; WKEW = Western Keweenaw; EKEW = Eastern Keweenaw; MISS = Michigan South Shore; WFBY = Whitefish Bay; ECAN = Eastern Canada; WCAN = Western Canada; NIPB = Nipigon Bay; BLKB = Black Bay; THBY = Thunder Bay; USGS, Lake Superior Biological Station, Ashland, WI).

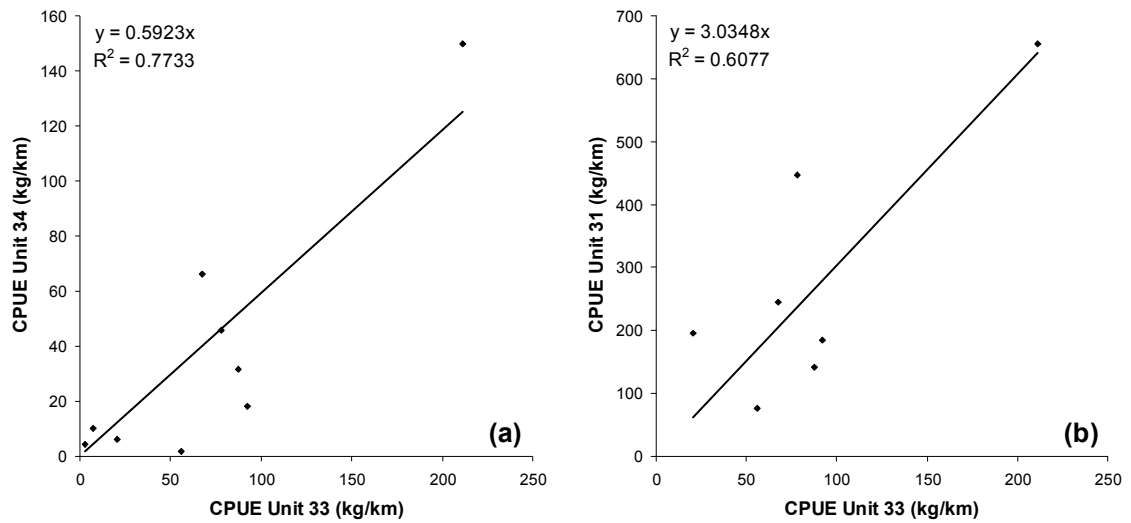


Figure 5. Relationship between targeted commercial fishery CPUE in (a) lake trout management units 33 and 34, and (b) lake trout management units 33 and 31.

Catch/effort in units 34 and 31 was strongly and linearly related to CPUE in unit 33 (passing through the origin). Linear regression was used to predict CPUE in eight years for both units 34 and 31.



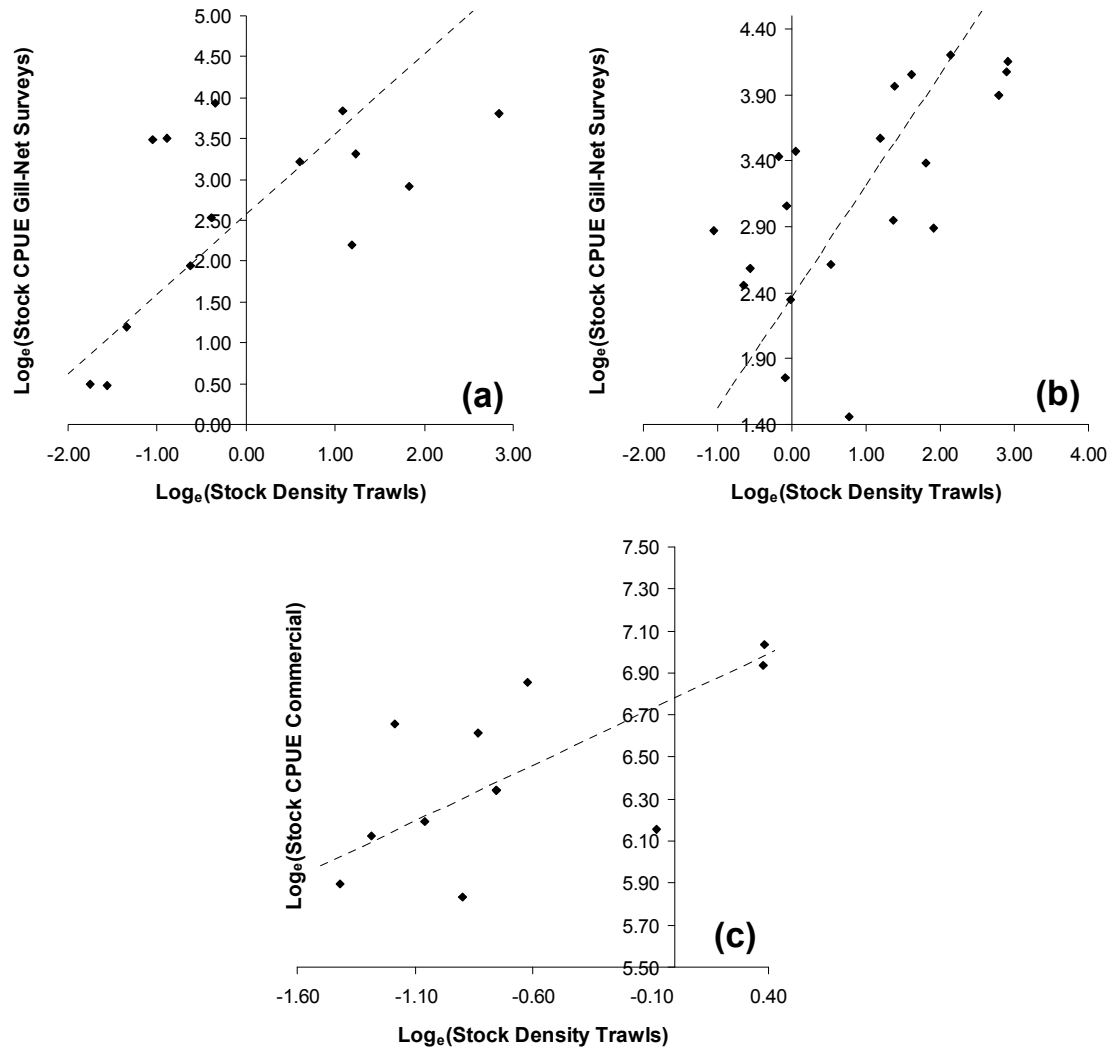


Figure 6. Relationship between  $\log_e$ -transformed adult cisco density and CPUE estimates in (a) bottom-trawls and fishery-independent gill-net surveys in the WI-2 spatial unit, (b) bottom-trawls and fishery-independent gill-net surveys in the MI-4 spatial unit, and (c) bottom-trawls and targeted commercial fisheries in the Nipigon Bay spatial unit. All relationships were significant ( $P \leq 0.05$ ) for both the slope and intercept terms.

Measurement-error models were used to predict gill-net CPUE from bottom-trawl density in 14 years for WI-2, seven years for MI-4, and five years for Nipigon Bay.

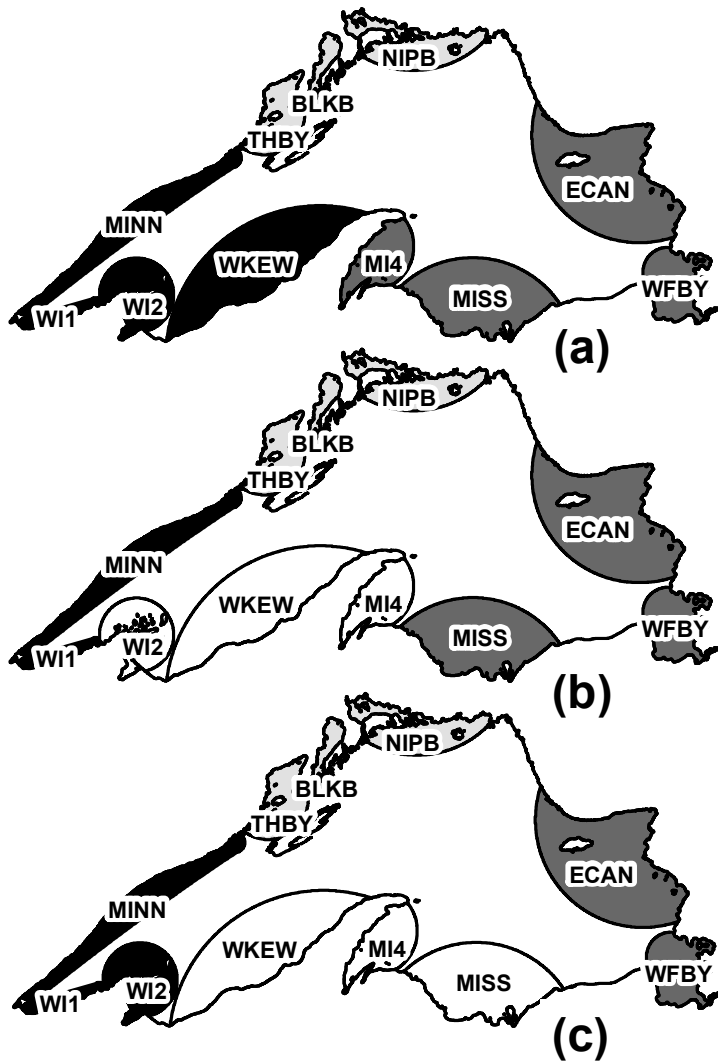


Figure 7. Regional stock groupings for (a) Model 3, (b) Model 4, and (c) Model 5. Like colors represent regional groupings for each model. Separate stock-recruitment curves were fitted to density estimates for each group of spatial units. The top-ranked model selected by Akaike's Information Criterion ( $AIC$ ) and likelihood statistics was Model 4. Regions identified for modeling were 230 km (Minnesota and WI-1), 240 km (WI-2, Western Keweenaw, and MI-4), 270 km (Michigan South Shore, Whitefish Bay, and Eastern Canada), and 290 km (Nipigon Bay, Black Bay, and Thunder Bay) measured at the widest point.

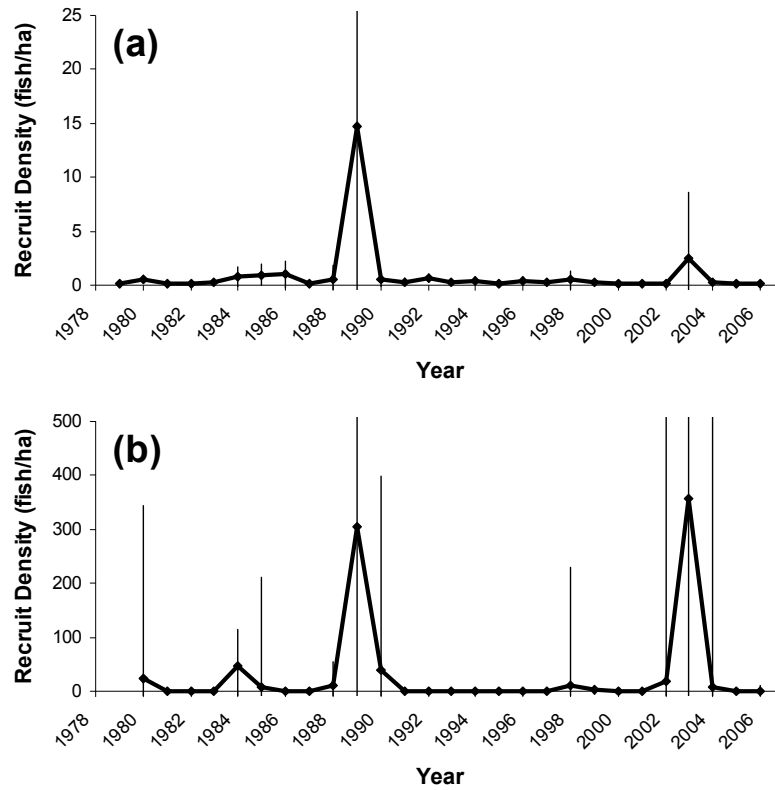


Figure 8. Geometric mean density of the 1979–2006 year-classes of cisco in (a) Minnesota and (b) WI-1 waters of Lake Superior. Years correspond to year of hatching. Density was indexed at age-1. Vertical bars represent standard errors and may be truncated due to scale.

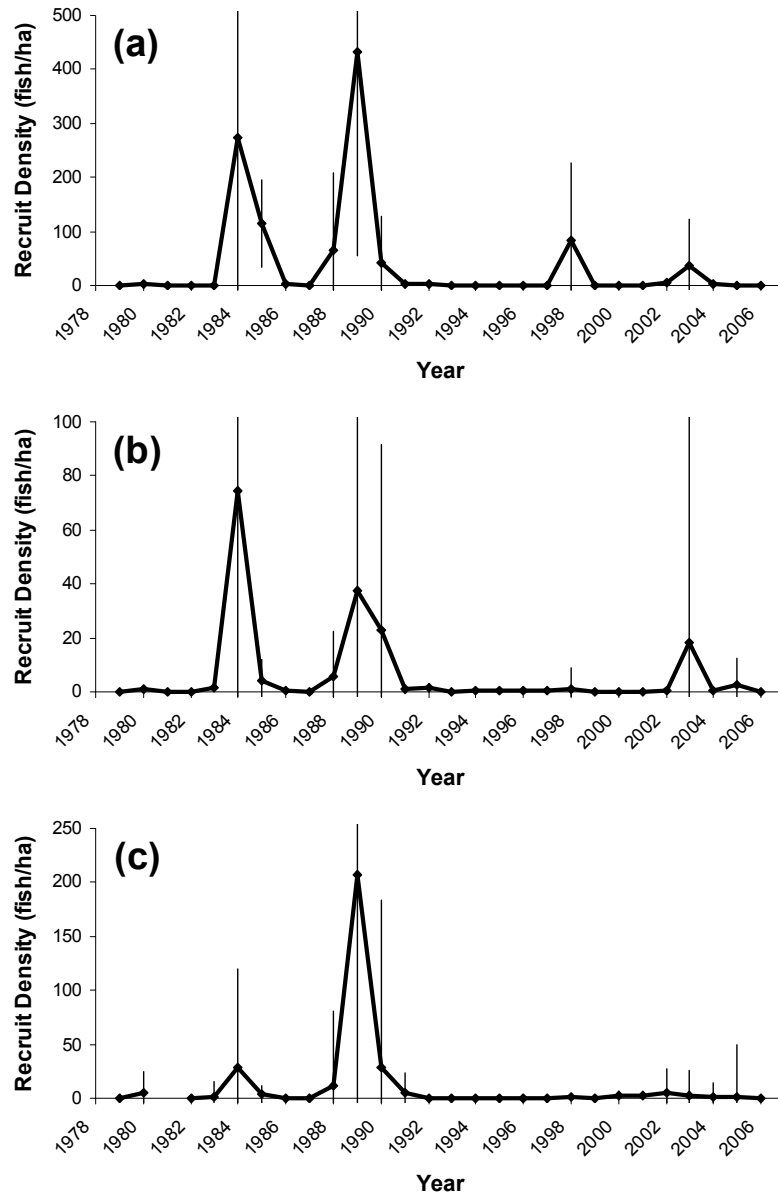


Figure 9. Geometric mean density of the 1979–2006 year-classes of cisco in (a) WI-2, (b) Western Keweenaw, and (c) MI-4 waters of Lake Superior. Years correspond to year of hatching. Density was indexed at age-1. Vertical bars represent standard errors and may be truncated due to scale.

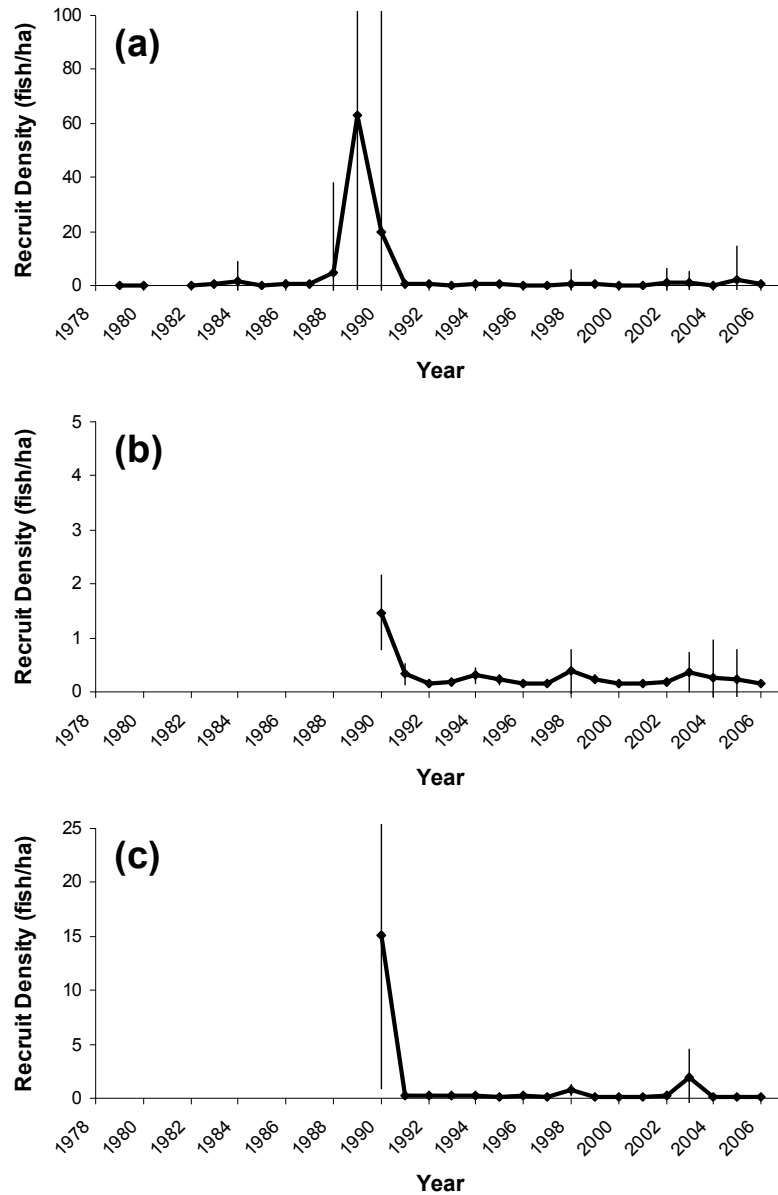


Figure 10. Geometric mean density of the 1979–2006 year-classes of cisco in (a) Michigan South Shore, (b) Whitefish Bay, and (c) Eastern Canada waters of Lake Superior. Years correspond to year of hatching. Density was indexed at age-1. Vertical bars represent standard errors and may be truncated due to scale.

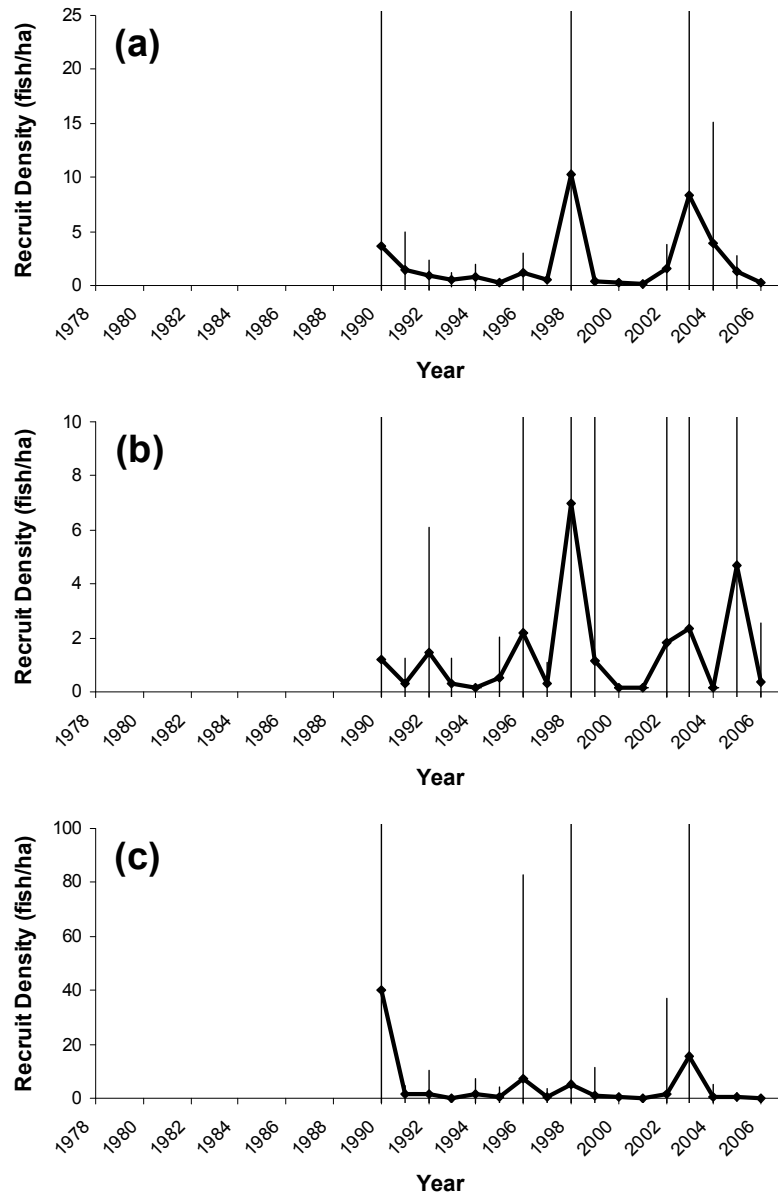


Figure 11. Geometric mean density of the 1979–2006 year-classes of cisco in (a) Nipigon Bay, (b) Black Bay, and (c) Thunder Bay waters of Lake Superior. Years correspond to year of hatching. Density was indexed at age-1. Vertical bars represent standard errors and may be truncated due to scale.

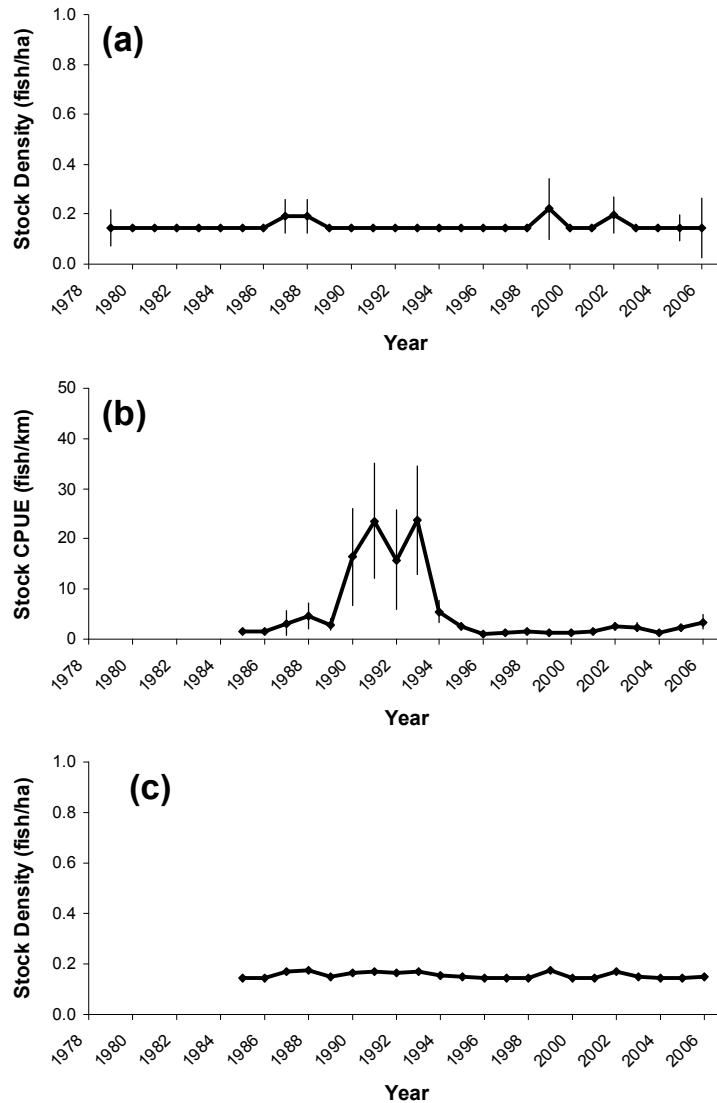


Figure 12. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Minnesota waters of Lake Superior estimated using (a) spring bottom-trawls, (b) fishery-independent gill-net surveys, and (c) combined spring bottom-trawls and fishery-independent gill-net surveys. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.

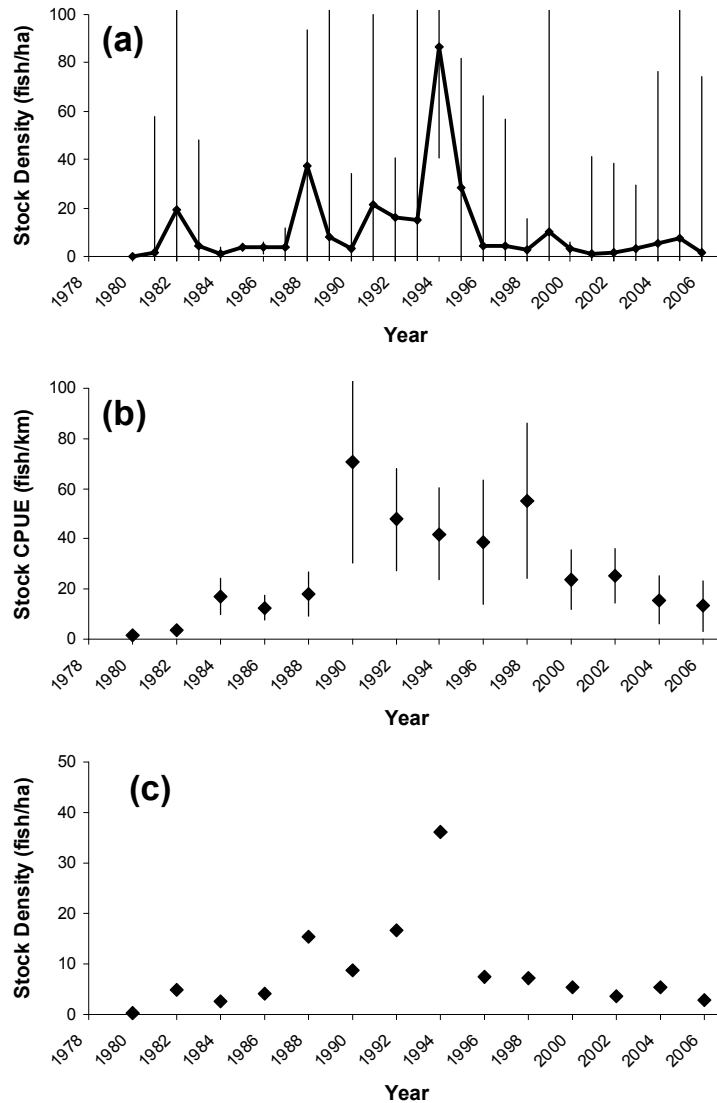


Figure 13. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in WI-1 waters of Lake Superior estimated using (a) spring bottom-trawls, (b) fishery-independent gill-net surveys, and (c) combined spring bottom-trawls and fishery-independent gill-net surveys. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.



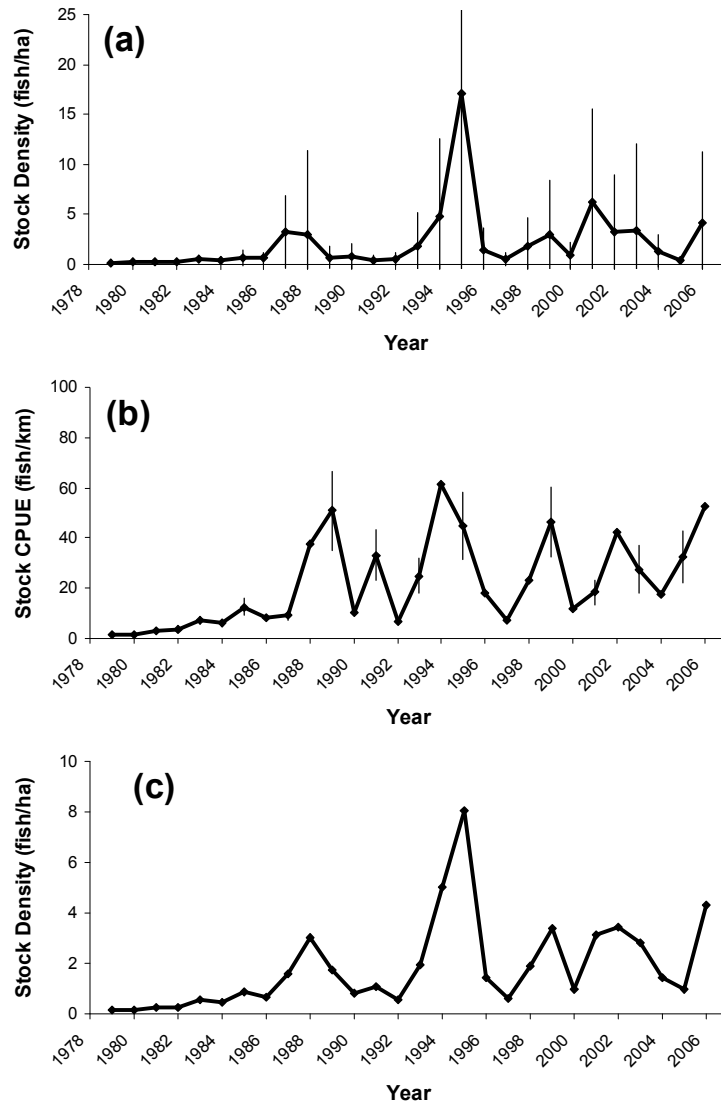


Figure 14. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in WI-2 waters of Lake Superior estimated using (a) spring bottom-trawls, (b) fishery-independent gill-net surveys, and (c) combined spring bottom-trawls and fishery-independent gill-net surveys. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006. In panel (b), points without error bars are predicted values.

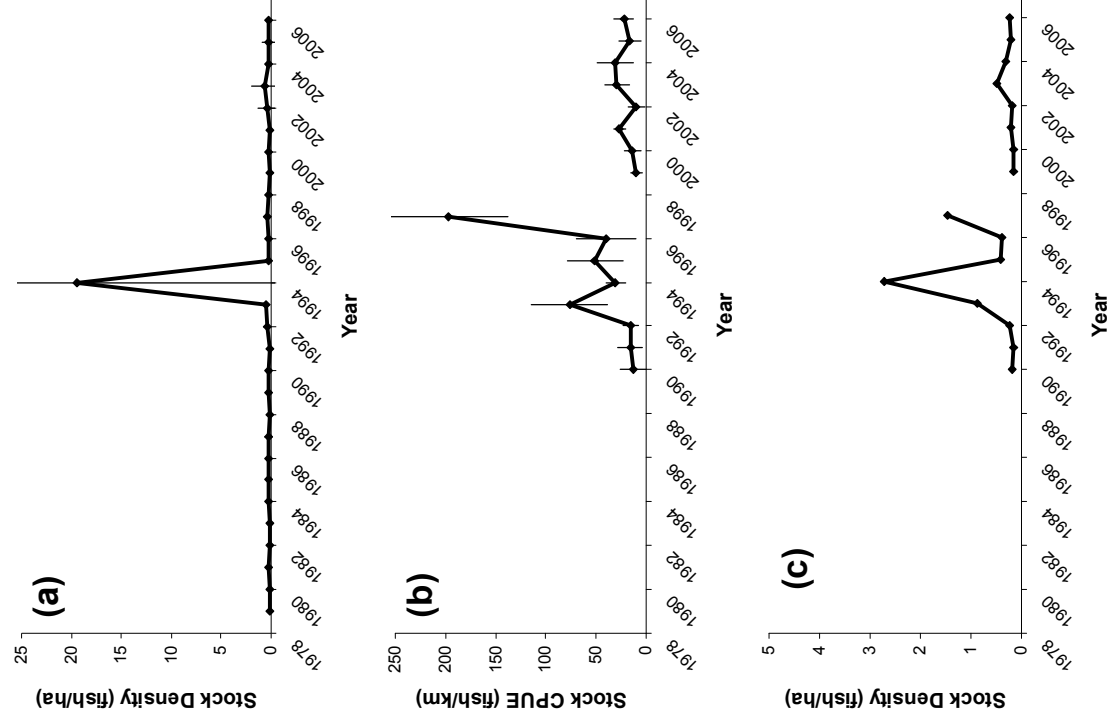


Figure 15. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Western Keweenaw waters of Lake Superior estimated using (a) spring bottom-trawls, (b) fishery-independent gill-net surveys, and (c) combined spring bottom-trawls and fishery-independent gill-net surveys. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.

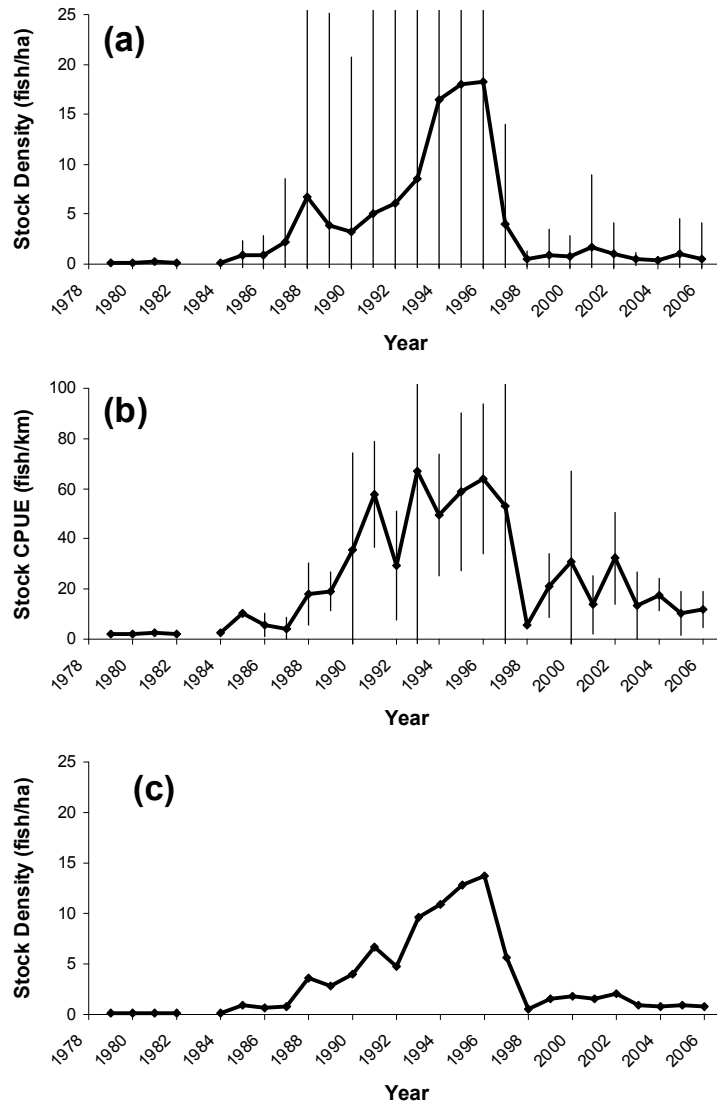


Figure 16. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in MI-4 waters of Lake Superior estimated using (a) spring bottom-trawls, (b) fishery-independent gill-net surveys, and (c) combined spring bottom-trawls and fishery-independent gill-net surveys. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006. In panel (b), points without error bars are predicted values.

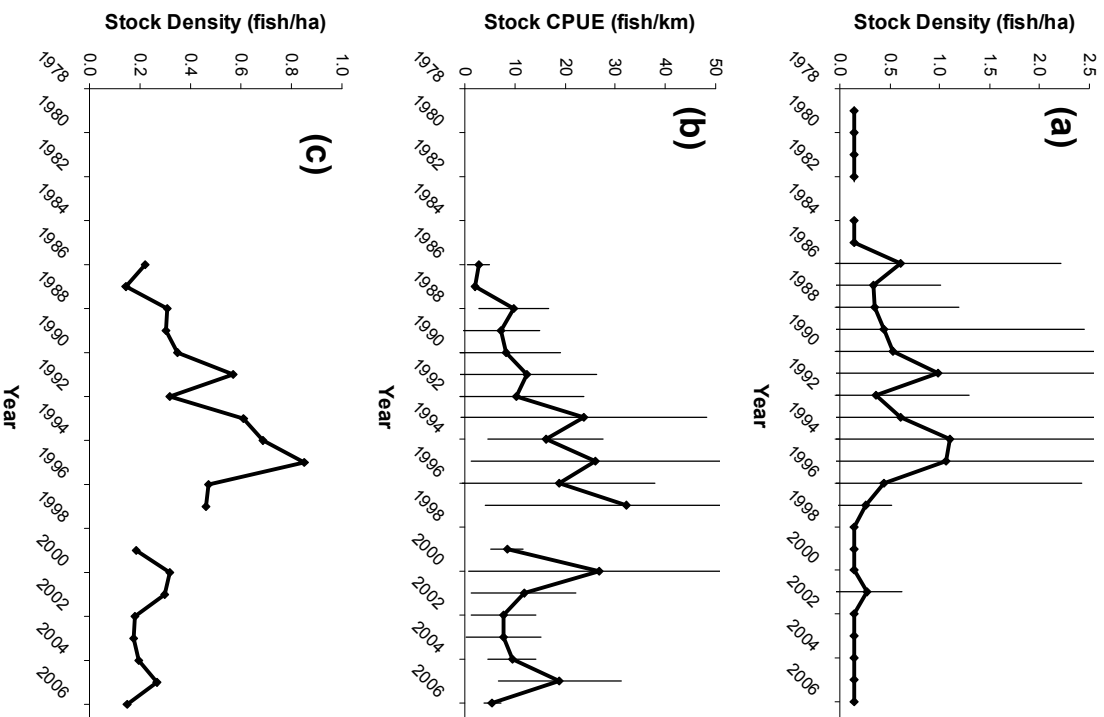


Figure 17. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Michigan South Shore waters of Lake Superior estimated using (a) spring bottom-trawls, (b) fishery-independent gill-net surveys, and (c) combined spring bottom-trawls and fishery-independent gill-net surveys. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.

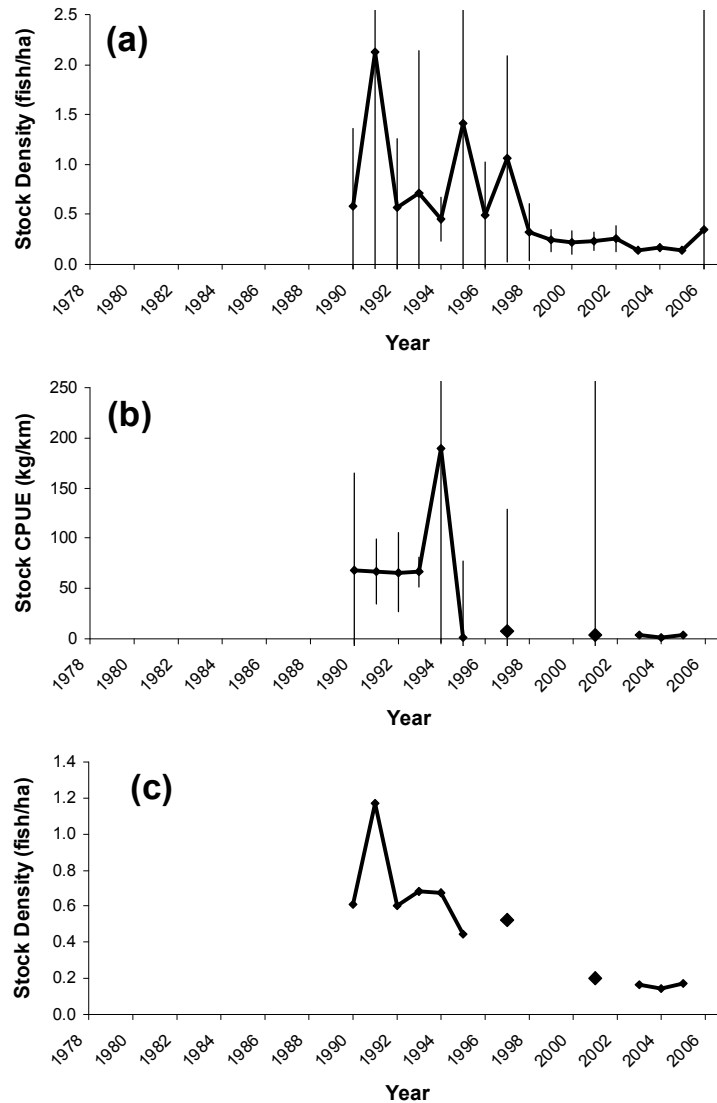


Figure 18. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Whitefish Bay waters of Lake Superior estimated using (a) spring bottom-trawls, (b) targeted commercial fisheries, and (c) combined spring bottom-trawls and targeted commercial fisheries. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.

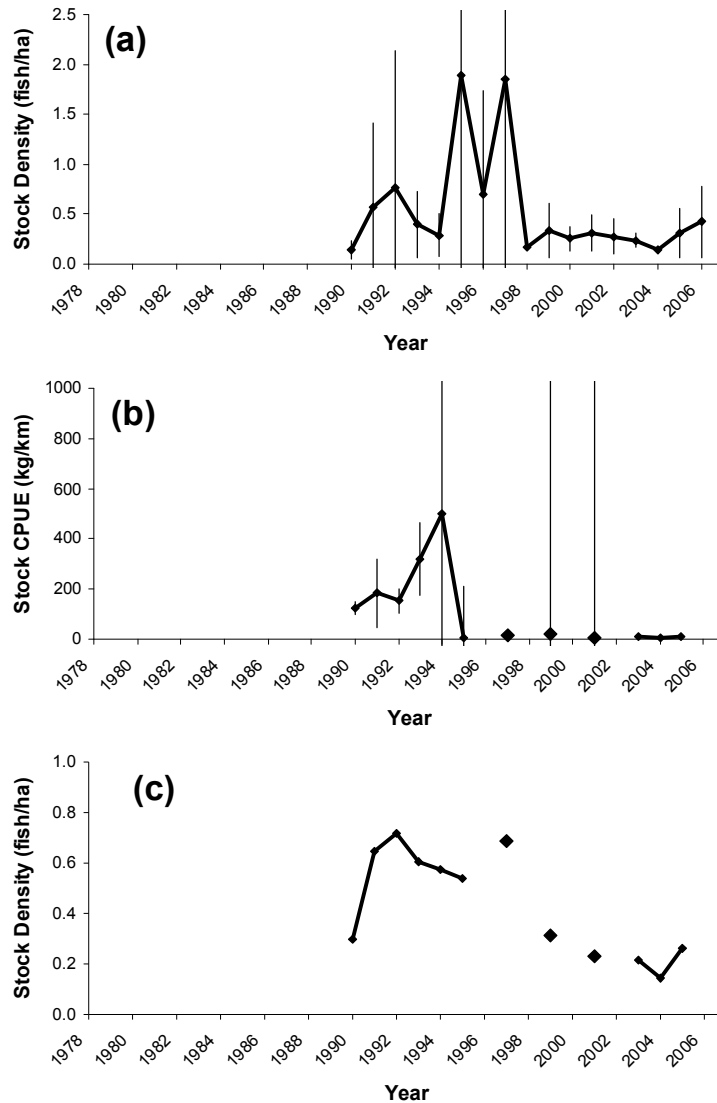


Figure 19. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Eastern Canada waters of Lake Superior estimated using (a) spring bottom-trawls, (b) targeted commercial fisheries, and (c) combined spring bottom-trawls and targeted commercial fisheries. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.

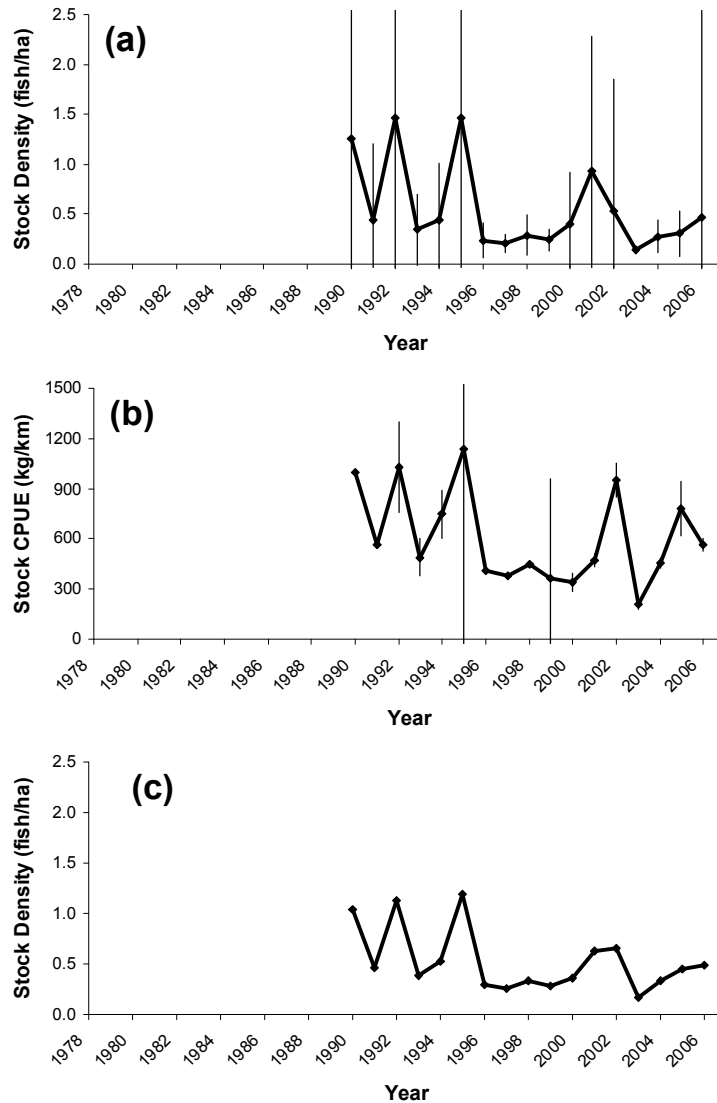


Figure 20. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Nipigon Bay waters of Lake Superior estimated using (a) spring bottom-trawls, (b) targeted commercial fisheries, and (c) combined spring bottom-trawls and targeted commercial fisheries. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006. In panel (b), points without error bars are predicted values.

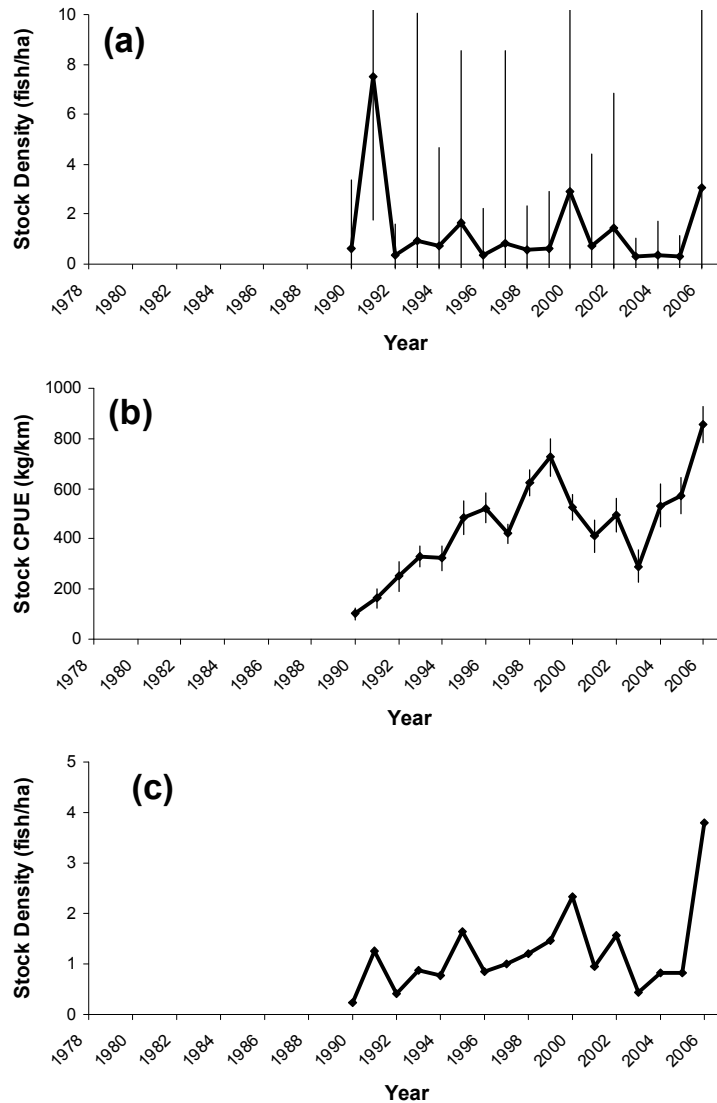


Figure 21. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Black Bay waters of Lake Superior estimated using (a) spring bottom-trawls, (b) targeted commercial fisheries, and (c) combined spring bottom-trawls and targeted commercial fisheries. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.



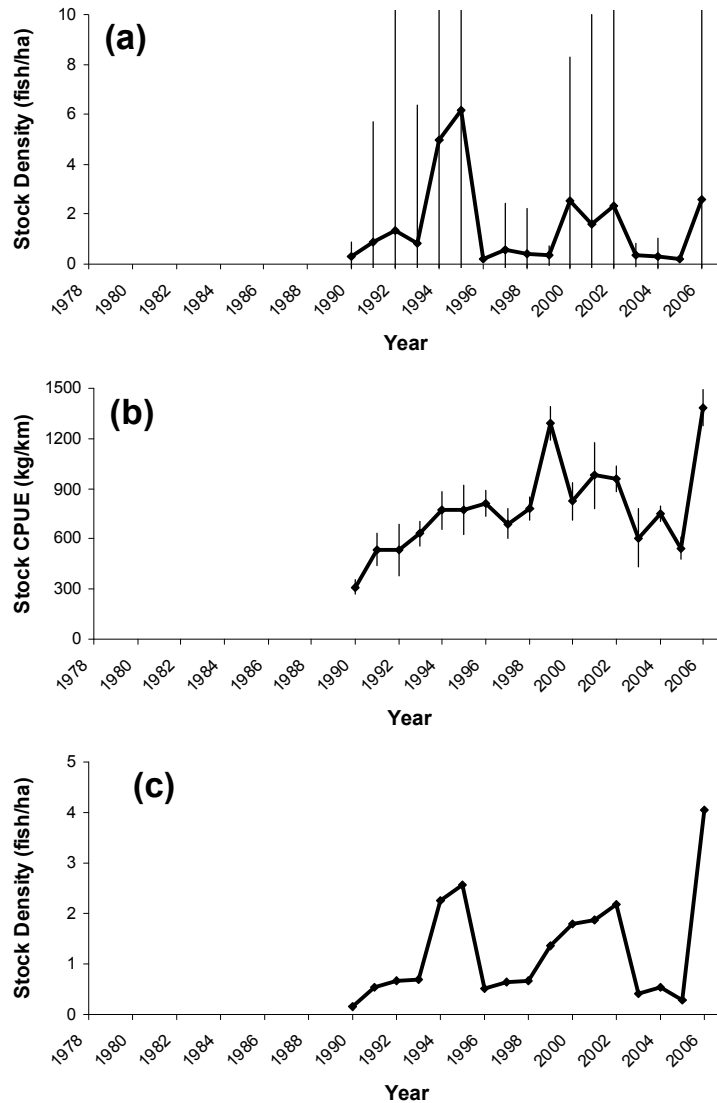


Figure 22. Spawning stock sizes that produced the 1979–2006 year-classes of cisco in Thunder Bay waters of Lake Superior estimated using (a) spring bottom-trawls, (b) targeted commercial fisheries, and (c) combined spring bottom-trawls and targeted commercial fisheries. Vertical bars represent standard errors and may be truncated due to scale. Years provided correspond to year of hatching for year-classes produced during 1979–2006.

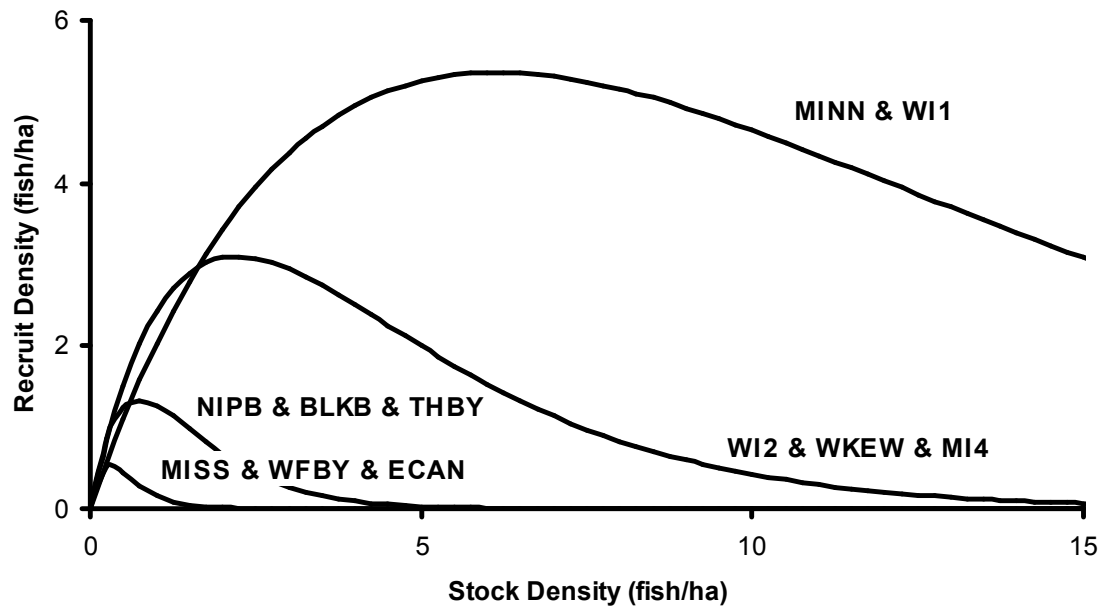


Figure 23. Comparison of regional stock-recruitment curves based on the top-ranked model describing age-1 cisco recruitment dynamics in Lake Superior. Differences among regional models were primarily driven by different levels of compensatory density-dependence in each region.

## **Chapter 2:**

### **Biotic and Abiotic Factors Regulating Cisco Recruitment Dynamics in Lake Superior during 1978–2007**

**Abstract** – The cisco (*Coregonus artedii*) was once the most abundant fish species in the Great Lakes, but currently, cisco populations are greatly reduced, and management agencies are attempting to restore the species throughout the basin. To increase understanding of biotic and abiotic factors regulating cisco recruitment dynamics in the Great Lakes, I used a generalized version of the Ricker stock-recruitment model to identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics within four different regions of Lake Superior. I found that recruitment variation of cisco in Lake Superior was correlated to adult spawning stock size in all four regions, the density of juvenile cisco during the year prior to cisco hatching in three of four regions, average April air temperature during spring when ciscoes were 11–12 months of age in three of four regions, average April wind speed during spring when ciscoes were hatching in two of four regions, and the biomass of rainbow smelt during the year of cisco hatching in one of four regions. My findings support the hypothesis that different biotic and abiotic factors regulate cisco recruitment within different regions of Lake Superior, suggest that air temperature during spring when ciscoes are 11–12 months of age drives recruitment variation on a lake-wide scale, whereas adult spawning stock size, intraspecific interactions with juvenile cisco, wind speed during spring when ciscoes are hatching, and interspecific interactions with rainbow smelt regulate recruitment variation on a regional scale in Lake Superior, and suggest that fishery managers

throughout Lake Superior and the entire Great Lakes basin should evaluate the potential effects of similar biotic and abiotic factors on recruitment prior to addressing cisco restoration and management efforts in each lake.

## INTRODUCTION

Historically, the cisco (*Coregonus artedii*) was the most abundant fish species in the Great Lakes (Smith 1995), but by the mid-1900s, cisco populations were greatly reduced throughout the basin (Fitzsimons and O’Gorman 2006). Over-fishing, habitat degradation, and interactions with exotic species caused cisco yield to decline by 80–99% in each lake (Edsall and DeSorcie 2002; Baldwin et al. 2006; Fitzsimons and O’Gorman 2006). Declining yields forced commercial fishers to target other species and brought about new regulations designed to prevent further losses, but except for a few strong year-classes in the 1990s, cisco stocks failed to recover in the lower Great Lakes (Fitzsimons and O’Gorman 2006). Reduced commercial fishing pressure enabled cisco to recover in portions of Lake Superior, but historic stock structure was altered (Goodyear et al. 1981; Selgeby 1982; Horns 2003), and abundance is now driven by highly erratic age-1 recruitment and few year-classes of adults (Bronte et al. 2003; Hoff 2004). Management agencies have begun exploring the feasibility of restoring cisco stocks throughout Lake Superior and the entire Great Lakes basin, but limited understanding of factors that drive recruitment variation and the spatial scale at which these factors operate remain barriers to establishing self-sustaining populations (Hoff 2004; Fitzsimons and O’Gorman 2006). Identifying major density-independent and density-dependent factors that regulate age-1 cisco recruitment dynamics in Lake Superior, and the spatial scale at which these factors operate, would be invaluable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin. A comprehensive analysis of cisco stock-recruitment in Lake Superior can provide a framework for addressing these questions.

The stock-recruitment relationship quantifies the ability of a fish stock to replace itself over a range of spawning stock sizes (Koslow 1991; Hilborn and Walters 1992), and is essential to many models used to estimate optimal fishing strategies (Koslow 1991). However, the stock-recruitment relationship is often obscured by the effects of environmental variation, thereby causing recruitment to appear independent of spawning stock size (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). Recruitment can be indexed at any life stage, but for many fish stocks, recruitment is established within the first year of life, primarily during egg and larval stages (Ricker 1975). Spawning stock size and environmental variation collectively determine egg and larval survival through density-dependent and density-independent mechanisms (Ricker 1975; Koslow 1991; Hilborn and Walters 1992). When annual variation in recruitment is driven by environmental variables, multi-factor stock-recruitment models can be used to quantify the separate effects of environmental variation and spawning stock size on recruitment (Ricker 1975; Walters et al. 1986; Madenjian et al. 1996; Hansen et al. 1998; Hoff 2004).

Cisco recruitment is not limited by habitat at any historic spawning sites in Lake Superior (Horns 2003). Over-fishing of discrete stocks (Selgeby 1982; Bronte et al. 2003) and interactions with rainbow smelt (*Osmerus mordax*; Anderson and Smith 1971; Selgeby et al. 1978; Cox and Kitchell 2004) are generally considered the two most likely factors contributing to cisco declines during the mid-1900s. Many studies have attempted to identify factors driving contemporary age-1 cisco recruitment dynamics in Lake Superior, but most have provided inconclusive or conflicting results. Factors that may regulate contemporary age-1 cisco recruitment include adult spawning stock size (Bronte et al. 2003; Horns 2003; Hoff 2004), commercial fishing mortality (Selgeby

1982), intraspecific and interspecific interactions (Dryer and Beil 1964; Dryer et al. 1965; Anderson and Smith 1971; Berst and Spangler 1973; Selgeby et al. 1978; Jensen 1996; Bronte et al. 2003; Horns 2003; Cox and Kitchell 2004; Hoff 2004), and environmental variation (Kinnunen 1997; Bronte et al. 2003; Hoff 2004). Highly synchronous, lake-wide recruitment events suggest that large-scale abiotic factors drive recruitment variation on a lake-wide scale, whereas small-scale biotic factors regulate recruitment variation on a regional scale in Lake Superior (Kinnunen 1997; Bronte et al. 2003; Stockwell et al. 2009).

My objective was to identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics in Lake Superior at spatial scales identified in Chapter 1. I used a generalized version of the Ricker stock-recruitment model (Ricker 1975; Hilborn and Walters 1992) to identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics within four different regions of Lake Superior. I expected to find a significant positive effect on age-1 cisco recruitment from wind speed during spring when ciscoes were hatching, and air temperature during spring when ciscoes were 11–12 months of age, because a previous study (Hoff 2004) showed that these factors were correlated to age-1 cisco recruitment in Lake Superior. I also expected to find a significant negative effect on age-1 cisco recruitment from slimy sculpin (*Cottus cognatus*) biomass during the year prior to cisco hatching, and lake trout (*Salvelinus namaycush*) biomass during the year of cisco hatching, because a previous study (Hoff 2004) showed that these factors were correlated to age-1 cisco recruitment in Lake Superior. Additionally, I expected to find significant negative effects on age-1 cisco recruitment from juvenile cisco density and rainbow smelt biomass during the year

of cisco hatching, because intraspecific interactions with other cisco age-classes and interspecific interactions with rainbow smelt are generally considered to limit age-1 cisco recruitment in Lake Superior (Anderson and Smith 1971; Selgeby et al. 1978; Jensen 1996; Bronte et al. 2003; Horns 2003; Cox and Kitchell 2004; Hoff 2004; Ebener et al. 2008; Stockwell et al. 2009). Finally, I expected to find that different variables explained variation in recruitment within different regions, because age-1 cisco recruitment has previously been observed to vary regionally in Lake Superior (Ebener et al. 2008; Stockwell et al. 2009).

## METHODS

### *Study Area*

Lake Superior is located near the head of the St. Lawrence River drainage, and is bordered by one Canadian province to the north (Ontario) and three U.S. states to the south (Michigan, Wisconsin, and Minnesota). A surface area of 8.24-million ha and a volume of 12,233 km<sup>3</sup> make Lake Superior the largest of the Great Lakes (Lawrie and Rahrer 1973). Lake Superior is highly oligotrophic (Hansen 1990). Primary production is near the low end of the range for freshwater lakes, so commercial fish production per unit of surface area is lower than in all other Great Lakes (Hansen 1990; Horns 2003). The native fish community of Lake Superior included 73 species in 18 families (Lawrie 1978), but biomass was dominated by lake trout, lake whitefish (*Coregonus clupeaformis*), cisco, and several species of related deepwater chubs (*Coregonus* spp.; Hansen 1990). Lake Superior has been little affected by point or non-point source pollution. The greatest influences from human development have been over-fishing and introductions of exotic species (Lawrie and Rahrer 1973).



### ***Cisco Recruitment and Spawning Stock Size***

Cisco recruitment was indexed using catch rates of age-1 cisco in spring bottom-trawl surveys when fish were 13–14 months of age and  $\leq 140$  mm total length (TL; Hoff 2004). Large cisco year-classes typically include a significant number of individuals  $>140$  mm TL (USGS, Lake Superior Biological Station, Ashland, WI), so length-frequency distributions were examined and the TL cut-off was adjusted to include all age-1 individuals. Spring bottom-trawl surveys of the Lake Superior near-shore fish community included an average of 49 sites (range = 32–53) in U.S. waters since 1978 and an average of 30 sites (range = 18–34) in Canadian waters since 1989 (Figure 1).

Yankee bottom-trawls with an 11.9-m head-rope and 12-mm mesh cod end were towed at a speed of 3.5 km per hour across contours at fixed sampling stations spaced every ~24 km along the U.S. and Canadian shorelines. Trawling began at a depth of 10–15 m and progressed in an offshore direction until 60 min elapsed or the trawl reached the maximum depth that would be attained at the end of 60 min. Trawling targeted all fish species during daylight hours. Catches from each trawl tow were grouped by species and measured in total length (mm) and weight (kg). Density (number/ha) and biomass (kg/ha) were computed from the total number and weight of fish caught and the area swept by each trawl tow. Data were summarized for each trawl tow (USGS, Lake Superior Biological Station, Ashland, WI).

Cisco spawning stock size was indexed using catch rates of adult cisco in bottom-trawls in U.S. and Canadian waters (methods described above), fishery-independent gill-net surveys in U.S. waters, and targeted commercial fisheries in Canadian waters. Most agencies with jurisdiction in Lake Superior conducted fishery-independent summer lake

trout surveys with graded-mesh bottom-set gill-nets placed at fixed sampling stations throughout lake trout management units (Figure 2). Although most surveys did not target cisco, the species was collected as by-catch (Ebener et al. 2008). Summer surveys were conducted in all Wisconsin lake trout management units since 1970 and all Minnesota and most Michigan lake trout management units since the mid-1980s. The average depth of summer survey nets was 34 m in Wisconsin (range = 18–61 m), 45 m in Minnesota (range = 36–57 m), and 46 m in Michigan (range = 15–105 m; Ebener et al. 2008). Soak times typically ranged 1–4 nights. Catch/effort (CPUE; number/km) was computed from the number of fish caught and net length. Data were summarized by mesh size and species for each gill-net gang. Prior to analysis, data were standardized to a soak time of one night by dividing by total number of nights. Fishery-independent gill-net surveys were not available for Canadian lake trout management units in Lake Superior (Ebener et al. 2008), so CPUE in targeted commercial fisheries was used to index cisco spawning stock size. In Ontario, the commercial cisco fishery was primarily a roe fishery and relied on floating gill-nets targeting adults during autumn spawning (Yule et al. 2006a). Commercial operators reported daily total biomass (kg) of cisco harvested, effort (km), and locations of harvest (Yule et al. 2006a). Catch/effort (kg/km) was computed from biomass caught and net length for each gill-net gang in each lake trout management unit (Yule et al. 2006a).

In Lake Superior, most ciscoes mature at 200 mm TL in spring (Hoff 2004) and 250 mm TL in autumn (Dryer and Beil 1964; Yule et al. 2006a). Therefore, cisco spawning stock size was indexed as the density of fish  $\geq 200$  mm TL in spring bottom-trawl surveys, CPUE of fish  $\geq 225$  mm TL in summer lake trout surveys, and CPUE of

fish  $\geq 250$  mm TL in autumn targeted commercial fisheries. Total length cut-offs were applied to density distribution data from spring bottom-trawl surveys to calculate the density of fish  $\geq 200$  mm TL. Mesh sizes used in summer lake trout surveys varied among agencies, so only mesh sizes from 2.0 to 2.5-inch stretch-measure were used to index cisco spawning stock CPUE. Based on a preliminary analysis of length-frequency distributions for various mesh sizes, this mesh-size range likely excludes smaller and larger adult cisco, but is the most appropriate standardized index of cisco spawning stock size ( $\geq 225$  mm TL) in summer. Mesh sizes used in the Ontario commercial fishery were not available, but the fishery targeted spawning fish (Yule et al. 2006a), so I assumed that commercial CPUE appropriately indexed cisco spawning stock size ( $\geq 250$  mm TL) in autumn.

I calculated summary statistics for each index of recruitment and spawning stock size in 11 pre-defined spatial units in U.S. and Canadian waters of Lake Superior using methods described in Chapter 1 (Figure 3). Spatial units were required to account for different spatial scales used for data collection and reporting, and were based on regional combinations of whole (U.S. and Canadian waters) and partial (Canadian waters) lake trout management units (described above) that loosely corresponded to U.S. Geological Survey Eco-Regions (Chapter 1). Summary statistics included the geometric mean ( $\mu$ ), coefficient of variation ( $CV$ ), relative standard error ( $RSE$ ), and a combined index of spawning stock size with units of bottom-trawl density (fish/ha), which was calculated by combining the geometric mean density of adult cisco in bottom-trawls and the geometric mean CPUE of adult cisco in fishery-independent gill-net surveys or targeted commercial fisheries (Zar 1999; Chapter 1). To account for zero catches, a value equal to  $\frac{1}{2}$  the

minimum observed density (0.145 fish/ha) was added to each observation of bottom-trawl density and a value of 1.0 was added to each observation of fishery-independent gill-net or targeted commercial fishery CPUE prior to calculating summary statistics (Chapter 1). In several spatial units, the number of years with CPUE from fishery-independent gill-net surveys (U.S. waters) or targeted commercial fisheries (Canadian waters) was much less than the number of years with density from bottom-trawling. Therefore, prior to calculating summary statistics for each spatial unit, a measurement-error model (Fuller 1987) was applied to  $\log_e$ -transformed relationships between adult cisco density in bottom-trawls and adult cisco CPUE in fishery-independent gill-net surveys or targeted commercial fisheries to predict missing gill-net CPUE (Chapter 1).

### ***Predators and Competitors***

Because recruitment of age-1 cisco in Lake Superior may be regulated by predators and competitors, the density and biomass of predators and competitors were indexed using catch rates in spring bottom-trawl surveys (methods described above). Juvenile cisco (age-1 and sub-adult), a potential source of egg predation, age-0 predation, and competition (based on studies of adults; Pritchard 1931; Dryer and Beil 1964; Anderson and Smith 1971; Jensen 1996; Hoff et al. 1997; Hoff 2004), were indexed as (1) the density of fish  $\leq 140$  mm TL (age-1; Hoff 2004) during the year prior to cisco hatching ( *AlCISS* ), (2) the density of fish  $\leq 140$  mm TL during the year of cisco hatching ( *AlCISH* ), (3) the density of fish  $>140$  and  $<200$  mm TL (sub-adult; USGS, Lake Superior Biological Station, Ashland, WI) during the year prior to cisco hatching ( *SACISS* ), and (4) the density of fish  $>140$  and  $<200$  mm TL during the year of cisco hatching ( *SACISH* ). Slimy sculpin, a potential source of egg predation (Anderson and

Smith 1971; Hoff 2004), were indexed as the biomass of fish during the year prior to cisco hatching ( *SSBI* ). Rainbow smelt, a potential source of age-0 predation and competition, were indexed as (1) the density of fish  $\leq 100$  mm TL (USGS, Lake Superior Biological Station, Ashland, WI) during the year after cisco hatching ( *SMLR* ; competition from rainbow smelt recruits during the year of cisco hatching; Anderson and Smith 1971) and (2) the biomass of fish during the year of cisco hatching ( *SMLBH* ; age-0 predation and competition from age-1+ rainbow smelt; Anderson and Smith 1971; Selgeby et al. 1978; Hrabik et al. 1998; Cox and Kitchell 2004). Bloater (*Coregonus hoyi*), a potential source of competition, were indexed as (1) the density of fish  $\leq 130$  mm TL (USGS, Lake Superior Biological Station, Ashland, WI) during the year after cisco hatching ( *BLTR* ; competition from bloater recruits during the year of cisco hatching; Anderson and Smith 1971; Davis and Todd 1992) and (2) the biomass of fish during the year of cisco hatching ( *BLTBH* ; competition from age-1+ bloater; Anderson and Smith 1971). Lake trout, a potential source of age-0 predation (Edsall and DeSorcie 2002; Hoff 2004; Fitzsimons and O’Gorman 2006), were indexed as the biomass of fish during the year of cisco hatching ( *LTBH* ). Summary statistics were calculated for each index of density and biomass using methods described above for bottom-trawls. If biomass was used instead of density, a value equal to  $\frac{1}{2}$  the minimum observed biomass (0.0001 kg/ha) was added to each observation to account for zero catches in place of  $\frac{1}{2}$  the minimum observed density (0.145 fish/ha).

### ***Temperature and Wind Speed***

Because recruitment of age-1 cisco in Wisconsin waters of Lake Superior was previously correlated to air temperature and wind speed (Hoff 2004), average air

temperature (°F; used as a surrogate for water temperature) and average wind speed (mph) were indexed using data from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC) online database (<http://www.ncdc.noaa.gov/oa/ncdc.html>). The two data products used in my study were (1) Surface Data U.S. Monthly and (2) Surface Data Global Summary of the Day. The Surface Data U.S. Monthly product was used to index (1) average April air temperature during spring when ciscoes were hatching ( *AATH* ), when sub-optimal temperatures were hypothesized to magnify the effects of predation and competition or prevent individuals from reaching adequate size for over-winter survival (Kinnunen 1997; Edsall and DeSorcie 2002; Pangle et al. 2004), and (2) average April air temperature during spring when ciscoes were 11–12 months of age ( *AATFY* ), when sub-optimal temperatures may place additional stress on new recruits following severe winters (Kinnunen 1997; Hoff 2004; Pangle et al. 2004). The Surface Data Global Summary of the Day product was used to index average air temperature (described above) and average April wind speed during spring when ciscoes were hatching ( *AAWH* ), when increased wind speeds may limit age-0 predation or mediate age-0 survival through transport to optimal or sub-optimal waters for growth and development (Hoff 2004; Oyadomari and Auer 2004). For the Surface Data Global Summary of the Day product, daily averages were used to calculate monthly averages for both temperature and wind speed. Monthly averages were only calculated when >20 days of observations were present in a given month. In most cases, monthly averages were calculated from a complete monthly series of observations or a monthly series missing 1–2 days of observations. All averages were calculated as arithmetic averages.

In U.S. waters, average air temperature was obtained from the Surface Data U.S. Monthly product and average wind speed was obtained from the Surface Data Global Summary of the Day product, whereas in Canadian waters, both average air temperature and average wind speed were obtained from the Surface Data Global Summary of the Day product. In some months, average air temperature from the Surface Data U.S. Monthly product was not available, so values from the same monitoring station and the Surface Data Global Summary of the Day product were used to fill in missing values (i.e. two different products were reported for the same monitoring station, so missing values for one product were obtained from the other product). Temperature values covering the required temporal distribution for analysis were available for nine monitoring stations along the U.S. and Canadian shorelines of Lake Superior (Figure 4), whereas wind speed values covering the required temporal distribution for analysis were available for six monitoring stations (Figure 5). Temperature and wind speed values were assigned to spatial units (described above) from the nearest monitoring station. Where multiple wind speed monitoring stations were similar distances from a spatial unit, wind speed values from the western-most station were assigned to the spatial unit.

### ***Ice Cover***

Because cisco hatching date may depend on spring ice cover (John and Hasler 1956), and recruitment of other coregonid species in the Great Lakes has been positively correlated to ice cover during the incubation period (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993), ice cover was indexed using Great Lakes Environmental Research Laboratory (GLERL, Ann Arbor, MI) ice cover records. The Great Lakes Environmental Research Laboratory maintains records of historic ice cover for the entire

Great Lakes region. Ice cover records were available in ~2.5 km resolution Arc/Info ASCII grid format for winters during 1973–2005 (Assel 2005). Yearly data included geo-referenced dates of first reported ice, last reported ice, and ice duration for each winter, reported at nine different threshold concentrations (10–90% ice cover in 10% increments; Assel et al. 2002). Due to a high degree of correlation, only dates of last reported ice cover for the 50% threshold concentration were used for analysis. All ASCII grids were converted to Environmental Systems Research Institute (ESRI, Redlands, CA) Arc/Info digital raster graphic (DRG) files (Figure 6) using Python programming language (Python Software Foundation, Hampton, NH).

Once ASCII grids were converted to Arc/Info DRG files, they were loaded into ArcMap (ESRI, Redlands, CA) and an overlay analysis was conducted for each year. ArcMap shapefiles containing point data for each bottom-trawl station (described above) and polygon data for the entire Lake Superior shoreline were loaded into ArcMap. Bottom-trawl stations were buffered to 16.5 km (average movement distance of cisco in a Lake Michigan tagging study; Smith and Van Oosten 1940) to create an ArcMap shapefile containing circular polygons (radius = 16.5 km) for each bottom-trawl station. The resulting file was then clipped to the boundary of the Lake Superior shoreline to create a new shapefile only covering the body of Lake Superior (Figure 7). The new shapefile was then split into multiple shapefiles to prevent overlap of polygons attributed to spatially distinct bottom-trawl stations (i.e. buffered bottom-trawl station polygons overlapped, so multiple shapefiles were used to avoid overlap during data extraction). The resulting shapefiles (9 total) were then loaded into ArcView (ESRI, Redlands, CA) and converted to Arc/Info DRG files (9 total) with grid extent and coordinate system



identical to Great Lakes Environmental Research Laboratory ice cover grids. These new Arc/Info DRG files were then loaded back into ArcMap and overlaid on each ice cover grid for each year (Figure 7).

Ice cover data corresponding to each ~2.5 km Great Lakes Environmental Research Laboratory grid within each bottom-trawl station buffer area were extracted using the Spatial Analyst → Extraction → Sample extension of ArcToolbox (ESRI, Redlands, CA). A geometric mean for the last day of 50% ice cover was then calculated for each bottom-trawl station and year based on 16.5 km buffer zones. First, to account for zero days of 50% ice cover (i.e. in some years 50% ice cover was not reached), a value of 1.0 was added to each observation. The resulting values were then  $\log_e$ -transformed and used to calculate an arithmetic average for each bottom-trawl station. The arithmetic average of the  $\log_e$ -transformed values was then back-transformed to obtain the geometric mean (Zar 1999). Geometric mean last day of 50% ice cover values for each bottom-trawl station were then used to calculate a geometric mean last day of 50% ice cover value for each spatial unit (described above). The resulting geometric mean last day of 50% ice cover values (*LST50H*) for each spatial unit were paired with density estimates for cisco recruits hatched during the spring of the same year.

### ***Model Description, Selection, and Validation***

To identify and quantify the effects of biotic and abiotic factors on age-1 cisco recruitment dynamics in Lake Superior at spatial scales identified in Chapter 1, estimates of spawner density (from the combined index of spawning stock size) were paired with estimates of recruit density two years later, and a sequence of generalized Ricker stock-recruitment models (Ricker 1975; Hilborn and Walters 1992) were fitted to test biotic and

abiotic variables for their explanation of overall age-1 cisco recruitment variation within four different regions of Lake Superior (Figure 8). The generalized version of the Ricker stock-recruitment model describes recruitment of the  $i^{\text{th}}$  year-class ( $R_i$ ) as a function of spawning stock size ( $S_i$ ) and other biotic or abiotic factors ( $X_i$ ; Walters et al. 1986; Hilborn and Walters 1992):

$$R_i = \alpha S_i e^{-\beta S_i - \delta X_i} e^{\varepsilon}$$

Where  $\alpha$  is the number of recruits produced per spawner at low spawning stock size,  $\beta$  is the rate at which the logarithm of recruits per spawner declines with spawning stock size,  $\delta$  is the rate at which the logarithm of recruits per spawner changes with other biotic or abiotic factors, and  $e^{\varepsilon}$  = multiplicative process error (Hilborn and Walters 1992). An insignificant  $\beta$ -coefficient indicates a density-independent recruitment rate, a negative  $\beta$ -coefficient indicates a compensatory density-dependent recruitment rate, and a positive  $\beta$ -coefficient indicates a depensatory density-dependent recruitment rate (Hilborn and Walters 1992). An insignificant  $\delta$ -coefficient indicates no other biotic or abiotic effect on recruitment rate, a negative  $\delta$ -coefficient indicates a negative other biotic or abiotic effect on recruitment rate, and a positive  $\delta$ -coefficient indicates a positive other biotic or abiotic effect on recruitment rate (Hilborn and Walters 1992). Stock-recruitment errors are usually lognormal (Peterman 1981), so parameters ( $\alpha$ ,  $\beta$ , and  $\delta$ ) were estimated using multiple-linear regression (Zar 1999) and the additive-error  $\log_e$ -transformed model:

$$\log_e(R_i / S_i) = \log_e(\alpha) - \beta S_i - \delta X_i + \varepsilon$$

All biotic and abiotic variables were selected for final multi-factor models using a two-phase process. First, because of the large number of variables ( $n = 15$ ) and possible two-way interaction terms between variables used for analysis ( $n = 105$ ), and to eliminate spurious variables and variables weakly correlated to age-1 cisco recruitment, simple-linear regression (Zar 1999) was used to test for a significant ( $P \leq 0.20$ ) relationship between the logarithm of cisco recruits per spawner and all biotic and abiotic variables. During the first phase of analysis, significant positive relationships between the logarithm of cisco recruits per spawner and biotic variables appeared to be a byproduct of sporadic consecutive years of strong cisco recruitment or related to some large-scale abiotic factor driving recruitment of multiple species, so insignificant ( $P > 0.20$ ) variables and significant biotic variables positively correlated to the logarithm of cisco recruits per spawner were eliminated from further analysis. Second, stepwise selection (Zar 1999; SYSTAT 2004) was used to select all best-fit models from significant candidate variables and all possible two-way interaction terms between significant candidate variables. For each region, partial correlations between explanatory variables (including interaction terms) and residuals were tested at each step for entry to ( $P_{\text{entry}} \leq 0.10$ ) or exit from ( $P_{\text{exit}} > 0.10$ ) final models. Modeling was stopped when significant improvements in model fit were not observed by adding or deleting additional variables (Zar 1999; SYSTAT 2004). Additional variables were not included in models if they were highly correlated (Pearson correlation coefficient  $\geq 0.50$ ) to variables already included in models (i.e. main effects or interaction terms added to models first or deleted from models last) or if tolerances were  $< 0.10$  (SYSTAT 2004). Normal probability plots (SYSTAT 2004) and time-series plots

(Hilborn and Walters 1992) were used to assess the normality and independence of residuals for each model.

For each regional best-fit model describing age-1 cisco recruitment dynamics in Lake Superior, peak recruitment ( $R_{\max}$ ) and the spawning stock size that produced peak recruitment ( $S_{\max}$ ) were estimated to show how cisco recruitment differed among regions. Peak recruitment was estimated as:

$$R_{\max} = \frac{\alpha}{\beta e}$$

Where  $\alpha$  and  $\beta$  are parameters estimated from the Ricker stock-recruitment model (Ricker 1975; Hilborn and Walters 1992). The spawning stock size that produced peak recruitment was estimated as:

$$S_{\max} = \frac{1}{\beta}$$

Where  $\beta$  is the density-dependent parameter estimated from the Ricker stock-recruitment model (Ricker 1975; Hilborn and Walters 1992).

## RESULTS

### *Spawner and Recruit Density*

In years used for model construction, estimates of recruit density ranged 317-fold in western stocks, 2,975-fold in southern stocks, 435-fold in eastern stocks, and 276-fold in northern stocks, whereas estimates of spawner density ranged 249-fold in western stocks, 94-fold in southern stocks, 8-fold in eastern stocks, and 28-fold in northern stocks. Average recruit density was greatest in southern stocks (20.4 fish/ha), followed

by western stocks (5.0 fish/ha), eastern stocks (2.8 fish/ha), and northern stocks (2.7 fish/ha; Table 1), whereas average spawner density was greatest in western stocks (3.4 fish/ha), followed by southern stocks (2.1 fish/ha), northern stocks (1.0 fish/ha), and eastern stocks (0.4 fish/ha; Table 2). Some of the weakest year-classes were produced by large parental stocks, whereas some of the strongest year-classes were produced by small parental stocks (Figures 9–10).

### ***Region 1 (Minnesota and WI-1)***

Simple-linear regression indicated a significant ( $P \leq 0.20$ ) relationship between the logarithm of cisco recruits per spawner and (1) the density of bloater recruits during the year of cisco hatching ( *BLTR* ), (2) the density of rainbow smelt recruits during the year of cisco hatching ( *SMLR* ), (3) average April air temperature during spring when ciscoes were 11–12 months of age ( *AATFY* ), (4) the density of age-1 cisco during the year prior to cisco hatching ( *AlCISS* ), and (5) the density of sub-adult cisco during the year prior to cisco hatching ( *SACISS* ). In years used for model construction, the density of bloater recruits ranged 204-fold, the density of rainbow smelt recruits ranged 352-fold, average April air temperature during spring when ciscoes were 11–12 months of age ranged 1.3-fold, the density of age-1 cisco during the year prior to cisco hatching ranged 316-fold, and the density of sub-adult cisco during the year prior to cisco hatching ranged 344-fold (Table 3). The density of bloater recruits and the density of rainbow smelt recruits were positively correlated to the logarithm of cisco recruits per spawner and were removed from further analysis.

The final multi-factor model for western stocks included (1) adult spawning stock size, (2) the density of age-1 cisco during the year prior to cisco hatching, and (3) average

April air temperature during spring when ciscoes were 11–12 months of age ( $F = 11.16$ ;  $df = 32$ ;  $P < 0.001$ ; Table 4):

$$R_i = (0.004)S_i e^{-(0.121)S_i - (0.080)A1CISS_i + (0.171)AATFY_i} e^{\varepsilon}$$

The model indicated that high age-1 cisco density reduced recruitment regardless of spawner density, whereas high April air temperature improved recruitment regardless of spawner density. The model predicted strong recruitment at low age-1 cisco density and high April air temperature, but weak recruitment at high age-1 cisco density and low April air temperature (Figure 11). The final multi-factor model indicated that cisco stock density should be maintained near 8.281 spawners/ha ( $S_{\max}$ ) to produce peak recruitment near 0.012 age-1 recruits/ha ( $R_{\max}$ ). The model underestimated strong recruitment events (Figure 12) and residuals were independent and approximately normally distributed (Figures 13-14). Adjusted  $R^2$  values were low for both linear and non-linear models (Table 4).

#### ***Region 2 (WI-2, Western Keweenaw, and MI-4)***

Simple-linear regression indicated a significant ( $P \leq 0.20$ ) relationship between the logarithm of cisco recruits per spawner and (1) the density of age-1 cisco during the year of cisco hatching ( $A1CISH$ ), (2) the density of bloater recruits during the year of cisco hatching ( $BLTR$ ), (3) average April air temperature during spring when ciscoes were hatching ( $AATH$ ), (4) average April wind speed during spring when ciscoes were hatching ( $AAWH$ ), (5) average April air temperature during spring when ciscoes were 11–12 months of age ( $AATFY$ ), and (6) the density of sub-adult cisco during the year prior to cisco hatching ( $SACISS$ ). In years used for model construction, the density of age-1 cisco during the year of cisco hatching ranged 2,459-fold, the density of bloater

recruits ranged 204-fold, average April air temperature during spring when ciscoes were hatching ranged 1.3-fold, average April wind speed during spring when ciscoes were hatching ranged 1.4-fold, average April air temperature during spring when ciscoes were 11–12 months of age ranged 1.3-fold, and the density of sub-adult cisco during the year prior to cisco hatching ranged 344-fold (Table 5). The density of age-1 cisco during the year of cisco hatching and the density of bloater recruits were positively correlated to the logarithm of cisco recruits per spawner and were removed from further analysis.

The final multi-factor model for southern stocks included (1) adult spawning stock size, (2) the interaction between average April wind speed during spring when ciscoes were hatching and average April air temperature during spring when ciscoes were 11–12 months of age, and (3) the interaction between the density of sub-adult cisco during the year prior to cisco hatching and average April wind speed during spring when ciscoes were hatching ( $F = 14.70$ ;  $df = 66$ ;  $P < 0.001$ ; Table 6):

$$R_i = (0.134)S_i e^{-(0.382)S_i + (0.009)AAWH_i \times AATFY_i - (0.002)SACISS_i \times AAWH_i} e^\varepsilon$$

The model indicated that high April wind speed and high April air temperature improved recruitment regardless of spawner density, whereas high sub-adult cisco density reduced recruitment regardless of spawner density. The model predicted strong recruitment at high April wind speed, high April air temperature, and low sub-adult cisco density, but weak recruitment at low April wind speed, low April air temperature, and high sub-adult cisco density (Figure 15). The final multi-factor model indicated that cisco stock density should be maintained near 2.617 spawners/ha ( $S_{\max}$ ) to produce peak recruitment near 0.129 age-1 recruits/ha ( $R_{\max}$ ). The model underestimated strong recruitment events (Figure 16) and residuals were independent and approximately normally distributed

(Figures 17–18). Adjusted  $R^2$  values were low for both linear and non-linear models (Table 6).

***Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada)***

Simple-linear regression indicated a significant ( $P \leq 0.20$ ) relationship between the logarithm of cisco recruits per spawner and (1) the density of age-1 cisco during the year of cisco hatching ( *AlCISH* ), (2) the density of bloater recruits during the year of cisco hatching ( *BLTR* ), (3) average April air temperature during spring when ciscoes were 11–12 months of age ( *AATFY* ), (4) the biomass of slimy sculpin during the year prior to cisco hatching ( *SSBI* ), and (5) the biomass of lake trout during the year of cisco hatching ( *LTBH* ). In years used for model construction, the density of age-1 cisco during the year of cisco hatching ranged 435-fold, the density of bloater recruits ranged 82-fold, average April air temperature during spring when ciscoes were 11–12 months of age ranged 1.4-fold, the biomass of slimy sculpin during the year prior to cisco hatching ranged 1,885-fold, and the biomass of lake trout during the year of cisco hatching ranged 12,298-fold (Table 7). The density of age-1 cisco during the year of cisco hatching and the density of bloater recruits were positively correlated to the logarithm of cisco recruits per spawner and were removed from further analysis.

The final model for eastern stocks included adult spawning stock size ( $F = 13.71$ ;  $df = 41$ ;  $P < 0.001$ ; Table 8):

$$R_i = (4.887)S_i e^{-(3.420)S_i} e^{\varepsilon}$$

The model predicted strong recruitment at low spawner density, but weak recruitment at high spawner density (Figure 19). The single-factor model indicated that cisco stock



density should be maintained near 0.292 spawners/ha ( $S_{\max}$ ) to produce peak recruitment near 0.526 age-1 recruits/ha ( $R_{\max}$ ). The model underestimated strong recruitment events (Figure 20) and residuals were independent and positively skewed (Figures 21–22). Adjusted  $R^2$  values were low for both linear and non-linear models (Table 8).

#### ***Region 4 (Nipigon Bay, Black Bay, and Thunder Bay)***

Simple-linear regression indicated a significant ( $P \leq 0.20$ ) relationship between the logarithm of cisco recruits per spawner and (1) the density of age-1 cisco during the year prior to cisco hatching ( $AlCISS$ ), (2) the density of bloater recruits during the year of cisco hatching ( $BLTR$ ), (3) average April wind speed during spring when ciscoes were hatching ( $AAWH$ ), (4) average April air temperature during spring when ciscoes were 11–12 months of age ( $AATFY$ ), (5) the density of sub-adult cisco during the year prior to cisco hatching ( $SACISS$ ), (6) the density of rainbow smelt recruits during the year of cisco hatching ( $SMLR$ ), and (7) the biomass of rainbow smelt during the year of cisco hatching ( $SMLBH$ ). In years used for model construction, the density of age-1 cisco during the year prior to cisco hatching ranged 336-fold, the density of bloater recruits ranged 21-fold, average April wind speed during spring when ciscoes were hatching ranged 2.3-fold, average April air temperature during spring when ciscoes were 11–12 months of age ranged 1.3-fold, the density of sub-adult cisco during the year prior to cisco hatching ranged 59-fold, the density of rainbow smelt recruits ranged 393-fold, and the biomass of rainbow smelt during the year of cisco hatching ranged 378-fold (Table 9). The density of age-1 cisco during the year prior to cisco hatching and the density of bloater recruits were positively correlated to the logarithm of cisco recruits per spawner and were removed from further analysis.

The final multi-factor model for northern stocks included (1) adult spawning stock size, (2) the interaction between average April wind speed during spring when ciscoes were hatching and average April air temperature during spring when ciscoes were 11–12 months of age, and (3) the interaction between the biomass of rainbow smelt during the year of cisco hatching and the density of sub-adult cisco during the year prior to cisco hatching ( $F = 16.36$ ;  $df = 47$ ;  $P < 0.001$ ; Table 10):

$$R_i = (0.181)S_i e^{-(1.260)S_i + (0.013)AAWH_i \times AATFY_i - (0.017)SMLBH_i \times SACISS_i} e^\varepsilon$$

The model indicated that high April wind speed and high April air temperature improved recruitment regardless of spawner density, whereas high rainbow smelt biomass and high sub-adult cisco density reduced recruitment regardless of spawner density. The model predicted strong recruitment at high April wind speed, high April air temperature, low rainbow smelt biomass, and low sub-adult cisco density, but weak recruitment at low April wind speed, low April air temperature, high rainbow smelt biomass, and high sub-adult cisco density (Figure 23). The final multi-factor model indicated that cisco stock density should be maintained near 0.793 spawners/ha ( $S_{\max}$ ) to produce peak recruitment near 0.053 age-1 recruits/ha ( $R_{\max}$ ). The model underestimated strong recruitment events (Figure 24) and residuals were independent and approximately normally distributed (Figures 25–26). Adjusted  $R^2$  values were low for both linear and non-linear models (Table 10).

## DISCUSSION

My findings are consistent with previous studies of cisco recruitment (Jensen 1996; Hoff 2004), and suggest that recruitment of age-1 cisco in Lake Superior is

regulated by compensatory density-dependence from adult cisco in all four regions and juvenile (age-1 and sub-adult) cisco in most (3 of 4) regions. Hoff (2004) found a significant compensatory density-dependent relationship between recruitment of age-1 cisco and adult spawning stock density, and concluded that recruitment of age-1 cisco was limited by predation from adult cisco in Wisconsin waters of Lake Superior. Similarly, Jensen (1996) found a significant negative correlation between recruitment of age-1 cisco and the biomass of age-1 through age-6+ cisco, and concluded that recruitment of age-1 cisco was limited by competition from adult and juvenile cisco in U.S. waters of Lake Superior. Evidence of larval predation by adult or juvenile ciscoes is rare for Lake Superior (Stockwell et al. 2009), but diet studies for cisco in the lower Great Lakes and inland lakes suggest that larval predation may be substantial under certain conditions (Pritchard 1931; Becker 1983). In contrast, evidence from Lake Superior and studies of inland lakes suggests that large cisco year-classes can limit zooplankton abundance and cause changes in zooplankton community structure (Rudstam et al. 1993; Link et al. 1995), thereby leading to increased intraspecific competition. Diet studies for cisco in Lake Superior and Lake Michigan suggest that egg predation during spawning may also lead to compensatory density-dependence (Smith 1956; Dryer and Beil 1964; Anderson and Smith 1971). My findings are correlative, so cause-and-effect cannot be established, but the inclusion of average April air temperature during spring when ciscoes were 11–12 months of age (described below) in most (3 of 4) regional models in my study, and previously observed density-dependent changes in growth and maturation for cisco stocks in Lake Superior (MacCallum and Selgeby 1987; Bowen et al. 1991; Coffin et al. 2003), are consistent with compensatory density-

dependence related to competition, and suggest that competition for limited resources may regulate recruitment of age-1 cisco in Lake Superior more than egg or larval predation. Regional variability in the relative importance of adult spawning stock size and the density of juvenile cisco during the year prior to cisco hatching suggests that compensatory density-dependence regulates recruitment of age-1 cisco in Lake Superior on a regional scale, possibly through regional differences in carrying capacity (Chapter 1).

I found that recruitment of age-1 cisco in Lake Superior was positively correlated to average April air temperature during spring when ciscoes were 11–12 months of age in most (3 of 4) regions, as was found in a previous study of cisco stock-recruitment in Wisconsin waters of Lake Superior (Hoff 2004). Hoff (2004) concluded that warmer April air temperatures shortened the duration of winter and were advantageous to cisco recruits with limited energy stores. In a study designed to test the effects of body size, physiological condition, energy stores, and food rations on the survival of age-0 cisco over a simulated 225-day winter, Pangle et al. (2004) concluded that body size, condition going into winter, and winter duration were all important factors regulating first-winter survival. Similarly, body size, condition, and winter duration have been found to regulate first-winter survival and recruitment of many other fish species (Oliver et al. 1979; Toney and Coble 1979; Post and Evans 1989; Johnson and Evans 1990; Thompson et al. 1991; Kirjasniemi and Valtonen 1997; Hurst and Conover 1998; O’Gorman et al. 2004). My findings suggest that first-winter duration drives recruitment variation of age-1 cisco in Lake Superior on a lake-wide scale, but multiple biotic and abiotic factors may also regulate body size and condition going into winter on a smaller scale (Pangle et al. 2004).

Fisher and Fielder (1998) found that cisco populations in Lake Superior had significantly lower ( $P < 0.001$ ) mean relative weight values than inland populations. Perhaps regional differences in temperature and productivity (Swenson and Heist 1981; Kinnunen 1997; Oyadomari and Auer 2004) interact with typically low temperatures (Bennett 1978; Hoff 2004) and productivity (Hansen 1990; Horns 2003) in Lake Superior to mediate the importance of first-winter duration as a final culling mechanism (Hoff 2004) before age-0 ciscoes recruit to age-1. Regional differences in competition from adult and juvenile cisco may also mediate the importance of first-winter duration by limiting the importance of spring warming in years of low cisco abundance and promoting the importance of spring warming in years of high cisco abundance.

I found that recruitment of age-1 cisco in Lake Superior was positively correlated to average April wind speed during spring when ciscoes were hatching in two of four regions, as was found in a previous study of cisco stock-recruitment in Wisconsin waters of Lake Superior (Hoff 2004). Hoff (2004) concluded that strong winds during hatching dispersed patches of newly hatched larvae, thereby limiting age-0 predation. However, studies of recruitment for marine fish species suggest that wind speed during hatching may be related to surface currents important for larval retention on spawning grounds or transport of newly hatched larvae away from spawning grounds to more productive nursery areas (Nelson et al. 1977; Bailey 1981; Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990; Warlen 1994). Alternatively, wind-driven currents may increase larval food supply (Bakun 1996) or enhance encounter rates between newly hatched larvae and their prey (Rothschild and Osborn 1988). In Lake Superior, both the highest concentrations of larval ciscoes and the highest growth rates for larval ciscoes were found

in near-shore waters with elevated temperatures and zooplankton abundance (Swenson and Heist 1981; Oyadomari and Auer 2004; Stockwell et al. 2009). Therefore, wind-driven mechanisms leading to larval retention on spawning grounds or transport of newly hatched larvae away from spawning grounds to more productive nursery areas may be more important in determining cisco recruitment in Lake Superior than wind-driven mechanisms controlling larval food supply, encounter rates between newly hatched larvae and their prey, or the limiting effects of wind speed on age-0 predation. Regional differences in the relative importance of average April wind speed during spring when ciscoes were hatching suggest that wind speed during hatching regulates recruitment of age-1 cisco in Lake Superior on a regional scale, possibly through regional differences in exposure to prevailing winds or wind-driven currents.

My findings are consistent with a previous study of cisco stock-recruitment (Hoff 2004) and diet studies for rainbow smelt (Selgeby et al. 1978; Swenson and Heist 1981; Gorman 2007; Myers 2008), but differ from a previous ecosystem modeling study (Cox and Kitchell 2004), and suggest that interspecific interactions with rainbow smelt regulate recruitment of age-1 cisco in the northern region of Lake Superior, but not in western, southern, or eastern regions. Previously, a study of cisco stock-recruitment in Wisconsin waters of Lake Superior found no significant correlation between recruitment of age-1 cisco and the density and biomass of rainbow smelt (Hoff 2004). Similarly, diet studies found no evidence of rainbow smelt predation on larval cisco in the Apostle Islands region of Lake Superior (0% of 1,711 stomachs contained larval cisco; Selgeby et al. 1978), and only limited evidence of rainbow smelt predation on larval cisco in western Lake Superior (13–30% estimated consumption of larval cisco; Swenson and Heist

1981). In contrast, diet studies found substantial rainbow smelt predation on larval cisco in Black Bay (17% of 1,195 stomachs contained larval cisco; Selgeby et al. 1978), where rainbow smelt showed a strong diet selectivity for larval cisco (69.3–99.5% of diet by weight; Gorman 2007), and consumption rates were estimated at up to 100% (Black Bay and Thunder Bay; Myers 2008). In contrast to my findings, Cox and Kitchell (2004) concluded that strong rainbow smelt predation regulated cisco populations in Lake Superior during 1929–1998, but the ecosystem model used was based on data for all of Lake Superior and failed to account for differences in predation rates among regions. In my study, regional differences in the relative importance of rainbow smelt biomass suggest that rainbow smelt predation regulates recruitment of age-1 cisco in Lake Superior on a regional scale, and differences may be related to the 7-fold greater average biomass of rainbow smelt in the northern region, compared to western, southern, and eastern regions. Alternatively, regional differences in the relative importance of rainbow smelt biomass may be related to abiotic factors leading to increased spatial and temporal overlap (Stockwell et al. 2009), sub-optimal conditions for larval growth leading to increased size-dependent predation (Selgeby et al. 1978; Kinnunen 1997), or increased predation in the relatively small confines of Nipigon Bay, Black Bay, and Thunder Bay, as was hypothesized as a mechanism leading to increased intraspecific interactions for alewives (*Alosa pseudoharengus*) in the Bay of Quinte, Lake Ontario (Ridgway et al. 1990; O’Gorman et al. 2004).

Biotic and abiotic variables included in my study were variables previously correlated to age-1 cisco recruitment or generally considered to regulate age-1 cisco recruitment in Lake Superior and variables previously correlated to recruitment of other

coregonid species in the Great Lakes, but low adjusted  $R^2$  values for both linear and non-linear models for all four regions in my study suggest that one or more important biotic or abiotic variables may be missing from each regional model. Therefore, future studies of cisco stock-recruitment in Lake Superior should focus on identifying biotic and abiotic factors regulating age-1 cisco recruitment that were not tested in my study. The positive linear relationship between the logarithm of cisco recruits per spawner and the density of bloater recruits in all four regions of Lake Superior suggests that environmental conditions promoting cisco recruitment are also important for promoting bloater recruitment, and field studies should be used to identify biotic and abiotic factors regulating recruitment of both species. Quantifying primary productivity or zooplankton abundance may serve as a good initial starting point for many field studies. My findings suggest that recruitment of age-1 cisco in Lake Superior is driven by large-scale abiotic factors, but both biotic and abiotic factors regulating recruitment of age-1 cisco in Lake Superior directly influence the recruitment process at smaller spatial scales. Therefore, developing multi-factor stock-recruitment models using more precise data collected at smaller spatial scales will likely improve model fit and could lend more or less support to biotic and abiotic factors already identified in my study.

## **MANAGEMENT IMPLICATIONS**

The fish-community objective for prey species in Lake Superior calls for rehabilitation of cisco stocks to historic levels of abundance to provide a forage base for lake trout and to support a commercial fishery (Busiahn 1990). Fishery management plans for the lower Great Lakes recognize the cisco as an important member of the native fish community and call for reestablishment of self-sustaining populations throughout the



species historic range (Edsall and DeSorcie 2002). Previously, studies of cisco stock-recruitment in the Great Lakes were limited to one study of the spatial scale for cisco recruitment dynamics in Lake Superior (Chapter 1) and one study of cisco stock-recruitment in Wisconsin waters of Lake Superior (Hoff 2004). The previous studies identified and quantified the spatial scale for cisco recruitment dynamics in Lake Superior (Chapter 1) and the effects of multiple biotic and abiotic factors correlated to age-1 cisco recruitment in Wisconsin waters of Lake Superior (Hoff 2004), but failed to identify or quantify the effects of biotic and abiotic factors on age-1 cisco recruitment in other regions of Lake Superior, and multi-factor models developed for cisco stocks in Wisconsin waters of Lake Superior were not broadly applicable to cisco stocks in other regions of Lake Superior or the lower Great Lakes. Therefore, fishery managers were forced to carry out cisco restoration and management efforts without reliable estimates of the effects of biotic and abiotic factors on age-1 cisco recruitment. My findings provide the first comprehensive estimates of the effects of biotic and abiotic factors on recruitment of age-1 cisco in Lake Superior, and are broadly applicable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin.

My findings suggest that air temperature during spring when ciscoes are 11–12 months of age drives recruitment of age-1 cisco in Lake Superior on a lake-wide scale, whereas adult spawning stock size, intraspecific interactions with juvenile cisco, wind speed during spring when ciscoes are hatching, and interspecific interactions with rainbow smelt regulate recruitment of age-1 cisco on a regional scale. Most (3 of 4) regional models in my study contained environmental variables, which are largely

beyond the control of fishery managers. Therefore, fishery managers are left with managing adult spawning stock size and the density and biomass of potential predators and competitors to achieve desired management goals. My findings suggest that cisco spawning stock size should be maintained near densities of 8.3 spawners/ha in western stocks, 2.6 spawners/ha in southern stocks, 0.3 spawners/ha in eastern stocks, and 0.8 spawners/ha in northern stocks, whereas the density of juvenile cisco should be maintained at the lowest levels possible in western, southern, and northern stocks, and the biomass of rainbow smelt should be maintained at the lowest levels possible in northern stocks, to produce peak recruitment of age-1 cisco in Lake Superior. Fishery managers should expect a similar suite of biotic and abiotic factors to regulate recruitment of age-1 cisco throughout the lower Great Lakes, and should evaluate the potential effects of similar biotic and abiotic factors on recruitment prior to addressing cisco restoration and management efforts in each lake.

Estimates of the spawning stock size that produced peak recruitment of age-1 cisco in Lake Superior can be used as targets for the restoration of remnant cisco populations throughout the lower Great Lakes, but because the productivity and fish-community structure of Lake Superior differs from many of the lower Great Lakes, fishery managers should exercise caution when applying management parameters estimated in my study to the lower Great Lakes. Because of Lake Superior's low productivity (Hansen 1990; Horns 2003), fishery managers should consider regional estimates of the spawning stock size that produced peak recruitment of age-1 cisco in Lake Superior as minimum targets for the restoration of cisco populations throughout the lower Great Lakes. Therefore, the spawning stock size that produced peak recruitment of

age-1 cisco in western stocks may be an appropriate minimum target for the restoration of cisco populations in Lake Ontario, Lake Erie, Lake Huron, and Lake Michigan. Because the fish-community structure of the lower Great Lakes is dominated by invasive species, such as the alewife (Fitzsimons and O’Gorman 2006; Stockwell et al. 2009), fishery managers throughout the lower Great Lakes should also evaluate the potential effects of increased interspecific predation and competition on cisco populations prior to addressing cisco restoration and management efforts in each lake.

Table 1. Summary statistics for estimated recruit densities used in model construction.

Number of density estimates used in model construction ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) recruit density, average coefficient of variation (Avg.  $CV$ ), and average relative standard error (Avg.  $RSE$ ) are provided for each region (Region 1 = western stocks; Region 2 = southern stocks; Region 3 = eastern stocks; Region 4 = northern stocks).

Region	Recruit Density Bottom-Trawls (fish/ha)					
	$n$	Avg.	Min.	Max.	Avg. $CV$	Avg. $RSE$
1	36	5.0	0.1	45.9	44.53	24.75
2	70	20.4	0.1	431.3	5.68	2.49
3	43	2.8	0.1	63.1	3.52	1.46
4	51	2.7	0.1	40.0	21.19	10.11

Table 2. Summary statistics for estimated spawner densities used in model construction. Number of density estimates used in model construction ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) spawner density, average coefficient of variation (Avg. *CV* Trawls) and relative standard error (Avg. *RSE* Trawls) for bottom-trawl density, and average coefficient of variation (Avg. *CV* Gill-Nets) and relative standard error (Avg. *RSE* Gill-Nets) for gill-net CPUE are provided for each region (Region 1 = western stocks; Region 2 = southern stocks; Region 3 = eastern stocks; Region 4 = northern stocks).

Region	$n$	Spawner Density (fish/ha)						
		Avg.	Min.	Max.	Avg. <i>CV</i> Trawls	Avg. <i>RSE</i> Trawls	Avg. <i>CV</i> Gill-Nets	Avg. <i>RSE</i> Gill-Nets
1	36	3.4	0.1	36.1	7.84	4.13	1.70	0.41
2	70	2.1	0.1	13.7	7.09	2.62	1.99	0.56
3	43	0.4	0.1	1.2	4.61	1.75	52.06	36.20
4	51	1.0	0.1	4.0	8.51	3.90	1.97	0.89

Table 3. Summary statistics for significant ( $P \leq 0.20$ ) biotic and abiotic variables identified using simple-linear regression in Region 1 (Minnesota and WI-1). Number of values used for analysis ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) values are provided for each variable. Shaded cells indicate variables used for final multi-factor analysis.

<b>Variable</b>	<b>Coefficient</b>	<b><i>n</i></b>	<b>Avg.</b>	<b>Min.</b>	<b>Max.</b>	<b>F</b>	<b>df</b>	<b>P</b>
BLTR	+	36	2.0	0.1	29.6	6.86	34	<0.02
SMLR	+	36	72.7	1.1	395.3	4.16	34	<0.05
AATFY	+	36	38.9	34.5	46.1	1.79	34	<0.20
A1CISS	–	36	5.0	0.1	45.9	9.74	34	<0.01
SACISS	–	36	2.9	0.1	49.9	6.72	34	<0.02

Table 4. Parameter estimates and standard errors ( $SE$ ) for the final multi-factor model for Region 1 (Minnesota and WI-1). Peak recruitment ( $R_{\max}$ ), the spawning stock size that produced peak recruitment ( $S_{\max}$ ), and adjusted  $R^2$  values for both linear and non-linear models are provided.

<b>Parameter</b>	<b>Value</b>	<b><math>SE</math></b>	<b><math>R_{\max}</math></b>	<b><math>S_{\max}</math></b>	<b>Adjusted <math>R^2</math> Linear Model</b>	<b>Adjusted <math>R^2</math> Non-Linear Model</b>
$\alpha$	0.004	1.32	0.012	8.281	0.47	0.10
$\beta$	-0.121	0.04				
$\delta_{A1CISS}$	-0.080	0.03				
$\delta_{AATFY}$	0.171	0.09				

Table 5. Summary statistics for significant ( $P \leq 0.20$ ) biotic and abiotic variables identified using simple-linear regression in Region 2 (WI-2, Western Keweenaw, and MI-4). Number of values used for analysis ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) values are provided for each variable. Shaded cells indicate variables used for final multi-factor analysis.

<b>Variable</b>	<b>Coefficient</b>	<b><i>n</i></b>	<b>Avg.</b>	<b>Min.</b>	<b>Max.</b>	<b>F</b>	<b>df</b>	<b>P</b>
A1CISH	+	69	21.2	0.1	431.3	8.10	67	<0.01
BLTR	+	70	4.2	0.1	145.9	6.85	68	<0.02
AATH	+	70	39.2	32.4	46.3	4.11	68	<0.05
AAWH	+	70	9.1	6.7	12.0	3.31	68	<0.08
AATFY	+	70	39.2	32.4	46.3	13.04	68	<0.01
SACISS	−	70	7.4	0.1	189.7	5.06	68	<0.03



Table 6. Parameter estimates and standard errors ( $SE$ ) for the final multi-factor model for Region 2 (WI-2, Western Keweenaw, and MI-4). Peak recruitment ( $R_{\max}$ ), the spawning stock size that produced peak recruitment ( $S_{\max}$ ), and adjusted  $R^2$  values for both linear and non-linear models are provided.

<b>Parameter</b>	<b>Value</b>	<b><math>SE</math></b>	<b><math>R_{\max}</math></b>	<b><math>S_{\max}</math></b>	<b>Adjusted <math>R^2</math> Linear Model</b>	<b>Adjusted <math>R^2</math> Non-Linear Model</b>
$\alpha$	0.134	0.65	0.129	2.617	0.37	0.02
$\beta$	-0.382	0.08				
$\delta_{AAWH*AAIFY}$	0.009	0.00				
$\delta_{SACISS*AAWH}$	-0.002	0.00				

Table 7. Summary statistics for significant ( $P \leq 0.20$ ) biotic and abiotic variables identified using simple-linear regression in Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada). Number of values used for analysis ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) values are provided for each variable. Shaded cells indicate variables used for final multi-factor analysis.

<b>Variable</b>	<b>Coefficient</b>	<b><i>n</i></b>	<b>Avg.</b>	<b>Min.</b>	<b>Max.</b>	<b>F</b>	<b>df</b>	<b>P</b>
A1CISH	+	43	3.1	0.1	63.1	8.61	41	<0.01
BLTR	+	43	0.8	0.1	11.9	30.77	41	<0.01
AATFY	+	43	38.8	31.3	45.9	3.95	41	<0.06
SSBI	–	43	0.0	0.0	0.2	3.55	41	<0.07
LTBH	–	43	0.1	0.0	1.2	1.81	41	<0.19

Table 8. Parameter estimates and standard errors ( $SE$ ) for the final model for Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada). Peak recruitment ( $R_{\max}$ ), the spawning stock size that produced peak recruitment ( $S_{\max}$ ), and adjusted  $R^2$  values for both linear and non-linear models are provided.

<b>Parameter</b>	<b>Value</b>	<b><math>SE</math></b>	<b><math>R_{\max}</math></b>	<b><math>S_{\max}</math></b>	<b>Adjusted <math>R^2</math> Linear Model</b>	<b>Adjusted <math>R^2</math> Non-Linear Model</b>
$\alpha$	4.887	2.44	0.526	0.292	0.23	0.02
$\beta$	-3.420	0.93				

Table 9. Summary statistics for significant ( $P \leq 0.20$ ) biotic and abiotic variables identified using simple-linear regression in Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Number of values used for analysis ( $n$ ), average (Avg.), minimum (Min.), and maximum (Max.) values are provided for each variable. Shaded cells indicate variables used for final multi-factor analysis.

<b>Variable</b>	<b>Coefficient</b>	<b><math>n</math></b>	<b>Avg.</b>	<b>Min.</b>	<b>Max.</b>	<b>F</b>	<b>df</b>	<b>P</b>
A1CISS	+	51	4.1	0.1	48.8	7.27	49	<0.01
BLTR	+	51	0.5	0.1	3.0	12.08	49	<0.01
AAWH	+	51	6.8	3.7	8.6	1.78	49	<0.19
AATFY	+	51	37.1	31.9	43.7	5.17	49	<0.03
SACISS	–	51	1.6	0.1	8.7	6.46	49	<0.02
SMLR	–	51	279.6	6.9	2699.4	5.60	49	<0.03
SMLBH	–	51	2.2	0.1	19.6	2.81	49	<0.11

Table 10. Parameter estimates and standard errors ( $SE$ ) for the final multi-factor model for Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Peak recruitment ( $R_{\max}$ ), the spawning stock size that produced peak recruitment ( $S_{\max}$ ), and adjusted  $R^2$  values for both linear and non-linear models are provided.

<b>Parameter</b>	<b>Value</b>	<b><math>SE</math></b>	<b><math>R_{\max}</math></b>	<b><math>S_{\max}</math></b>	<b>Adjusted <math>R^2</math> Linear Model</b>	<b>Adjusted <math>R^2</math> Non-Linear Model</b>
$\alpha$	0.181	0.58	0.053	0.793	0.48	0.01
$\beta$	-1.260	0.22				
$\delta_{AAWH*AATFY}$	0.013	0.00				
$\delta_{SMLBH*SACISS}$	-0.017	0.01				

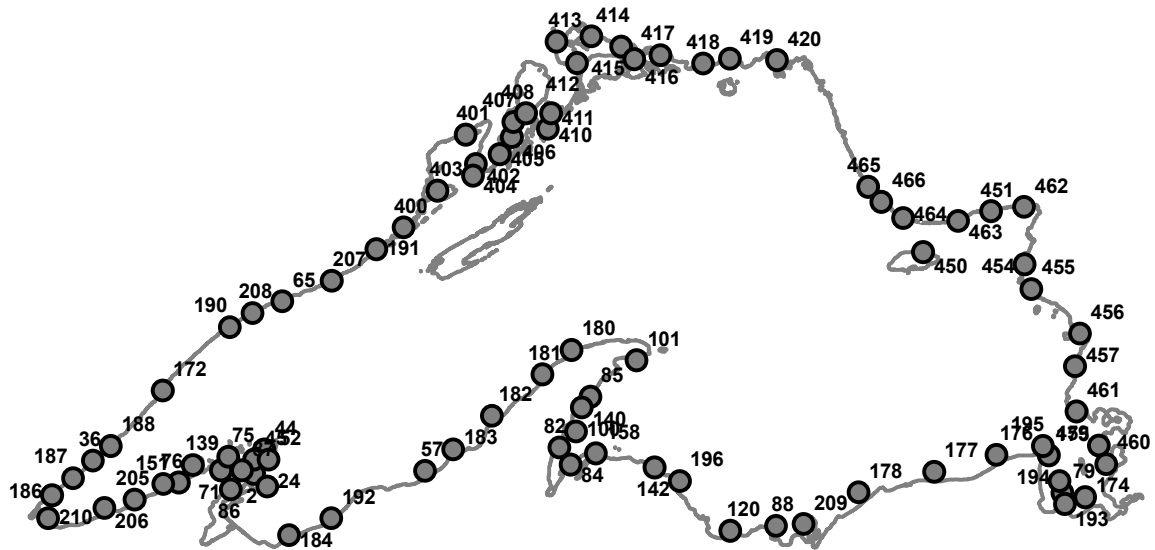


Figure 1. Locations of spring bottom-trawl survey stations in Lake Superior. Individual survey stations are denoted by a unique numeric code. Survey stations in U.S. waters are numbered  $<300$  and survey stations in Canadian waters are numbered  $\geq 400$  (USGS, Lake Superior Biological Station, Ashland, WI).

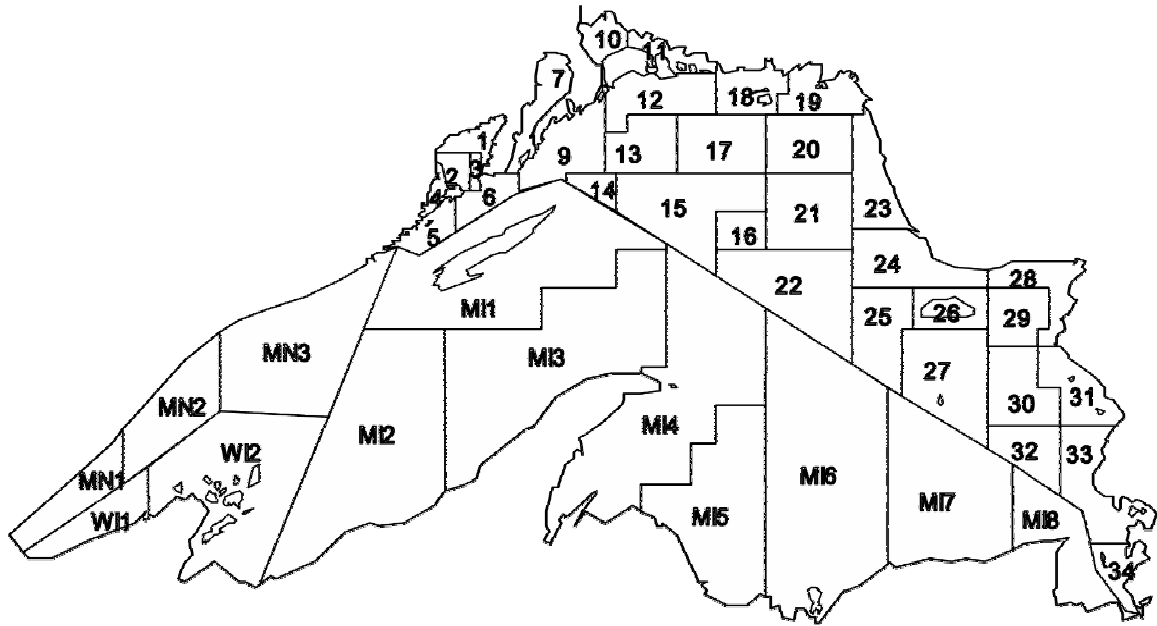


Figure 2. Locations of lake trout management units in Lake Superior. Jurisdictions in U.S. waters are denoted by a unique alpha-numeric code (MI = Michigan, WI = Wisconsin, and MN = Minnesota) and jurisdictions in Canadian waters are denoted by a unique numeric code (Hansen 1996).

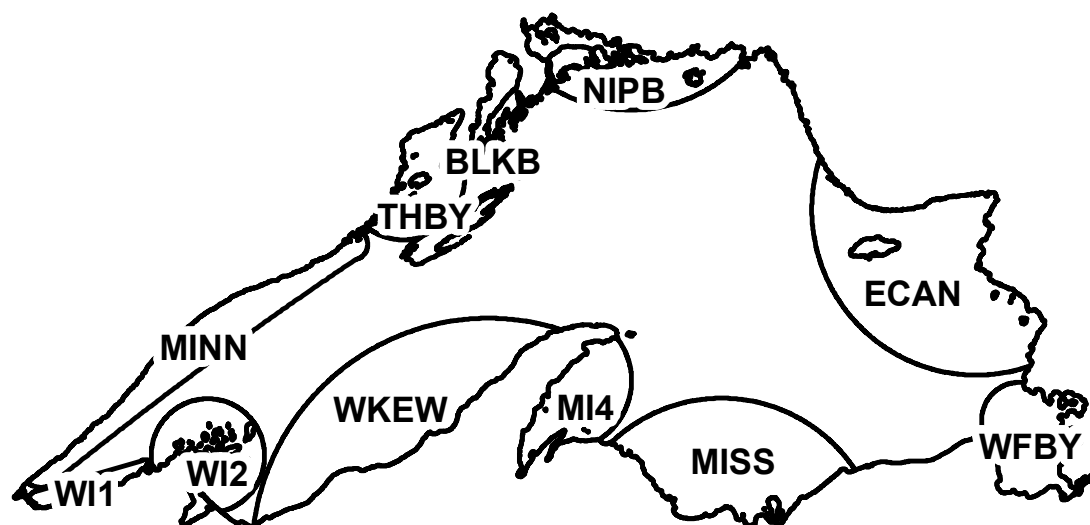


Figure 3. Spatial units used for stock-recruitment analysis (Minnesota-MINN corresponds to a combination of lake trout management units MN-1, MN-2, and MN-3; WI-1 corresponds to lake trout management unit WI-1; WI-2 corresponds to lake trout management unit WI-2; Western Keweenaw-WKEW corresponds to a combination of lake trout management units MI-2 and MI-3; MI-4 corresponds to lake trout management unit MI-4; Michigan South Shore-MISS corresponds to a combination of lake trout management units MI-5 and MI-6; Whitefish Bay-WFBY corresponds to a combination of lake trout management units MI-8, 34, and the southern 63.5% of unit 33; Eastern Canada-ECAN corresponds to a combination of lake trout management units 23, 24, 26, 28, 29, 31, and the northern 36.5% of unit 33; Nipigon Bay-NIPB corresponds to a combination of lake trout management units 10, 11, 12, 18, and 19; Black Bay-BLKB corresponds to a combination of lake trout management unit 7, the eastern 41.2% of unit 6, and the western 28.8% of unit 9; Thunder Bay-THBY corresponds to a combination of lake trout management units 1, 2, 3, 4, 5, and the western 58.8% of unit 6).



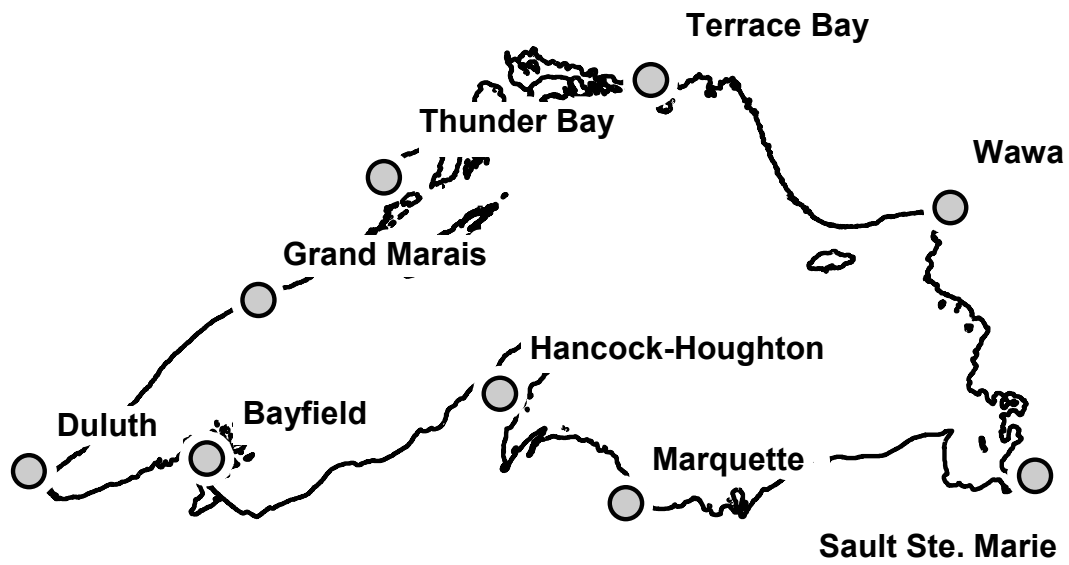


Figure 4. Locations of National Climatic Data Center (NCDC) monitoring stations used for temperature data (temperatures from Grand Marais were assigned to Minnesota-MINN; temperatures from Duluth were assigned to WI-1; temperatures from Bayfield were assigned to WI-2; temperatures from Hancock-Houghton were assigned to Western Keweenaw-WKEW and MI-4; temperatures from Marquette were assigned to Michigan South Shore-MISS; temperatures from Sault Ste. Marie were assigned to Whitefish Bay-WFBY; temperatures from Wawa were assigned to Eastern Canada-ECAN; temperatures from Terrace Bay were assigned to Nipigon Bay-NIPB; temperatures from Thunder Bay were assigned to Black Bay-BLKB and Thunder Bay-THBY).

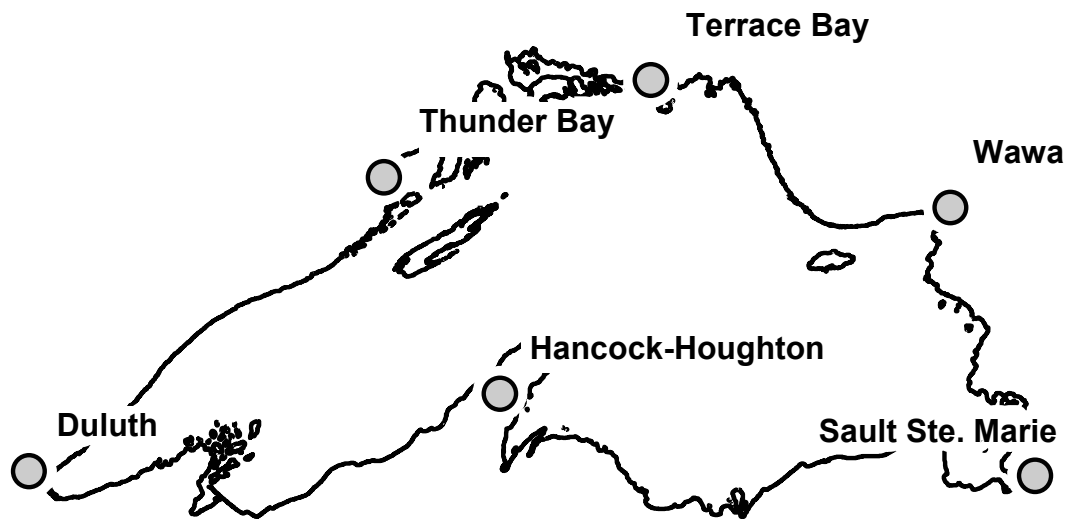


Figure 5. Locations of National Climatic Data Center (NCDC) monitoring stations used for wind speed data (wind speeds from Duluth were assigned to Minnesota-MINN, WI-1, and WI-2; wind speeds from Hancock-Houghton were assigned to Western Keweenaw-WKEW, MI-4, and Michigan South Shore-MISS; wind speeds from Sault Ste. Marie were assigned to Whitefish Bay-WFBY; wind speeds from Wawa were assigned to Eastern Canada-ECAN; wind speeds from Terrace Bay were assigned to Nipigon Bay-NIPB; wind speeds from Thunder Bay were assigned to Black Bay-BLKB and Thunder Bay-THBY).

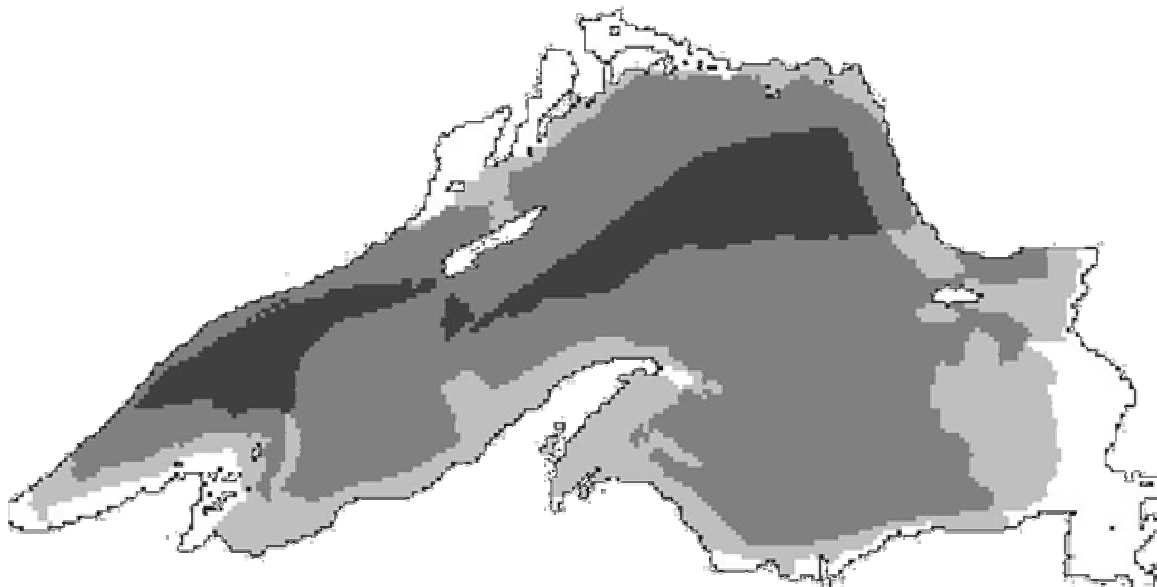


Figure 6. Example Great Lakes Environmental Research Laboratory (GLERL) ice cover digital raster graphic (DRG) file clipped to the Lake Superior shoreline. Lighter colors indicate areas of extended ice cover (GLERL, Ann Arbor, MI).

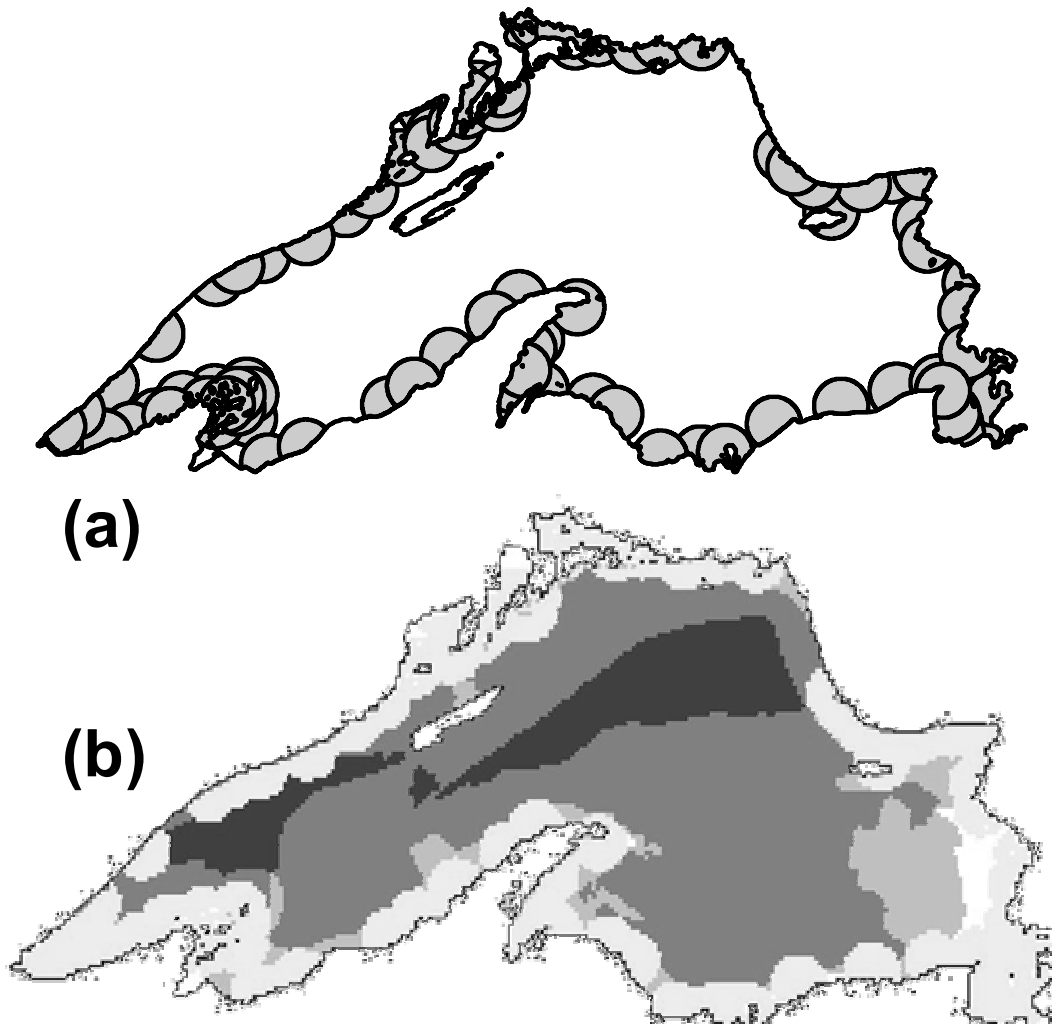


Figure 7. Buffered bottom-trawl stations clipped to the Lake Superior shoreline (a), and an overlay of a bottom-trawl digital raster graphic (DRG) file on an ice cover DRG file clipped to the Lake Superior shoreline (b). In (a), each circle has a radius of 16.5 km (average movement distance of cisco in a Lake Michigan tagging study; Smith and Van Oosten 1940). In (b), lighter colored circles indicate the extent of the bottom-trawl DRG file. Data from ice cover DRG file grids corresponding to overlaying bottom-trawl DRG file grids were extracted for analysis. Ice cover values were extracted for each bottom-trawl station to allow as much flexibility as possible for data analysis.

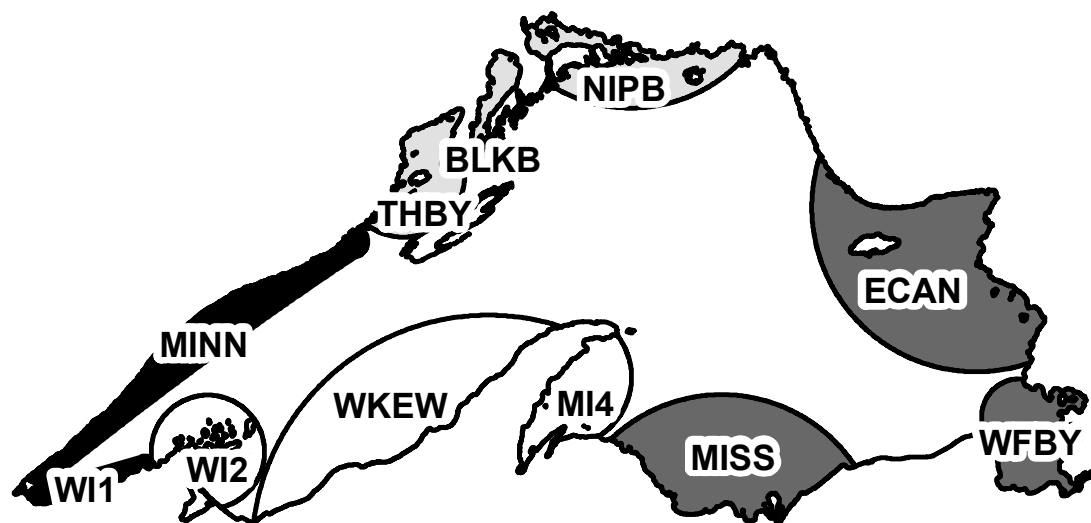


Figure 8. Regional stock groupings identified in Chapter 1 (black = western stocks; white = southern stocks; dark gray = eastern stocks; light gray = northern stocks). Separate multi-factor models were fitted to data from each regional group of spatial units.

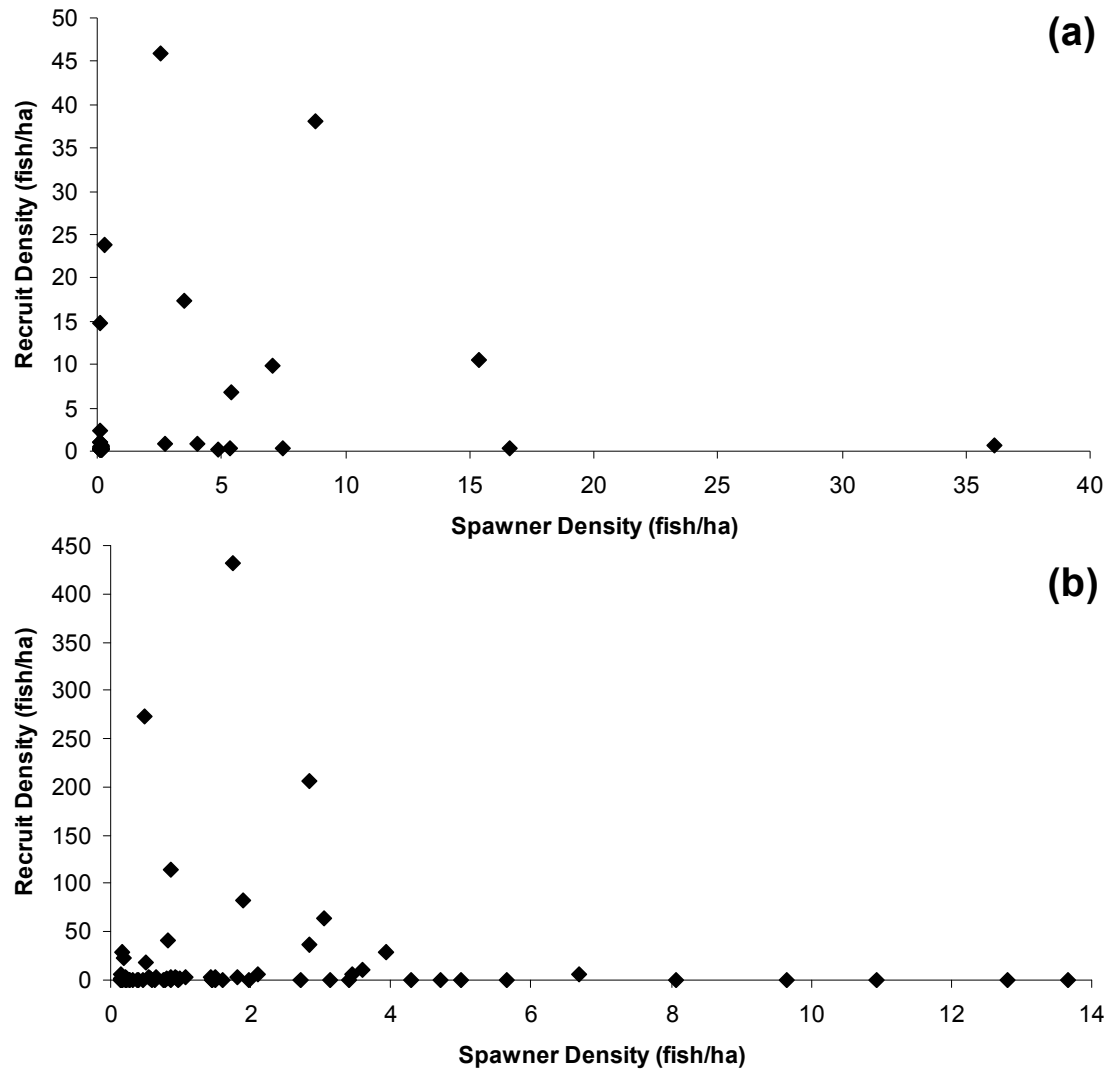


Figure 9. Relationship between estimated recruit density in bottom-trawls and spawner density indexed using combined bottom-trawl and gill-net data in (a) Region 1 (Minnesota and WI-1) and (b) Region 2 (WI-2, Western Keweenaw, and MI-4).

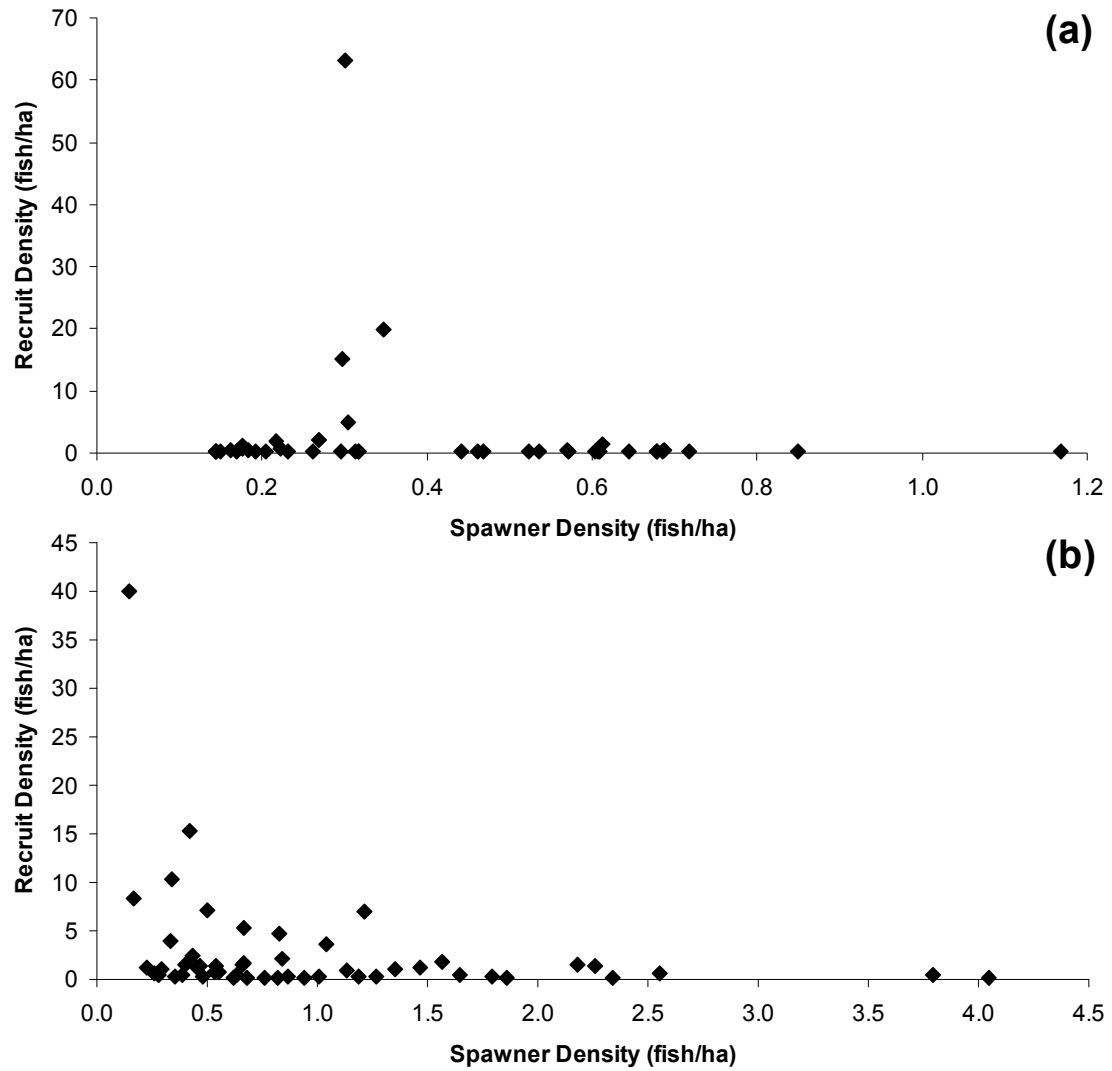


Figure 10. Relationship between estimated recruit density in bottom-trawls and spawner density indexed using combined bottom-trawl and gill-net data in (a) Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada) and (b) Region 4 (Nipigon Bay, Black Bay, and Thunder Bay).

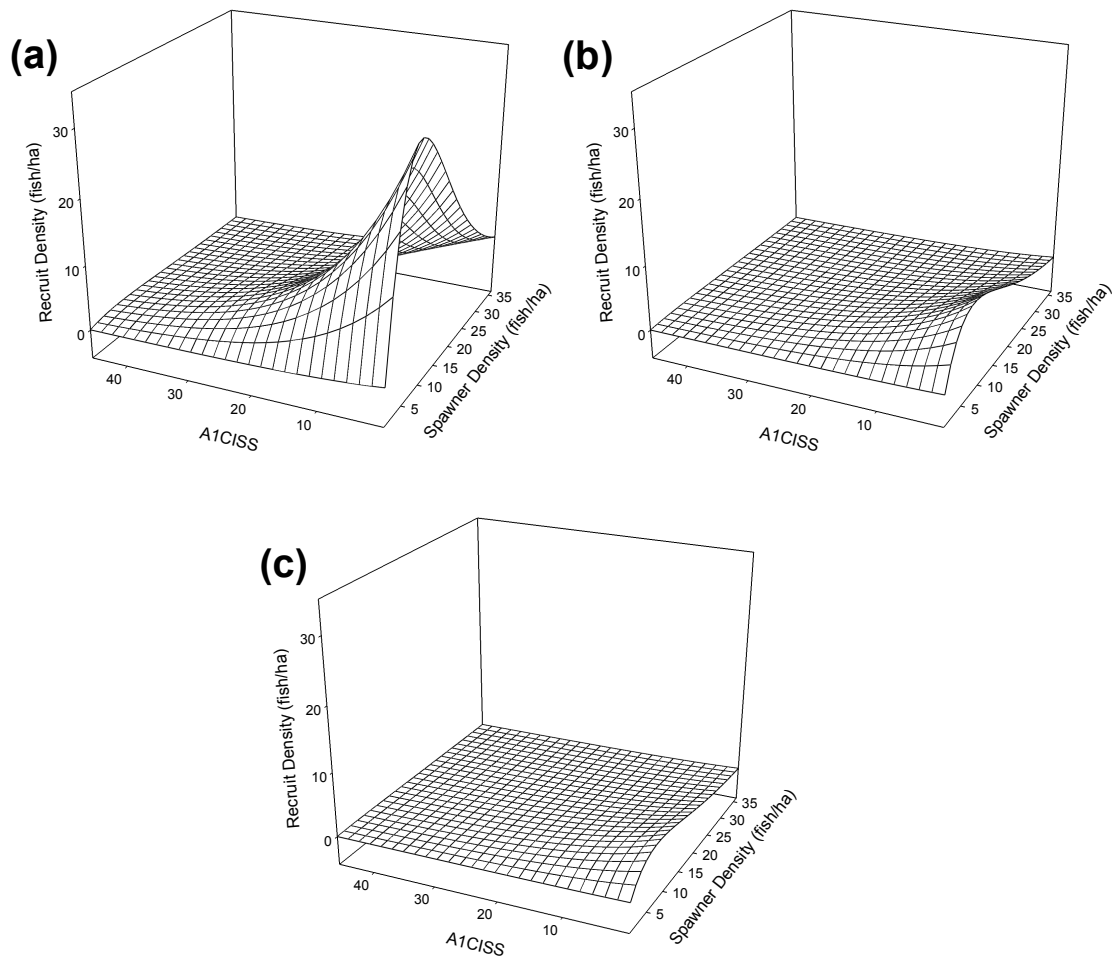


Figure 11. Relationship between recruit density, spawner density, and the density of age-1 cisco during the year prior to cisco hatching ( *A1C1SS* ) in Region 1 (Minnesota and WI-1). Average April air temperature during spring when ciscoes were 11–12 months of age was held at (a) 46.1°F, (b) 38.9°F, and (c) 34.5°F to illustrate the effect of age-1 cisco density on recruitment at the maximum, average, and minimum observed April air temperatures.



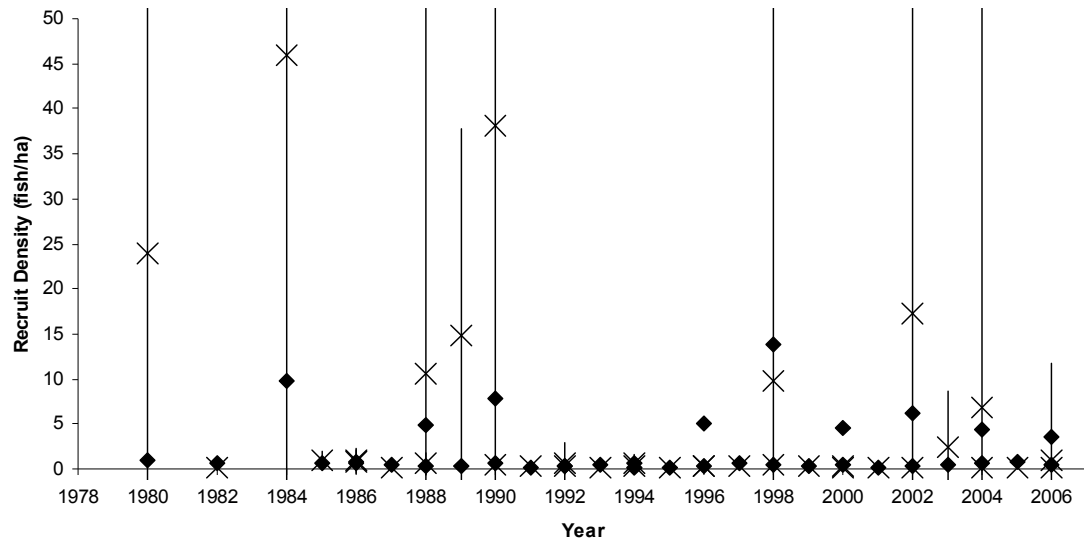


Figure 12. Plot of observed (x) and predicted (solid) recruit densities from Region 1 (Minnesota and WI-1). Standard errors are provided for observed values. Years provided correspond to year of hatching. The final model appears to underestimate strong recruitment events.

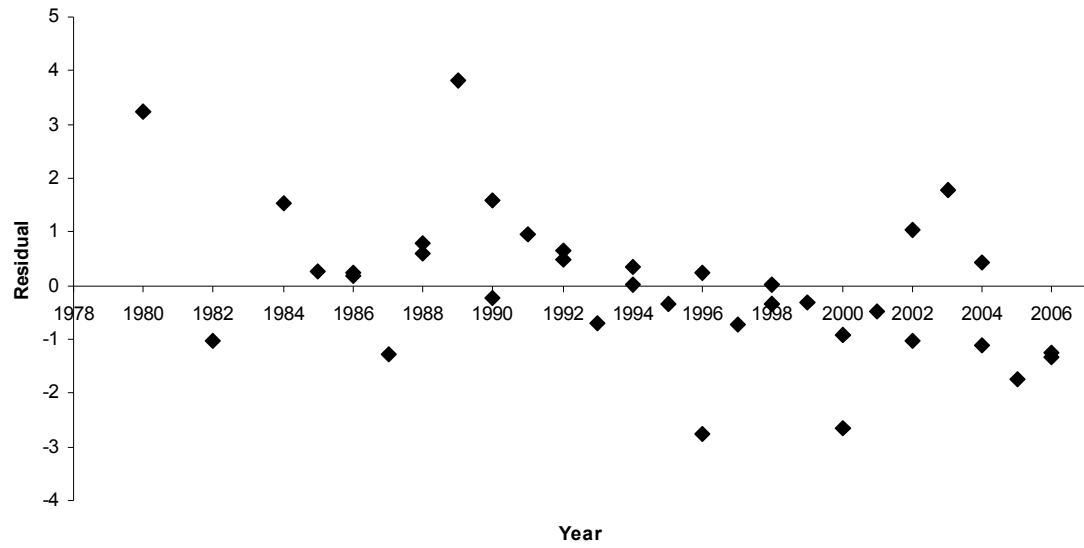


Figure 13. Time-series plot of residuals from Region 1 (Minnesota and WI-1). Years provided correspond to year of hatching. Residuals appear independent.

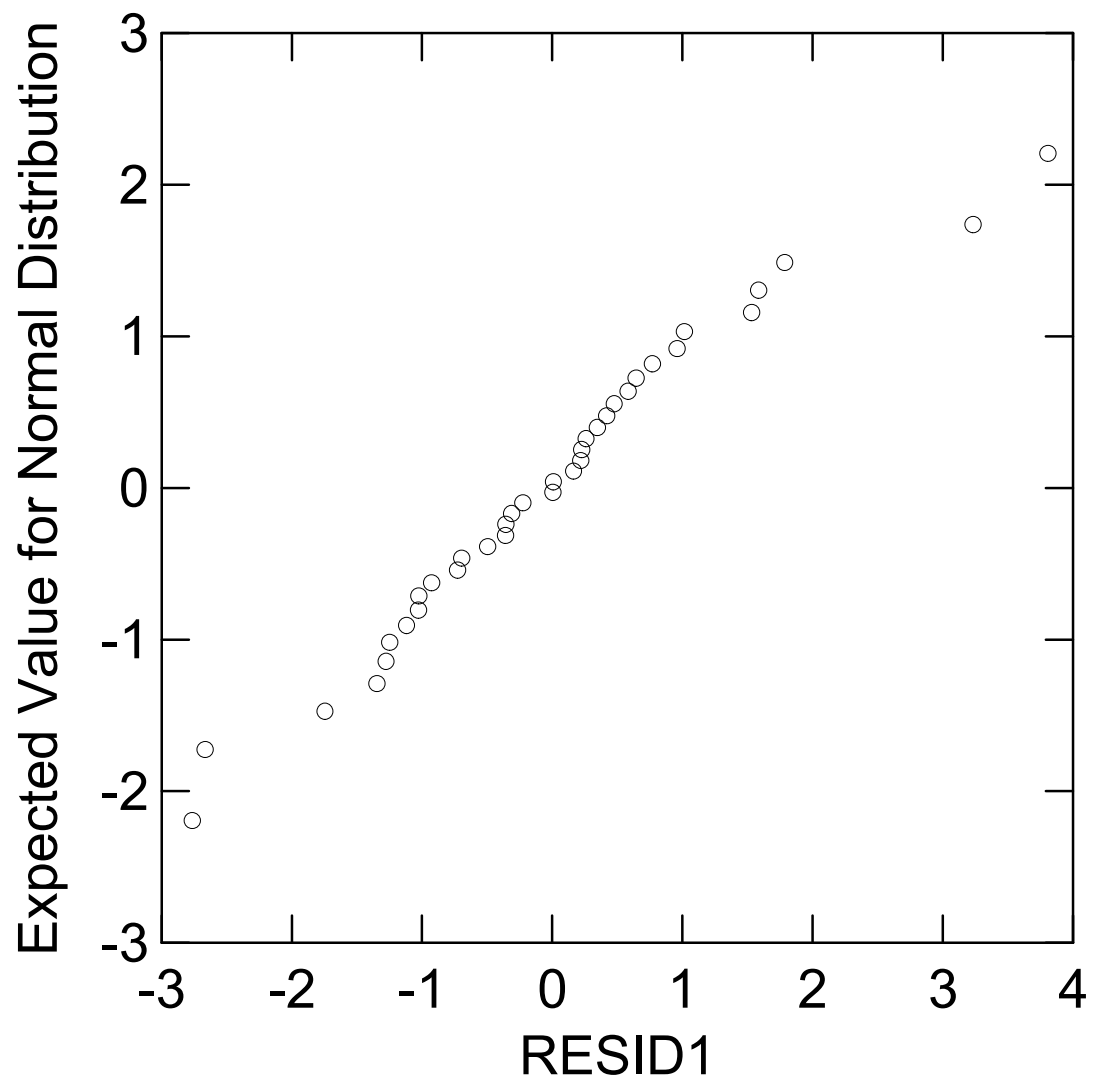


Figure 14. Normal probability plot of residuals from Region 1 (Minnesota and WI-1).

Residuals appear approximately normally distributed.

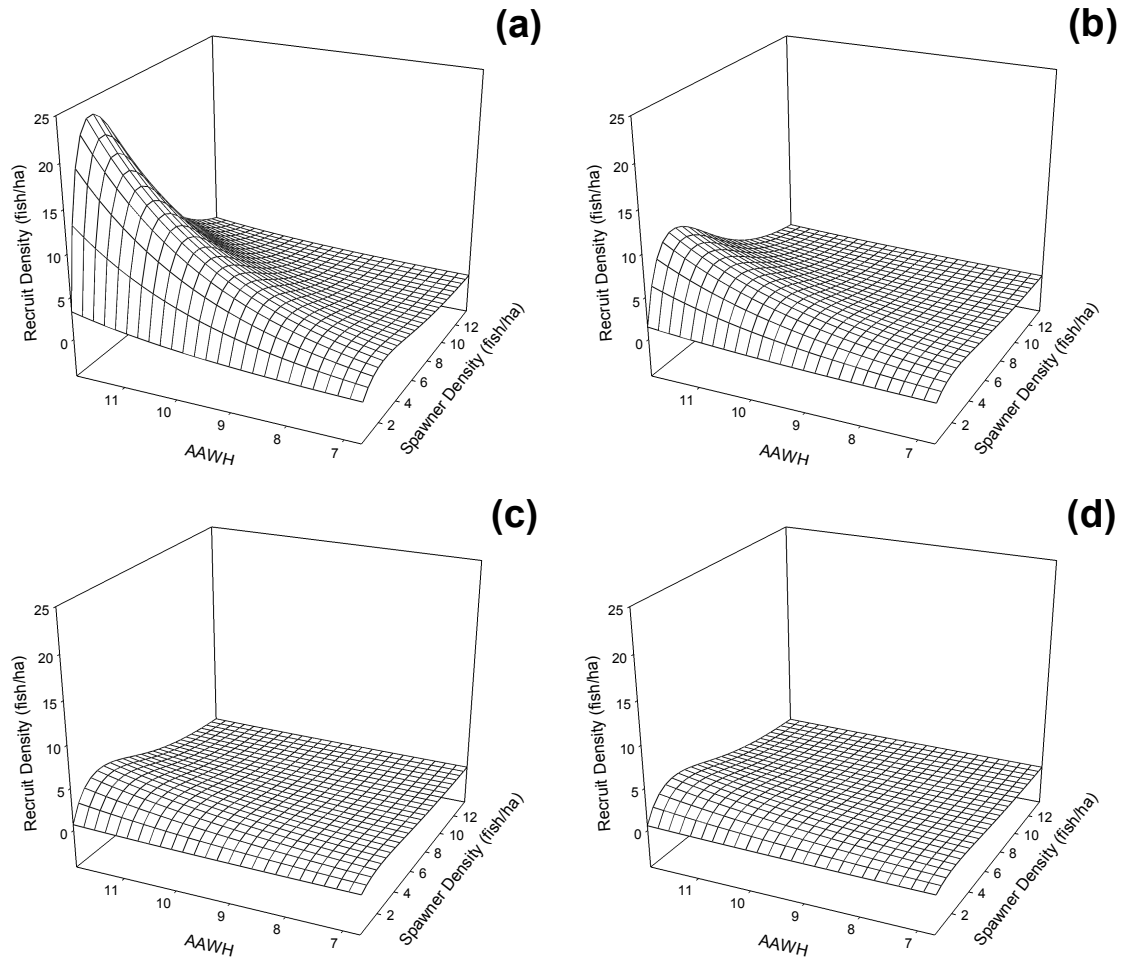


Figure 15. Relationship between recruit density, spawner density, and (a)–(d) average April wind speed during spring when ciscoes were hatching ( *AAWH* ) in Region 2 (WI-2, Western Keweenaw, and MI-4). Average April air temperature during spring when ciscoes were 11–12 months of age and the density of sub-adult cisco during the year prior to cisco hatching were held at (a) 46.3°F and 0.145 fish/ha, (b) 39.2°F and 0.145 fish/ha, (c) 32.4°F and 0.145 fish/ha, and (d) 32.4 °F and 7.447 fish/ha to illustrate the combined effects of April wind speed, April air temperature, and sub-adult cisco density on recruitment.

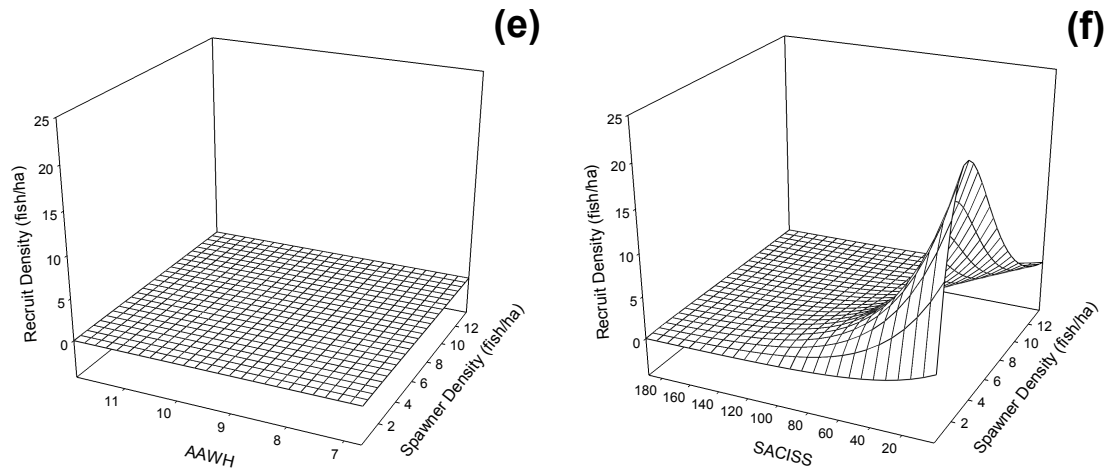


Figure 15. (*continued*) Relationship between recruit density, spawner density, and (e) average April wind speed during spring when ciscoes were hatching ( *AAWH* ) or (f) the density of sub-adult cisco during the year prior to cisco hatching ( *SACISS* ) in Region 2 (WI-2, Western Keweenaw, and MI-4). Average April air temperature during spring when ciscoes were 11–12 months of age and the density of sub-adult cisco during the year prior to cisco hatching were held at (e) 32.4°F and 189.673 fish/ha, whereas average April wind speed during spring when ciscoes were hatching and average April air temperature during spring when ciscoes were 11–12 months of age were held at (f) 11.95 mph and 46.3°F, to illustrate the combined effects of April wind speed, April air temperature, and sub-adult cisco density on recruitment.

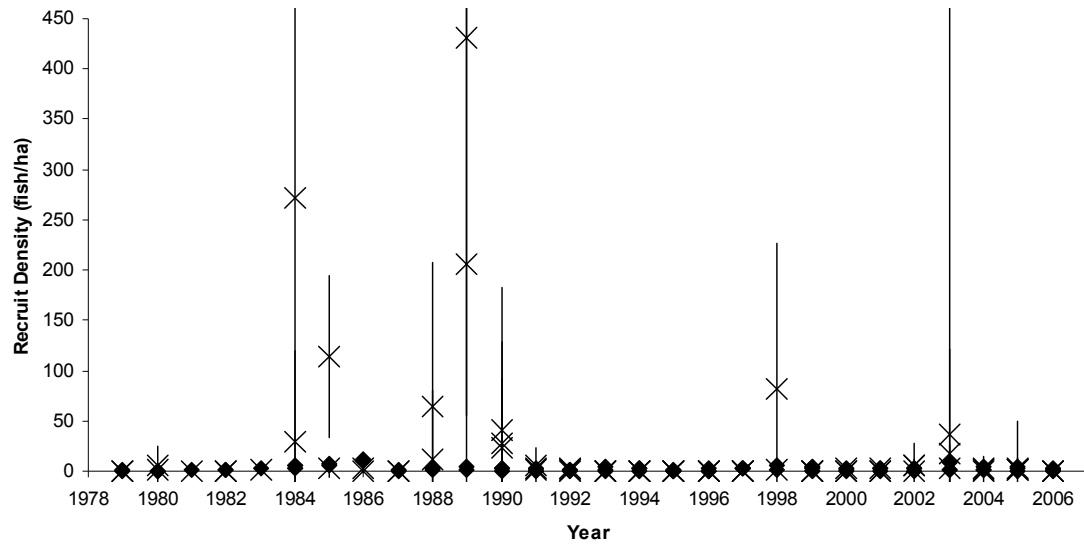


Figure 16. Plot of observed (x) and predicted (solid) recruit densities from Region 2 (WI-2, Western Keweenaw, and MI-4). Standard errors are provided for observed values. Years provided correspond to year of hatching. The final model appears to underestimate strong recruitment events.

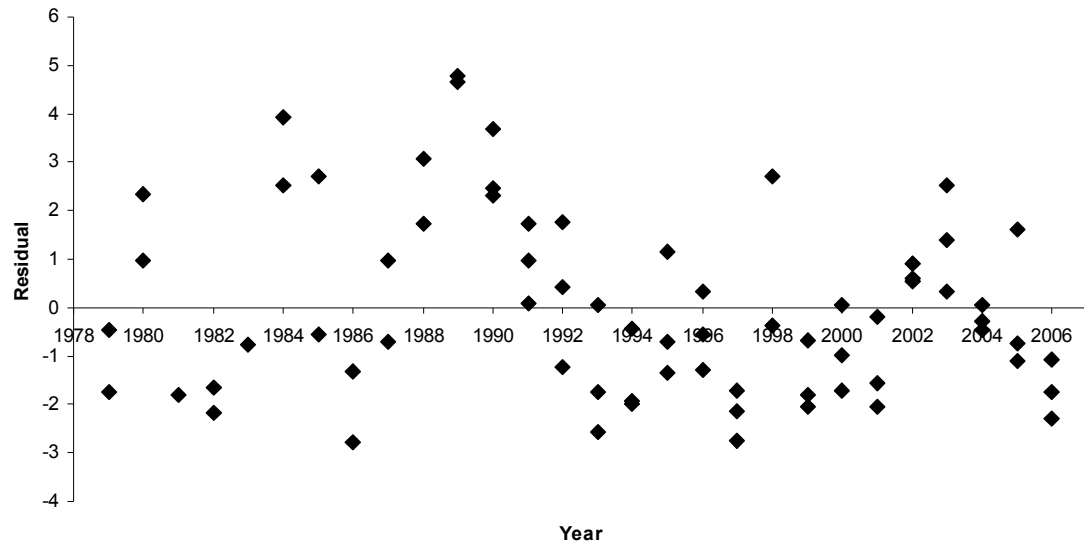


Figure 17. Time-series plot of residuals from Region 2 (WI-2, Western Keweenaw, and MI-4). Years provided correspond to year of hatching. Residuals appear independent.

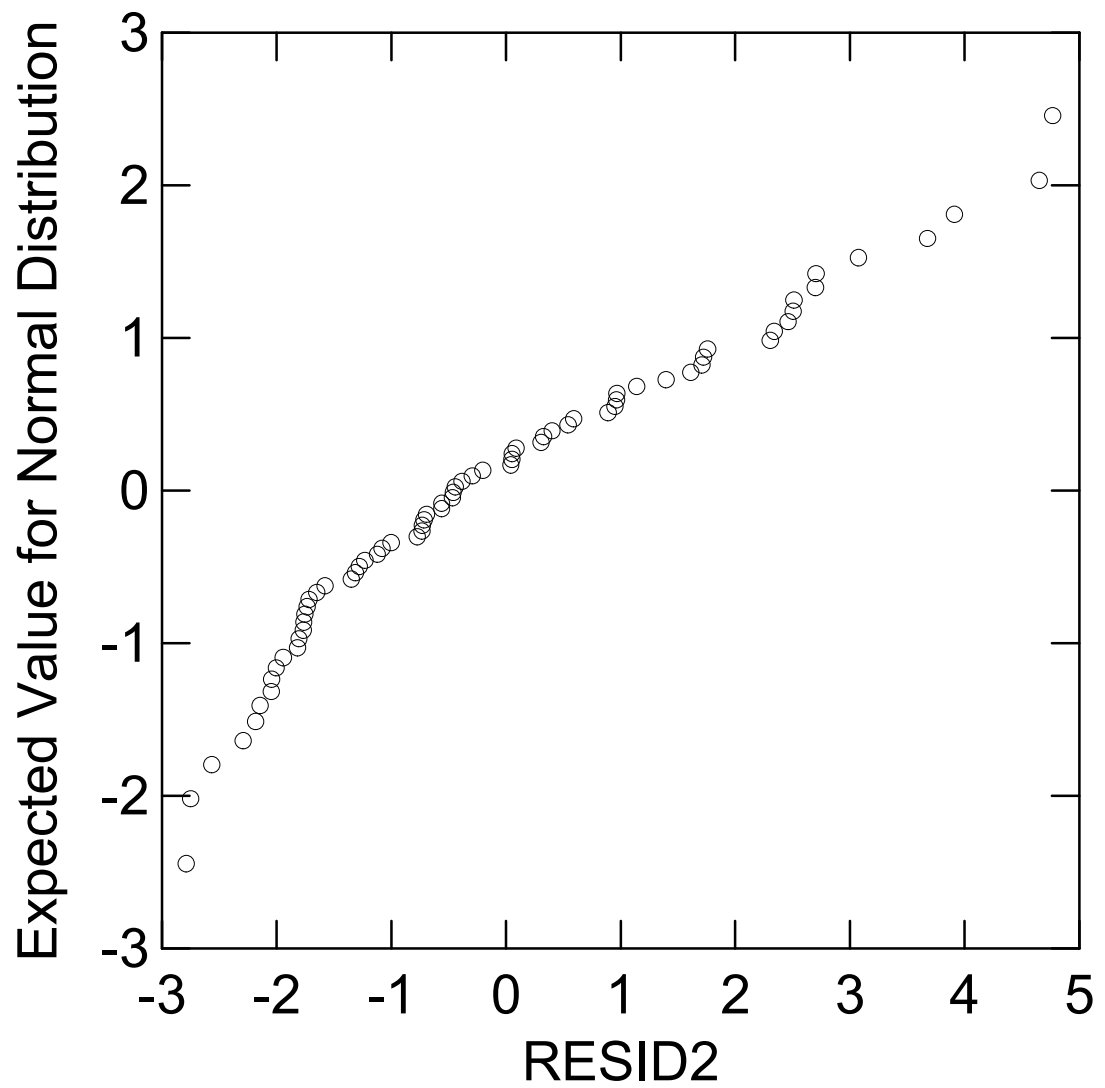


Figure 18. Normal probability plot of residuals from Region 2 (WI-2, Western Keweenaw, and MI-4). Residuals appear approximately normally distributed.



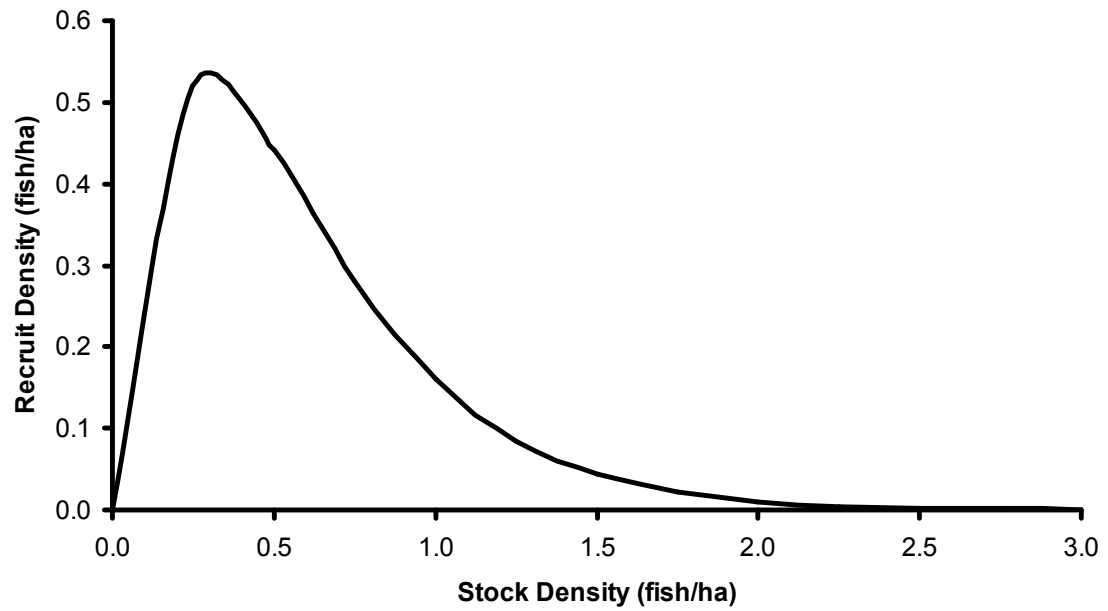


Figure 19. Single-factor stock-recruitment relationship for cisco stocks in Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada). Low stock densities are predicted to produce stronger recruitment than high stock densities.

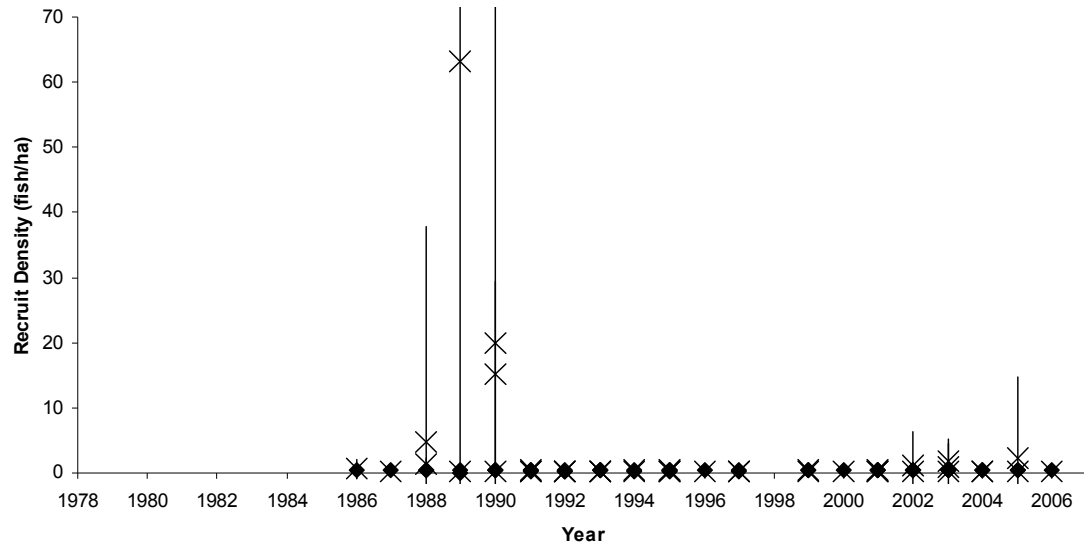


Figure 20. Plot of observed (x) and predicted (solid) recruit densities from Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada). Standard errors are provided for observed values. Years provided correspond to year of hatching. The final model appears to underestimate strong recruitment events.

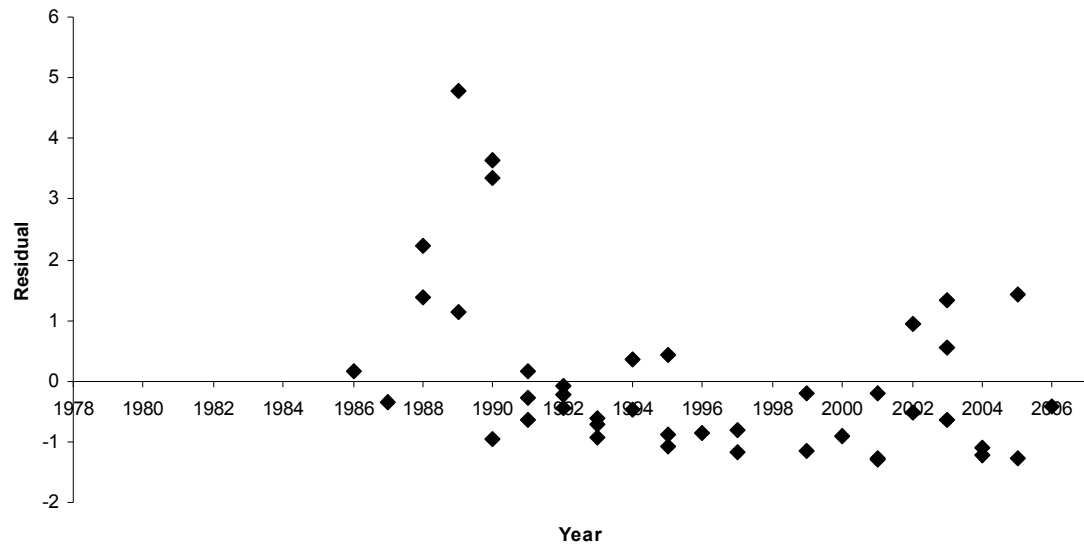


Figure 21. Time-series plot of residuals from Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada). Years provided correspond to year of hatching. Residuals appear independent.

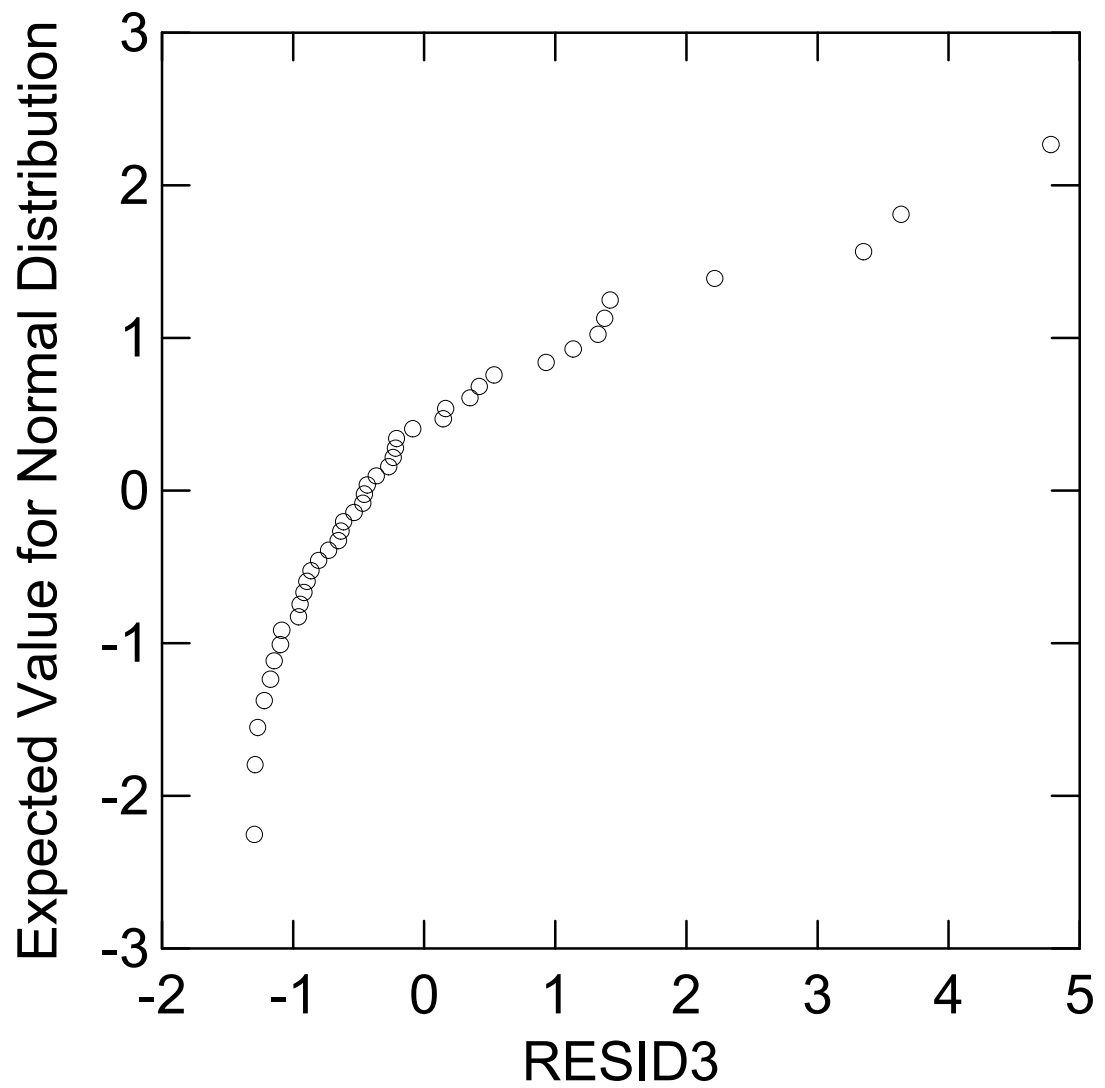


Figure 22. Normal probability plot of residuals from Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada). Residuals appear positively skewed.

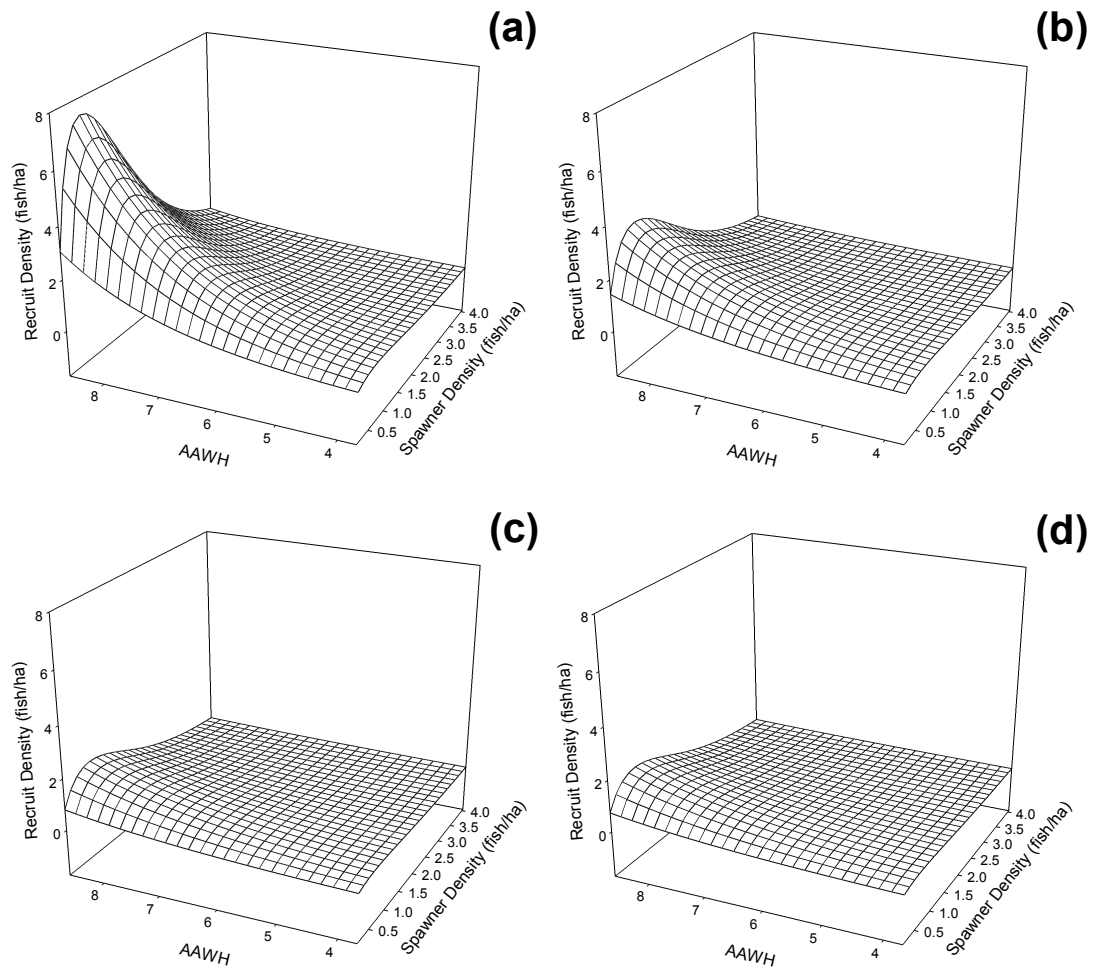


Figure 23. Relationship between recruit density, spawner density, and (a)–(d) average April wind speed during spring when ciscoes were hatching (*AAWH*) in Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Average April air temperature during spring when ciscoes were 11–12 months of age and the interaction between the biomass of rainbow smelt during the year of cisco hatching and the density of sub-adult cisco during the year prior to cisco hatching were held at (a) 43.7°F and 0.012, (b) 37.1°F and 0.012, (c) 31.9°F and 0.012, and (d) 31.9 °F and 5.477 to illustrate the combined effects of April wind speed, April air temperature, rainbow smelt biomass, and sub-adult cisco density on recruitment.

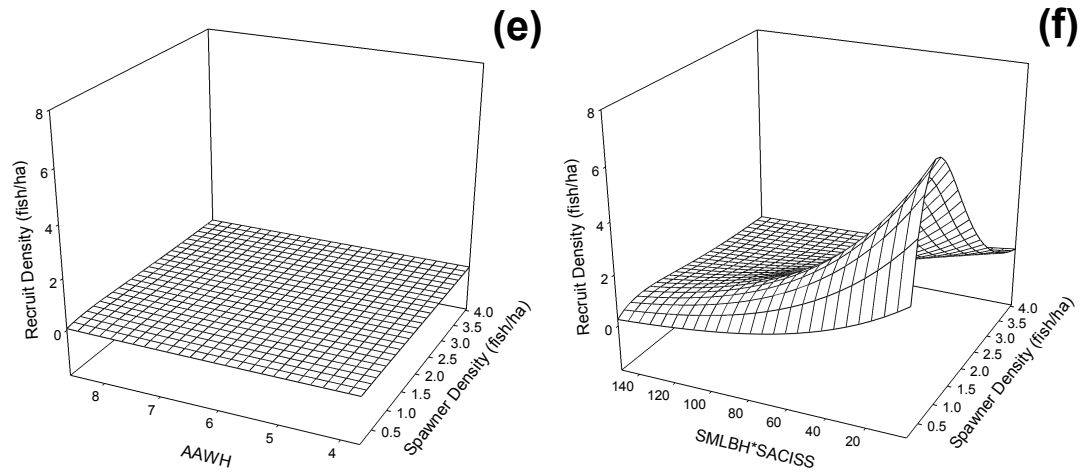


Figure 23. (*continued*) Relationship between recruit density, spawner density, and (e) average April wind speed during spring when ciscoes were hatching ( *AAWH* ) or (f) the interaction between the biomass of rainbow smelt during the year of cisco hatching ( *SMLBH* ) and the density of sub-adult cisco during the year prior to cisco hatching ( *SACISS* ) in Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Average April air temperature during spring when ciscoes were 11–12 months of age and the interaction between the biomass of rainbow smelt during the year of cisco hatching and the density of sub-adult cisco during the year prior to cisco hatching were held at (e) 31.9°F and 150.247, whereas average April wind speed during spring when ciscoes were hatching and average April air temperature during spring when ciscoes were 11–12 months of age were held at (f) 8.6 mph and 43.7°F, to illustrate the combined effects of April wind speed, April air temperature, rainbow smelt biomass, and sub-adult cisco density on recruitment.

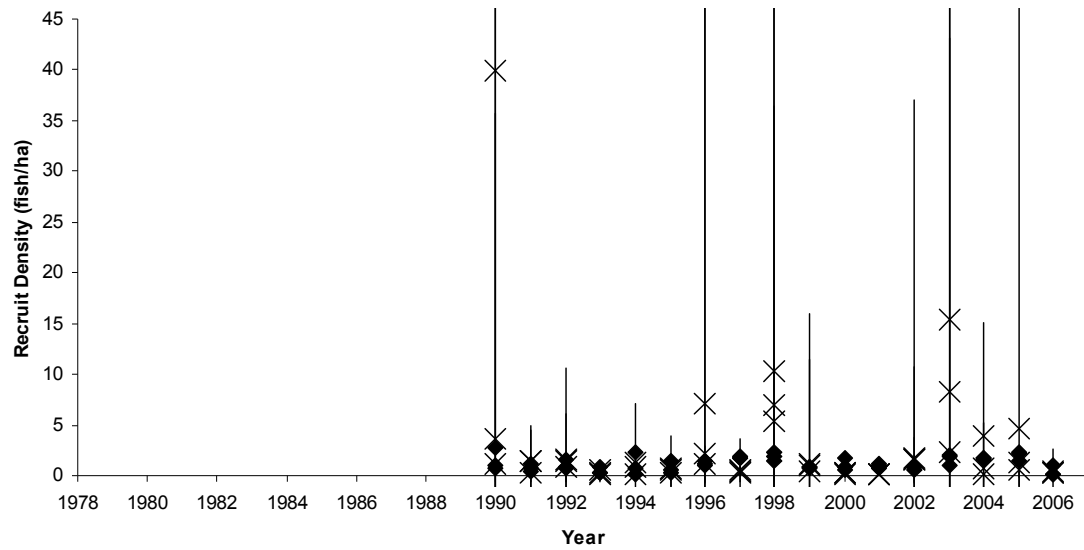


Figure 24. Plot of observed (x) and predicted (solid) recruit densities from Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Standard errors are provided for observed values. Years provided correspond to year of hatching. The final model appears to underestimate strong recruitment events.

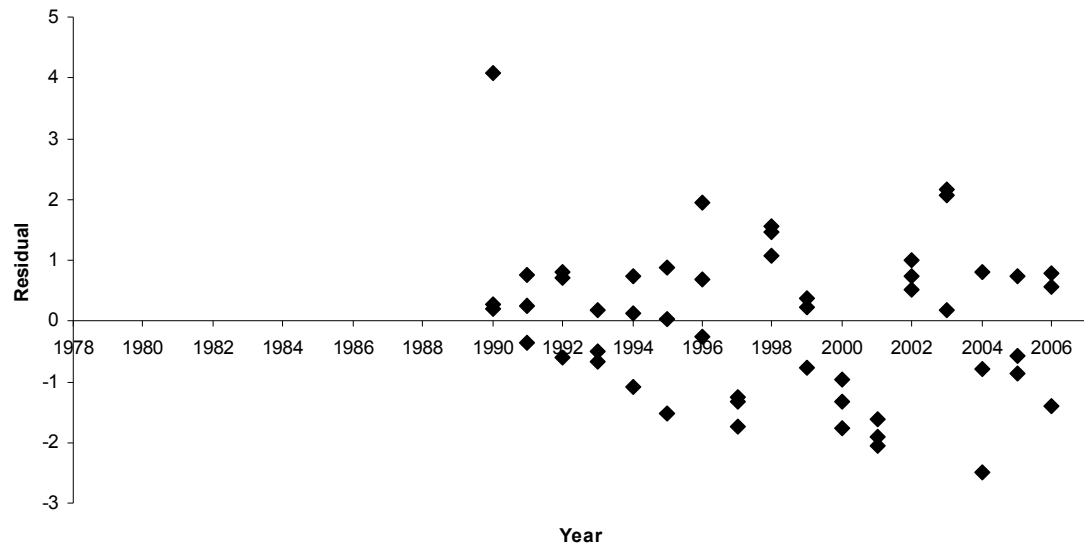


Figure 25. Time-series plot of residuals from Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Years provided correspond to year of hatching. Residuals appear independent.



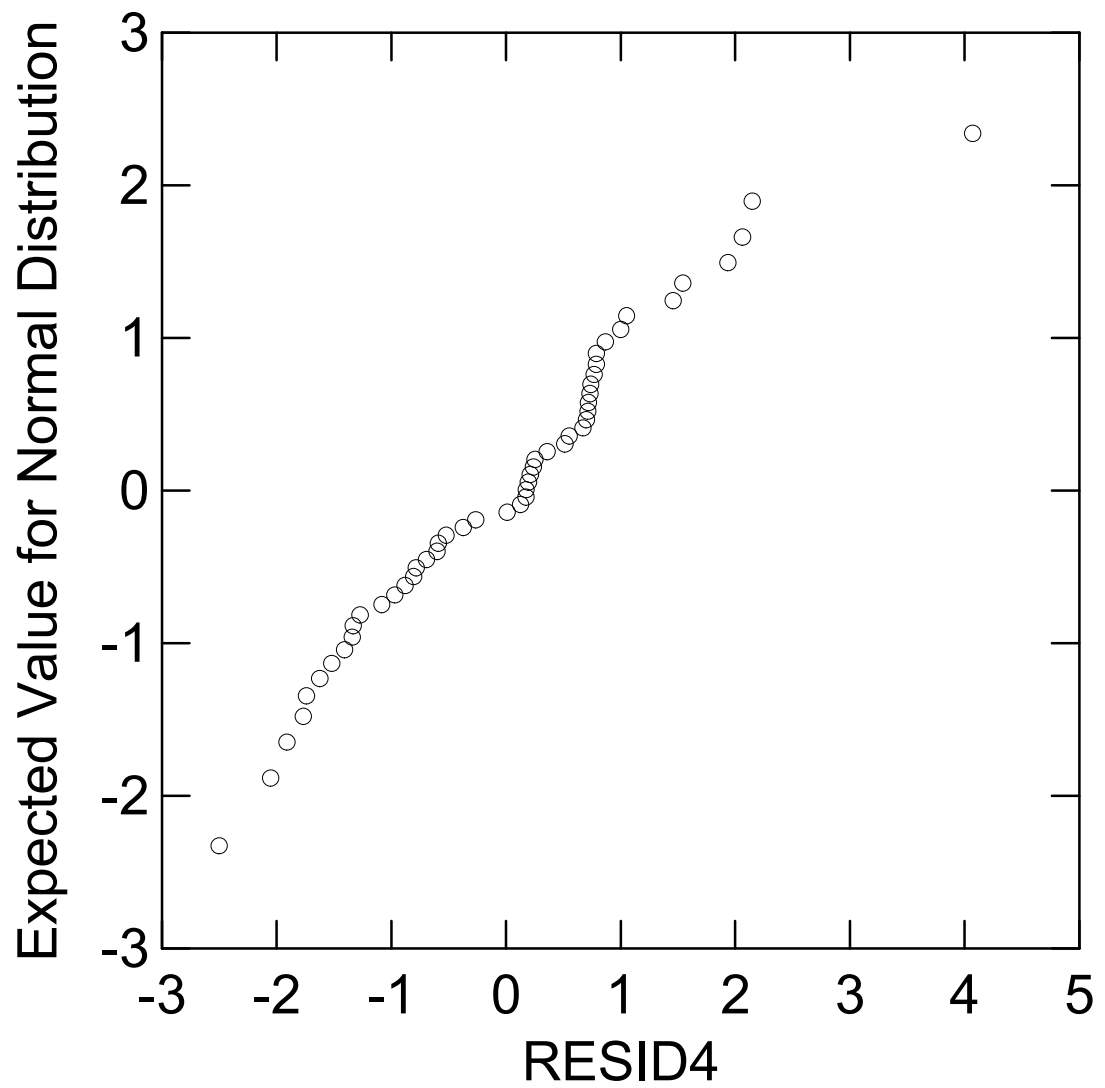


Figure 26. Normal probability plot of residuals from Region 4 (Nipigon Bay, Black Bay, and Thunder Bay). Residuals appear approximately normally distributed.

## CONCLUSIONS

The fish-community objective for prey species in Lake Superior calls for rehabilitation of cisco stocks to historic levels of abundance to provide a forage base for lake trout and to support a commercial fishery (Busiahn 1990). Fishery management plans for the lower Great Lakes recognize the cisco as an important member of the native fish community and call for reestablishment of self-sustaining populations throughout the species historic range (Edsall and DeSorcie 2002). Previously, studies of cisco stock-recruitment in the Great Lakes were limited to one study of cisco stock-recruitment in Wisconsin waters of Lake Superior (Hoff 2004). The previous study identified and quantified the effects of multiple biotic and abiotic factors correlated to age-1 cisco recruitment, but failed to identify or quantify the spatial scale for cisco recruitment dynamics, and management parameters estimated for cisco stocks in Wisconsin waters of Lake Superior were not broadly applicable to cisco stocks in other regions of Lake Superior or the lower Great Lakes. My findings provide the first estimate of the spatial scale for cisco recruitment dynamics and the first comprehensive estimates of the effects of biotic and abiotic factors on recruitment of age-1 cisco in Lake Superior, and are broadly applicable to cisco restoration and management efforts throughout Lake Superior and the entire Great Lakes basin.

In Chapter 1, I found that recruitment variation of cisco in Lake Superior was best described by an 8-parameter regional model with separate stock-recruitment relationships for western, southern, eastern, and northern stocks. The regional scale identified for modeling suggests that large-scale abiotic factors are more important than small-scale biotic factors in regulating cisco recruitment in Lake Superior, and that fishery managers

throughout Lake Superior and the entire Great Lakes basin should address cisco restoration and management efforts on a regional scale in each lake. I also found that the density-independent recruitment rate and the rate of compensatory density-dependence varied among regions at different rates. Relatively constant density-independent recruitment rates among regions in my study suggest that the ability to reproduce at low spawning stock size may be genetically pre-determined and similar for cisco stocks throughout Lake Superior, whereas highly variable rates of compensatory density-dependence among regions in my study suggest that large-scale abiotic factors drive regional differences in age-1 cisco year-class strength and regional deviations from normal patterns of recruitment synchrony in Lake Superior through regional differences in compensatory density-dependence. Finally, I found that peak recruitment and the spawning stock size that produced peak recruitment varied among regions. Estimates of peak recruitment and the spawning stock size that produced peak recruitment in my study were greatest for the most productive and lowest for the least productive regions of Lake Superior, which suggests that carrying capacity may be an important underlying factor driving regional differences in rates of compensatory density-dependence for cisco stocks in Lake Superior.

In Chapter 2, I found that recruitment variation of cisco in Lake Superior was correlated to adult spawning stock size in all four regions, the density of juvenile cisco during the year prior to cisco hatching in three of four regions, average April air temperature during spring when ciscoes were 11–12 months of age in three of four regions, average April wind speed during spring when ciscoes were hatching in two of four regions, and the biomass of rainbow smelt during the year of cisco hatching in one

of four regions. My findings support the hypothesis that different biotic and abiotic factors regulate cisco recruitment within different regions of Lake Superior, suggest that air temperature during spring when ciscoes are 11–12 months of age drives recruitment variation on a lake-wide scale, whereas adult spawning stock size, intraspecific interactions with juvenile cisco, wind speed during spring when ciscoes are hatching, and interspecific interactions with rainbow smelt regulate recruitment variation on a regional scale in Lake Superior. Laboratory and field studies suggest that air temperature during spring when ciscoes are 11–12 months of age may positively influence recruitment by shortening the duration of winter, whereas adult spawning stock size and the density of juvenile cisco may negatively influence recruitment by increasing competition for limited resources, wind speed during spring when ciscoes are hatching may positively influence recruitment by promoting larval retention on spawning grounds or transport of newly hatched larvae away from spawning grounds to more productive nursery areas, and the biomass of rainbow smelt may negatively influence recruitment through larval predation. The variety of biotic and abiotic variables included in final multi-factor models in my study suggests that fishery managers throughout Lake Superior and the entire Great Lakes basin should evaluate the potential effects of similar biotic and abiotic factors on recruitment prior to addressing cisco restoration and management efforts in each lake.

**APPENDIX A**  
**ADDITIONAL TABLES – CHAPTER 1**

**Table 1. Results of the linear regression for cisco recruitment in Region 1 (Minnesota and WI-1).**

---

```

>MODEL LNRAST = CONSTANT+AST

>ESTIMATE / TOL=1e-012
Data for the following results were selected according to:
  (MINN = 1) OR (WI1 = 1)
28 case(s) deleted due to missing data.

Eigenvalues of unit scaled X'X
      1      2
1.446656175 0.553343825

Condition indices
      1      2
1.000000000 1.616907326

Variance proportions
      1      2
CONSTANT    0.276671912 0.723328088
AST          0.276671912 0.723328088

Dep Var: LNRAST   N: 36   Multiple R: 0.581122069   Squared multiple R: 0.337702859
Adjusted squared multiple R: 0.318223531   Standard error of estimate: 1.617942369

Effect          Coefficient    Std Error    Std Coef Tolerance    t    P(2 Tail)
CONSTANT        0.866821287    0.301391917    0.000000000    .    2.87606    0.00690
AST             -0.163291478    0.039217791   -0.581122069    1.00E+00 -4.16371    0.00020

Effect          Coefficient    Lower 95%    Upper 95%
CONSTANT        0.866821287    0.254319209    1.479323364
AST             -0.163291478   -0.242991620   -0.083591335

Correlation matrix of regression coefficients
              CONSTANT      AST
CONSTANT      1.000000000
AST           -0.446656175 1.000000000

Analysis of Variance
Source          Sum-of-Squares    df    Mean-Square    F-ratio    P
Regression      4.53823E+01      1    4.53823E+01    1.73365E+01    0.000202045
Residual        8.90031E+01      34    2.617737511

-----
*** WARNING ***
Case          50 has large leverage    (Leverage = 0.656670169)

Durbin-Watson D Statistic    2.875124717
First Order Autocorrelation -0.456289855

```

Table 2. Results of the linear regression for cisco recruitment in Region 2 (WI-2, Western Keweenaw, and MI-4).

```

>MODEL LNRAST = CONSTANT+AST

>ESTIMATE / TOL=1e-012
Data for the following results were selected according to:
      (WI2 = 1) OR (WKEW = 1) OR (MI4 = 1)
26 case(s) deleted due to missing data.

Eigenvalues of unit scaled X'X
      1          2
1.587320842 0.412679158

Condition indices
      1          2
1.000000000 1.961218997

Variance proportions
      1          2
CONSTANT    0.206339579 0.793660421
AST          0.206339579 0.793660421

Dep Var: LNRAST   N: 70   Multiple R: 0.549204544   Squared multiple R: 0.301625631
Adjusted squared multiple R: 0.291355420   Standard error of estimate: 2.028049553

Effect          Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)
CONSTANT        1.333620480    0.299495923    0.000000000      .      4.45288    0.00003
AST             -0.450260713    0.083084426   -0.549204544    1.00E+00 -5.41932    0.00000

Effect          Coefficient      Lower 95%      Upper 95%
CONSTANT        1.333620480    0.735985655    1.931255306
AST             -0.450260713   -0.616053108   -0.284468318

Correlation matrix of regression coefficients
      CONSTANT      AST
CONSTANT    1.000000000
AST         -0.587320842 1.000000000

Analysis of Variance
Source          Sum-of-Squares      df      Mean-Square      F-ratio      P
Regression      1.20794E+02          1      1.20794E+02    2.93690E+01    0.000000851
Residual        2.79683E+02          68      4.112984987

-----
*** WARNING ***
Case          147 has large leverage (Leverage = 0.206183913)
Case          148 has large leverage (Leverage = 0.237716584)

Durbin-Watson D Statistic    1.465496346
First Order Autocorrelation  0.255923400

```

**Table 3. Results of the linear regression for cisco recruitment in Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada).**

---

```
>MODEL LNRAST = CONSTANT+AST

>ESTIMATE / TOL=1e-012
Data for the following results were selected according to:
(MISS = 1) OR (WFBY = 1) OR (ECAN = 1)
19 case(s) deleted due to missing data.

Eigenvalues of unit scaled X'X
      1      2
1.869849995 0.130150005

Condition indices
      1      2
1.000000000 3.790367230

Variance proportions
      1      2
CONSTANT    0.065075003 0.934924997
AST          0.065075003 0.934924997

Dep Var: LNRAST   N: 43   Multiple R: 0.500652678   Squared multiple R: 0.250653104
Adjusted squared multiple R: 0.232376351   Standard error of estimate: 1.410766735

Effect          Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)
CONSTANT        1.586552732    0.436109457    0.000000000      .      3.63797    0.00076
AST             -3.420445732    0.923625019   -0.500652678    1.00E+00 -3.70328    0.00063

Effect          Coefficient      Lower 95%      Upper 95%
CONSTANT        1.586552732    0.705811803    2.467293662
AST             -3.420445732   -5.285744331   -1.555147133

Correlation matrix of regression coefficients
      CONSTANT      AST
CONSTANT    1.000000000
AST         -0.869849995 1.000000000

Analysis of Variance
Source          Sum-of-Squares      df      Mean-Square      F-ratio      P
Regression      2.72951E+01          1      2.72951E+01    1.37143E+01    0.000628112
Residual        8.16008E+01          41      1.990262781

-----
*** WARNING ***
Case          150 is an outlier      (Studentized Residual = 4.034585164)
Case          169 has large leverage (Leverage = 0.269333102)

Durbin-Watson D Statistic    1.265258262
First Order Autocorrelation  0.357162590
```



**Table 4. Results of the linear regression for cisco recruitment in Region 4 (Nipigon Bay, Black Bay, and Thunder Bay).**

---

```

>MODEL LNRAST = CONSTANT+AST

>ESTIMATE / TOL=1e-012
Data for the following results were selected according to:
      (NIPB = 1) OR (BLKB = 1) OR (THBY = 1)

Eigenvalues of unit scaled X'X
      1          2
      1.761234438 0.238765562

Condition indices
      1          2
      1.000000000 2.715956069

Variance proportions
      1          2
      CONSTANT    0.119382781 0.880617219
      AST          0.119382781 0.880617219

Dep Var: LNRAST   N: 51   Multiple R: 0.628373554   Squared multiple R: 0.394853323

Adjusted squared multiple R: 0.382503391   Standard error of estimate: 1.426687582

Effect            Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)
CONSTANT          1.577124971    0.308069969    0.000000000      .      5.11937    0.00001
AST               -1.338784362    0.236769097   -0.628373554    1.00E+00 -5.65439    0.00000

Effect            Coefficient      Lower 95%      Upper 95%
CONSTANT          1.577124971    0.958035178    2.196214764
AST               -1.338784362    -1.814589686   -0.862979037

Correlation matrix of regression coefficients
      CONSTANT      AST
CONSTANT    1.000000000
AST         -0.761234438 1.000000000

Analysis of Variance
Source          Sum-of-Squares      df      Mean-Square      F-ratio      P
Regression      6.50772E+01      1      6.50772E+01    3.19721E+01    0.000000794
Residual        9.97364E+01      49      2.035437457

-----
*** WARNING ***
Case      235 has large leverage      (Leverage = 0.236396846)
Case      236 is an outlier            (Studentized Residual = 3.326279771)
Case      252 has large leverage      (Leverage = 0.276421091)

Durbin-Watson D Statistic      1.871450013
First Order Autocorrelation      0.054121510

```

**APPENDIX B**  
**ADDITIONAL TABLES – CHAPTER 2**

Table 1. Python code used for ASCII grid conversions.

---

```

"""
    Purpose: Converts NOAA ASCII Grids to ArcInfo grids

    Features:

"""

__author__ = "Alan Bond"
__version__ = "1.0"
__date__ = "10-24-2007"

import os, sys, glob
import arcgisscripting

#.....
#.....
#..
#.. Input parameters or variables
#..
#..
#.....
#.....

gp = arcgisscripting.create()
convertedGridFolderName = 'ReformattedGrids'
arcInfoGridFolderName = 'ArcInfoGrids'
noaaGridExtension = '.dat'
logFileName = 'GridConversionLog.log'

# Items needed for header
numberOfColumns = '516'
numberOfRows = '510'
lowerLeftXCoord = '-649446.25'
lowerLeftYCoord = '3306260'
cellSize = '2550'
noDataValue = '-99'

#.....
#.....
#..
#.. Functions
#..
#.....
#.....

```

```

def MakeGrid(InAsciiFilePath, OutRasterPath):
    try:
        gp.ASCIIToRaster_conversion(InAsciiFilePath, OutRasterPath, "INTEGER")
        status = 1
    except:
        status = 0
    return status

def WriteHeader():
    l = []
    l.append('ncols %s' %(numberOfColumns))
    l.append('nrows %s' %(numberOfRows))
    l.append('xllcorner %s' %(lowerLeftXCoord))
    l.append('yllcorner %s' %(lowerLeftYCoord))
    l.append('cellsize %s' %(cellSize))
    l.append('nodata_value %s\n' %(noDataValue))
    return '\n'.join(l)

def ReFormatLine(LineOfAscii):
    l = []
    for i in range(3,len(LineOfAscii)+3, 3):
        l.append(LineOfAscii[i-3:i].strip())
    #print l
    reFormattedLine = ''.join(l)
    reFormattedLine = '%s%s' %(reFormattedLine, '\n')
    return reFormattedLine

if __name__ == '__main__':

    # check to make sure we have an input folder specified on the cmd line
    if len(sys.argv) != 2:
        print 'You must specify a folder that contains the grids to be converted.'
        sys.exit
    elif os.path.isdir(sys.argv[1]):
        inputFolder = sys.argv[1]
    else:
        print '%s is not a valid directory.' %(sys.argv[1])
        sys.exit

    # open log file
    logFilePath = '%s%s%s' %(inputFolder, os.sep, logFileName)
    logFile = file(logFilePath, 'w')

```

```

# get list of noaa grids
logFile.write('Getting list of files to convert.\n')
noaaGrids = glob.glob1(inputFolder, '*%s' %(noaaGridExtension))
logFile.write('Found %s files to convert.\n\n' %(len(noaaGrids)))

# create output folders for reformatted ascii grids and arcinfo grids
logFile.write('Making sure output folders exist.\n')
convertedGridFolderPath = '%s%s%s' %(inputFolder, os.sep,
convertedGridFolderName)
if not os.path.exists(convertedGridFolderPath):
    os.mkdir(convertedGridFolderPath)
arcInfoFolderPath = '%s%s%s' %(inputFolder, os.sep, arcInfoGridFolderName)
if not os.path.exists(arcInfoFolderPath):
    os.mkdir(arcInfoFolderPath)
logFile.write('Output folders exist.\n\n')

# reformat old grid and write to new file
for f in noaaGrids:
    # create a new file to put the converted data into
    try:
        logFile.write('Begining to convert file named %s . . . ' %(f))
        print "
        print 'Begining to convert file named %s . . . ' %(f)
        convertedFileName = '%s%s%s' %(os.path.splitext(f)[0], 'C', '.ASC')
        convertedPath = os.path.join(convertedGridFolderPath, convertedFileName)
        convertedFile = file(convertedPath, 'w')

        # write the header
        convertedFile.write(WriteHeader())

        # read each line in the file, convert it, and then write it out to the converted file.
        oldFilePath = os.path.join(inputFolder, f)
        oldFile = file(oldFilePath, 'r')
        for line in oldFile.readlines():
            convertedFile.write(ReFormatLine(line[:-1]))

        convertedFile.close()
        oldFile.close()
        logFile.write('Conversion of %s finished.\n' %(f))
        print 'Conversion of %s finished.' %(f)

        logFile.write('Starting creation of the ArcInfo grid %s . . . '
%(os.path.splitext(f)[0]))
        print 'Starting creation of the ArcInfo grid %s . . . ' %(os.path.splitext(f)[0])

        gridPath = os.path.join(arcInfoFolderPath, os.path.splitext(f)[0])

```

```

        # create arcinfo grids
        if MakeGrid(convertedPath, gridPath):
            logFile.write('creation of ArcInfo grid %s completed.\n\n'
%(os.path.splitext(f)[0]))
            print 'creation of ArcInfo grid %s completed.\n' %(os.path.splitext(f)[0])
        else:
            logFile.write('CREATION OF ARCINFO GRID %s FAILED!!\n\n'
%(os.path.splitext(f)[0]))
            print 'CREATION OF ARCINFO GRID %s FAILED!!\n\n'
%(os.path.splitext(f)[0])
        except:
            logFile.write('THERE WERE PROBLEMS WITH THE CONVERSTION
FOR FILE %s' %(oldFilePath))

    logFile.close()
    print 'Finished processing files %s.' %(inputFolder)

```

**Table 2. Results of the multiple-regression for cisco recruitment in Region 1 (Minnesota and WI-1).**

```

MODEL LNRAST = CONSTANT+AST+A1CISS+AATFY
>ESTIMATE / TOL=0.1
Data for the following results were selected according to:
    (MINN = 1) OR (WI1 = 1)
13 case(s) deleted due to missing data.

Eigenvalues of unit scaled X'X
      1          2          3          4
    2.618143445  0.759896333  0.619674779  0.002285443

Condition indices
      1          2          3          4
    1.000000000  1.856177672  2.055487350  3.38463E+01

Variance proportions
      1          2          3          4
    CONSTANT    0.000580852  0.001008322  0.000000980  0.998409846
    AST          0.044835754  0.297859543  0.574571397  0.082733305
    A1CISS       0.044050397  0.312575089  0.548948458  0.094426056
    AATFY        0.000580598  0.000998771  0.000003739  0.998416892

Dep Var: LNRAST   N: 36   Multiple R: 0.715095423   Squared multiple R: 0.511361464
Adjusted squared multiple R: 0.465551601   Standard error of estimate: 1.432501002

Effect          Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)
CONSTANT        -5.528983706    3.531950100    0.000000000      .      -1.56542    0.12732
AST             -0.120758116    0.037132737   -0.429754247    0.8744120   -3.25207    0.00270
A1CISS          -0.079812153    0.024554986   -0.435766779    0.8495485   -3.25034    0.00271
AATFY           0.171087269    0.090694686    0.250807328    0.8638314    1.88641    0.06834

Effect          Coefficient      Lower 95%      Upper 95%
CONSTANT        -5.528983706   -1.27233E+01   1.665363307
AST             -0.120758116   -0.196395027   -0.045121205
A1CISS          -0.079812153   -0.129829023   -0.029795283
AATFY           0.171087269   -0.013651764    0.355826302

Correlation matrix of regression coefficients
      CONSTANT      AST      A1CISS      AATFY
CONSTANT    1.000000000
AST         -0.298881724  1.000000000
A1CISS       0.293615360 -0.300430398  1.000000000
AATFY       -0.996831024  0.273794684 -0.318224013  1.000000000

Analysis of Variance
Source          Sum-of-Squares      df      Mean-Square      F-ratio      P
Regression      6.87195E+01         3      2.29065E+01    1.11627E+01    0.000035842
Residual        6.56659E+01        32      2.052059120
-----
*** WARNING ***
Case          5 is an outlier      (Studentized Residual = 3.070530757)
Case          29 has large leverage (Leverage = 0.522125803)
Case          35 has large leverage (Leverage = 0.378514845)
Case          37 has large leverage (Leverage = 0.727308691)

Durbin-Watson D Statistic 2.160944523
First Order Autocorrelation -0.094654001

```

**Table 3. Results of the multiple-regression for cisco recruitment in Region 2 (WI-2, Western Keweenaw, and MI-4).**

---

```

MODEL LNRST = CONSTANT+AST+AAWHAATFY+AAWSACISS
>ESTIMATE / TOL=0.1
Data for the following results were selected according to:
    (WI2 = 1) OR (WKEW = 1) OR (MI4 = 1)
3 case(s) deleted due to missing data.

Eigenvalues of unit scaled X'X
              1              2              3              4
      2.565323958  0.865011888  0.557331582  0.012332572

Condition indices
              1              2              3              4
      1.000000000  1.722106756  2.145429667  1.44226E+01

Variance proportions
              1              2              3              4
CONSTANT      0.003269272  0.000794092  0.003855580  0.992081055
AST            0.051176592  0.009682661  0.822627768  0.116512979
AAWHAATFY     0.003436260  0.001099123  0.006587314  0.988877303
AAWSACISS     0.027828879  0.953479533  0.000795830  0.017895759

Dep Var: LNRST   N: 70   Multiple R: 0.632875963   Squared multiple R: 0.400531984

Adjusted squared multiple R: 0.373283438   Standard error of estimate: 1.907216139

Effect          Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)
CONSTANT        -2.010827954    1.488370492    0.000000000      .      -1.35103    0.18130
AST             -0.382188272    0.081669216   -0.466173330    0.9153036   -4.67971    0.00001
AAWHAATFY       0.009357532    0.003929584    0.238562319    0.9049984    2.38130    0.02014
AAWSACISS       -0.002272962    0.001135649   -0.192492406    0.9819538   -2.00147    0.04946

Effect          Coefficient      Lower 95%      Upper 95%
CONSTANT        -2.010827954   -4.982455599    0.960799691
AST             -0.382188272   -0.545246128   -0.219130417
AAWHAATFY       0.009357532    0.001511864    0.017203200
AAWSACISS       -0.002272962   -0.004540358   -0.000005566

Correlation matrix of regression coefficients
              CONSTANT      AST      AAWHAATFY      AAWHSACISS
CONSTANT      1.000000000
AST           -0.380595941  1.000000000
AAWHAATFY     -0.981152282  0.282346474  1.000000000
AAWSACISS     -0.149470636-0.038269817  0.112724830  1.000000000

Analysis of Variance
Source          Sum-of-Squares      df      Mean-Square      F-ratio      P
Regression      1.60404E+02          3      5.34680E+01    1.46992E+01    0.000000197
Residual        2.40073E+02          66      3.637473402
-----
*** WARNING ***
Case           58 has large leverage (Leverage = 0.800418423)
Case          112 has large leverage (Leverage = 0.240557616)

Durbin-Watson D Statistic    1.473163926
First Order Autocorrelation  0.250640309

```



**Table 4. Results of the regression for cisco recruitment in Region 3 (Michigan South Shore, Whitefish Bay, and Eastern Canada).**

---

```

MODEL LNRAST = CONSTANT+AST
>ESTIMATE / TOL=0.1
Data for the following results were selected according to:
    (MISS = 1) OR (WFBY = 1) OR (ECAN = 1)
10 case(s) deleted due to missing data.

Eigenvalues of unit scaled X'X
      1      2
    1.869849995 0.130150005

Condition indices
      1      2
    1.000000000 3.790367230

Variance proportions
      1      2
    CONSTANT    0.065075003 0.934924997
    AST          0.065075003 0.934924997

Dep Var: LNRAST   N: 43   Multiple R: 0.500652678   Squared multiple R: 0.250653104
Adjusted squared multiple R: 0.232376351   Standard error of estimate: 1.410766735

Effect      Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)
CONSTANT    1.586552732    0.436109457    0.000000000      .      3.63797    0.00076
AST         -3.420445732    0.923625019   -0.500652678    1.00E+00 -3.70328    0.00063

Effect      Coefficient      Lower 95%      Upper 95%
CONSTANT    1.586552732    0.705811803    2.467293662
AST         -3.420445732   -5.285744331   -1.555147133

Correlation matrix of regression coefficients
      CONSTANT      AST
CONSTANT    1.000000000
AST         -0.869849995 1.000000000

Analysis of Variance
Source      Sum-of-Squares      df      Mean-Square      F-ratio      P
Regression    2.72951E+01      1      2.72951E+01    1.37143E+01    0.000628112
Residual      8.16008E+01      41      1.990262781
-----
*** WARNING ***
Case      126 is an outlier      (Studentized Residual = 4.034585164)
Case      145 has large leverage      (Leverage = 0.269333102)

Durbin-Watson D Statistic    1.265258262
First Order Autocorrelation    0.357162590

```

**Table 5. Results of the multiple-regression for cisco recruitment in Region 4 (Nipigon Bay, Black Bay, and Thunder Bay).**

---

```

MODEL LNRST = CONSTANT+AST+AAWHAATFY+SMLBHSACISS
>ESTIMATE / TOL=0.1
Data for the following results were selected according to:
      (NIPB = 1) OR (BLKB = 1) OR (THBY = 1)

Eigenvalues of unit scaled X'X
      1          2          3          4
      2.765432123 0.901853079 0.321783560 0.010931238

Condition indices
      1          2          3          4
      1.000000000 1.751110715 2.931565323 1.59055E+01

Variance proportions
      1          2          3          4
      CONSTANT    0.002565114 0.000414163 0.008230170 0.988790553
      AST          0.041150417 0.007382054 0.915807824 0.035659706
      AAWHAATFY    0.002700113 0.000466044 0.011395218 0.985438625
      SMLBHSACISS 0.017794095 0.981270967 0.000036607 0.000898331

Dep Var: LNRST   N: 51   Multiple R: 0.714761059   Squared multiple R: 0.510883371

Adjusted squared multiple R: 0.479663160   Standard error of estimate: 1.309645877

Effect          Coefficient      Std Error      Std Coef Tolerance      t      P(2 Tail)

CONSTANT        -1.707624643    1.267781313    0.000000000    .      -1.34694    0.18446
AST              -1.260354360    0.218644781   -0.591561547   0.9881476  -5.76439    0.00000
AAWHAATFY        0.013093085    0.004817491    0.278639108   0.9900855   2.71782    0.00917
SMLBHSACISS      -0.016574076    0.008724125   -0.194051902   0.9974559  -1.89980    0.06361

Effect          Coefficient      Lower 95%      Upper 95%

CONSTANT        -1.707624643   -4.258071720    0.842822434
AST              -1.260354360   -1.700210933   -0.820497788
AAWHAATFY        0.013093085    0.003401544    0.022784626
SMLBHSACISS      -0.016574076   -0.034124752    0.000976599

Correlation matrix of regression coefficients
      CONSTANT      AST      AAWHAATFY      SMLBHSACISS
CONSTANT      1.000000000
AST            -0.262571218 1.000000000
AAWHAATFY      -0.974357836 0.097697687 1.000000000
SMLBHSACISS    -0.043756093 -0.046600671 0.014653873 1.000000000

Analysis of Variance
Source          Sum-of-Squares      df      Mean-Square      F-ratio      P

Regression      8.42006E+01          3      2.80669E+01    1.63639E+01    0.000000203
Residual        8.06131E+01          47      1.715172322

-----
*** WARNING ***
Case          197 has large leverage      (Leverage = 0.955364946)
Case          210 is an outlier          (Studentized Residual = 3.551154198)
Case          226 has large leverage      (Leverage = 0.294357185)

Durbin-Watson D Statistic      1.827010044
First Order Autocorrelation     0.084117572

```

Table 6. Values for biotic and abiotic variables used in multi-factor stock-recruitment analysis. Years provided correspond to year of hatching for recruit density estimates. Variable descriptions are provided in Chapter 2.

Year	Spatial Unit	AICISS	SACISS	AICISH	SACISH	BLTR	BLTBH	SMLR	SMLBH	SSBI	LTBH	LST50H	AATH	AAWH	AATFY
1979	MINN	0.145	0.145	0.469	0.145	0.258	0.006	64.342	0.524	0.009	0.000	148.389	35.000	9.300	43.100
1980	MINN	0.469	0.145	0.145	0.145	0.219	0.000	103.421	0.093	0.008	0.000	91.409	43.100	8.767	39.100
1981	MINN	0.145	0.145	0.585	0.145	0.186	0.000	34.421	0.087	0.010	0.003	98.718	39.100	10.097	35.200
1982	MINN	0.585	0.145	0.145	0.145	0.375	0.000	32.765	0.028	0.013	0.000	104.597	35.200	10.117	36.200
1983	MINN	0.145	0.145	0.145	0.145	0.272	0.000	62.872	0.033	0.002	0.001	43.113	36.200	9.477	41.400
1984	MINN	0.145	0.145	0.236	0.145	0.327	0.000	194.205	0.066	0.004	0.001	128.103	41.400	11.143	39.500
1985	MINN	0.236	0.145	0.777	0.145	0.145	0.000	59.888	0.148	0.002	0.000	95.720	39.500	10.870	41.900
1986	MINN	0.777	0.145	0.942	0.226	0.435	0.000	188.179	0.074	0.002	0.002	108.320	41.900	11.830	42.700
1987	MINN	0.942	0.226	1.000	0.145	0.173	0.001	65.906	0.247	0.006	0.003	0.263	42.700	8.210	39.300
1988	MINN	1.000	0.145	0.145	0.145	0.366	0.000	130.869	0.109	0.006	0.000	115.069	39.300	9.120	36.400
1989	MINN	0.145	0.145	0.575	0.258	0.145	0.000	349.232	0.202	0.004	0.001	132.509	36.400	8.950	37.100
1990	MINN	0.575	0.258	14.766	0.229	0.145	0.000	30.731	0.347	0.004	0.000	113.426	37.100	9.487	40.500
1991	MINN	14.766	0.229	0.500	0.145	0.145	0.000	163.998	0.033	0.005	0.000	118.164	40.500	9.700	36.900
1992	MINN	0.500	0.145	0.291	0.145	0.145	0.000	151.786	0.074	0.007	0.001	116.421	36.900	9.843	36.600
1993	MINN	0.291	0.145	0.614	0.145	0.145	0.000	154.991	0.141	0.005	0.001	103.165	36.600	9.637	37.900
1994	MINN	0.614	0.145	0.209	0.145	0.145	0.000	395.301	0.129	0.004	0.000	112.077	37.900	10.990	35.300
1995	MINN	0.209	0.145	0.340	0.145	0.145	0.000	175.592	0.541	0.001	0.000	113.848	35.300	10.213	34.500
1996	MINN	0.340	0.145	0.145	0.145	0.145	0.000	128.390	0.141	0.004	0.000	142.563	34.500	8.990	36.100
1997	MINN	0.145	0.145	0.332	0.145	0.145	0.000	77.816	0.124	0.002	0.001	125.959	36.100	8.587	41.400
1998	MINN	0.332	0.145	0.325	0.145	0.145	0.000	42.790	0.086	0.001	0.002	0.254	41.400	9.650	39.400
1999	MINN	0.325	0.145	0.472	0.279	0.213	0.000	8.577	0.096	0.001	0.000	2.393	39.400	9.910	37.200
2000	MINN	0.472	0.279	0.281	0.213	0.145	0.000	7.840	0.007	0.003	0.000	55.745	37.200	9.087	39.300
2001	MINN	0.281	0.213	0.181	0.145	0.145	0.000	24.772	0.012	0.000	0.001	107.042	39.300	9.677	35.400
2002	MINN	0.181	0.145	0.145	0.145	0.145	0.000	1.122	0.021	0.001	0.000	0.305	35.400	9.157	37.500
2003	MINN	0.145	0.145	0.145	0.145	1.387	0.000	23.723	0.001	0.001	0.000	118.058	37.500	11.737	38.500
2004	MINN	0.145	0.145	2.458	0.403	0.145	0.002	25.568	0.021	0.000	0.000	83.443	38.500	8.633	40.900
2005	MINN	2.458	0.403	0.201	0.145	0.145	0.000	7.780	0.020	0.004	0.036	114.915	40.900	8.910	43.700
2006	MINN	0.201	0.145	0.145	0.145	0.145	0.000	18.327	0.007	0.000	0.000	43.700	40.900	9.670	39.600
1980	W11	0.145	0.145	0.227	2.993	29.589	0.828	26.363	0.767	0.038	0.775	104.301	41.400	8.767	39.200
1981	W11	0.227	2.993	23.891	3.677	1.430	1.509	15.036	0.406	0.002	2.612	111.432	39.200	10.097	35.700
1982	W11	23.891	3.677	0.339	5.006	0.333	0.705	9.358	0.316	0.008	0.338	111.975	35.700	10.117	35.100

1983 W11	0.339	5.006	0.233	0.203	0.785	0.461	5.799	0.258	0.004	0.345	88.652	35.100	9.477	42.400
1984 W11	0.233	0.203	0.526	0.319	17.906	0.288	7.408	0.097	0.007	0.006	139.274	42.400	11.143	42.100
1985 W11	0.526	0.319	45.900	1.152	0.345	0.186	1.581	0.108	0.003	0.399	104.198	42.100	10.870	42.100
1986 W11	45.900	1.152	8.359	14.985	0.596	0.000	3.297	0.212	0.007	0.158	114.856	42.100	11.830	46.100
1987 W11	8.359	14.985	0.797	30.403	0.325	0.724	21.386	0.036	0.005	0.117	61.842	46.100	8.210	40.100
1988 W11	0.797	30.403	0.145	0.312	3.466	0.436	4.746	0.386	0.003	0.028	118.338	40.100	9.120	36.800
1989 W11	0.145	0.312	10.550	0.523	1.007	0.023	29.648	0.030	0.003	0.028	138.950	36.800	8.950	40.200
1990 W11	10.550	0.523	305.438	97.026	2.258	0.012	33.655	2.217	0.007	0.063	124.110	40.200	9.487	42.700
1991 W11	305.438	97.026	38.057	49.932	1.255	0.039	10.679	0.250	0.030	0.043	133.026	42.700	9.700	36.200
1992 W11	38.057	49.932	0.470	11.683	0.145	0.543	13.554	0.175	0.007	0.070	117.937	36.200	9.843	37.200
1993 W11	0.470	11.683	0.401	4.020	0.390	0.000	2.143	0.398	0.003	0.152	116.965	37.200	9.637	39.600
1994 W11	0.401	4.020	0.145	0.207	0.145	0.184	67.843	0.184	0.006	0.099	133.471	39.600	10.990	34.700
1995 W11	0.145	0.207	0.680	0.207	0.382	0.002	50.256	1.320	0.002	0.723	124.266	34.700	10.213	33.700
1996 W11	0.680	0.207	0.145	0.235	0.145	0.110	23.107	0.489	0.011	0.471	161.732	33.700	8.990	35.700
1997 W11	0.145	0.235	0.325	0.233	0.883	0.006	7.260	0.112	0.008	0.055	137.535	35.700	8.587	44.100
1998 W11	0.325	0.233	0.575	0.207	0.262	0.361	35.652	0.147	0.005	1.239	72.337	44.100	9.650	41.400
1999 W11	0.575	0.207	9.795	2.154	0.262	0.095	1.307	0.108	0.002	0.038	50.900	41.400	9.910	38.100
2000 W11	9.795	2.154	1.949	12.071	0.211	0.014	1.953	0.670	0.001	0.004	88.507	38.100	9.087	39.800
2001 W11	1.949	12.071	0.324	1.328	0.244	0.067	12.641	0.122	0.000	0.053	117.321	39.800	9.677	37.200
2002 W11	0.324	1.328	0.145	0.281	0.145	0.115	21.307	0.077	0.022	0.007	102.796	37.200	9.157	38.300
2003 W11	0.145	0.281	17.299	0.223	7.932	0.258	40.884	0.099	0.001	0.011	123.764	38.300	11.737	39.400
2004 W11	17.299	0.223	356.555	1.152	11.642	0.124	36.936	0.279	0.002	0.388	96.365	39.400	8.633	43.100
2005 W11	356.555	1.152	6.850	7.729	0.440	0.090	33.311	0.500	0.004	0.726	119.666	43.100	8.910	45.700
2006 W11	6.850	7.729	0.268	0.328	1.633	0.032	97.828	0.078	0.009	0.002	45.700	45.700	9.670	38.900
1979 W12	0.145	0.177	0.145	0.145	0.853	0.299	41.652	2.558	0.009	0.400	161.286	37.600	9.300	42.900
1980 W12	0.145	0.145	0.145	0.260	3.640	0.027	70.138	0.351	0.030	0.044	114.096	42.900	8.767	42.700
1981 W12	0.145	0.260	1.889	0.184	0.657	0.022	79.207	0.093	0.022	0.004	121.937	42.700	10.097	39.100
1982 W12	1.889	0.184	0.215	0.407	0.648	0.010	47.493	0.192	0.008	0.019	123.560	39.100	10.117	38.500
1983 W12	0.215	0.407	0.145	0.366	3.451	0.010	191.919	0.059	0.010	0.058	71.567	38.500	9.477	42.500
1984 W12	0.145	0.366	1.225	0.339	19.998	0.144	151.795	0.594	0.002	0.194	138.650	42.500	11.143	44.300
1985 W12	1.225	0.339	272.411	0.794	4.156	0.088	62.377	0.468	0.021	0.160	113.544	44.300	10.870	44.500
1986 W12	272.411	0.794	113.961	189.673	1.422	0.187	86.201	1.407	0.032	0.223	121.346	44.500	11.830	46.200
1987 W12	113.961	189.673	3.006	2.764	0.227	0.051	201.497	0.221	0.034	0.086	62.751	46.200	8.210	39.500
1988 W12	3.006	2.764	0.186	0.336	11.338	0.001	359.046	0.544	0.017	0.059	118.354	39.500	9.120	37.500
1989 W12	0.186	0.336	64.428	6.937	0.946	0.080	155.989	1.089	0.023	0.021	143.459	37.500	8.950	42.200
1990 W12	64.428	6.937	431.307	9.135	0.935	0.006	102.363	0.576	0.007	0.019	127.503	42.200	9.487	44.000

1991 W12	431.307	9.135	40.873	5.055	0.342	0.005	82.780	0.247	0.019	0.014	124.724	44.000	9.700	37.200
1992 W12	40.873	5.055	2.515	3.612	0.145	0.029	251.409	0.215	0.017	0.047	118.560	37.200	9.843	36.500
1993 W12	2.515	3.612	2.301	2.273	0.252	0.001	69.513	0.457	0.008	0.226	123.601	36.500	9.637	40.000
1994 W12	2.301	2.273	0.328	0.621	0.145	0.037	345.621	0.247	0.012	0.412	129.565	40.000	10.990	34.500
1995 W12	0.328	0.621	0.470	0.201	0.145	0.001	77.961	0.658	0.007	0.100	116.550	34.500	10.213	34.800
1996 W12	0.470	0.201	0.355	0.203	0.184	0.002	148.266	0.183	0.008	0.049	159.318	34.800	8.990	37.500
1997 W12	0.355	0.203	0.729	0.228	0.145	0.002	47.867	0.271	0.001	0.341	134.674	37.500	8.587	44.400
1998 W12	0.729	0.228	0.397	0.466	0.145	0.011	90.965	0.136	0.001	0.077	58.358	44.400	9.650	42.100
1999 W12	0.397	0.466	82.046	65.133	0.274	0.003	3.320	0.343	0.005	0.009	74.872	42.100	9.910	38.600
2000 W12	82.046	65.133	0.575	17.316	0.221	0.049	26.763	0.032	0.001	0.003	88.906	38.600	9.087	41.600
2001 W12	0.575	17.316	0.145	1.777	0.305	0.031	49.770	0.092	0.000	0.005	124.012	41.600	9.677	39.000
2002 W12	0.145	1.777	0.385	0.436	0.145	0.016	18.142	0.121	0.002	0.009	63.832	39.000	9.157	37.500
2003 W12	0.385	0.436	5.395	0.198	2.643	0.003	34.858	0.049	0.000	0.002	138.296	37.500	11.737	38.900
2004 W12	5.395	0.198	37.056	1.806	2.156	0.036	12.275	0.069	0.001	0.001	105.714	38.900	8.633	43.400
2005 W12	37.056	1.806	2.346	16.052	0.519	0.268	76.942	0.029	0.004	0.028	119.583	43.400	8.910	44.829
2006 W12	2.346	16.052	1.202	1.018	0.251	0.003	55.959	0.125	0.001	0.001	44.829	44.829	9.670	37.766
1979 WKEW	0.145	0.145	0.145	0.145	0.176	0.009	16.301	0.151	0.035	0.004	163.118	34.800	9.653	39.900
1980 WKEW	0.145	0.145	0.145	0.327	0.145	0.000	10.949	0.300	0.010	0.020	117.051	39.900	9.003	40.000
1981 WKEW	0.145	0.327	0.807	0.179	0.145	0.000	5.709	0.016	0.024	0.000	126.832	40.000	10.033	34.200
1982 WKEW	0.807	0.179	0.197	0.200	0.377	0.001	51.363	0.015	0.001	0.001	107.475	34.200	11.403	34.900
1983 WKEW	0.197	0.200	0.190	0.214	0.554	0.001	24.136	0.101	0.009	0.007	66.025	34.900	9.913	40.300
1984 WKEW	0.190	0.214	1.710	0.145	0.621	0.013	3.140	0.088	0.016	0.056	127.578	40.300	11.950	42.000
1985 WKEW	1.710	0.145	74.294	0.275	0.320	0.001	4.810	0.016	0.005	0.014	112.214	42.000	10.473	42.600
1986 WKEW	74.294	0.275	4.019	18.565	0.379	0.002	135.848	0.039	0.014	0.013	123.943	42.600	11.630	46.300
1987 WKEW	4.019	18.565	0.607	0.145	0.211	0.001	50.151	0.238	0.004	0.001	6.492	46.300	8.153	39.700
1988 WKEW	0.607	0.145	0.145	0.176	0.802	0.000	68.261	0.160	0.009	0.003	111.985	39.700	8.693	36.100
1989 WKEW	0.145	0.176	5.538	0.782	1.350	0.002	46.124	0.154	0.003	0.005	139.962	36.100	6.707	41.800
1990 WKEW	5.538	0.782	37.346	0.770	0.658	0.003	27.647	0.108	0.002	0.000	119.876	41.800	8.057	43.200
1991 WKEW	37.346	0.770	22.920	0.757	0.329	0.001	14.737	0.074	0.007	0.010	117.104	43.200	8.407	36.000
1992 WKEW	22.920	0.757	0.822	1.832	0.145	0.003	16.447	0.064	0.006	0.002	118.481	36.000	6.943	35.500
1993 WKEW	0.822	1.832	1.667	5.948	0.145	0.000	38.733	0.292	0.006	0.014	118.742	35.500	6.757	36.900
1994 WKEW	1.667	5.948	0.145	0.176	0.145	0.000	45.306	0.170	0.007	0.002	135.802	36.900	9.990	33.500
1995 WKEW	0.145	0.176	0.351	0.145	0.181	0.000	4.694	0.169	0.006	0.003	52.366	33.500	9.100	32.400
1996 WKEW	0.351	0.145	0.351	0.145	0.145	0.001	39.703	0.128	0.017	0.030	148.824	32.400	8.180	36.100
1997 WKEW	0.351	0.145	0.400	0.145	0.145	0.000	7.327	0.048	0.011	0.015	142.152	36.100	7.807	44.600
1998 WKEW	0.400	0.145	0.342	0.145	0.145	0.000	0.683	0.028	0.008	0.007	37.386	44.600	7.700	41.900

1999 WKEW	0.342	0.145	1.125	1.311	0.145	0.000	13.549	0.002	0.002	0.000	65.571	41.900	8.367	38.300
2000 WKEW	1.125	1.311	0.185	0.221	0.145	0.000	0.865	0.032	0.001	0.001	60.856	38.300	7.893	40.200
2001 WKEW	0.185	0.221	0.145	0.145	0.145	0.001	0.684	0.001	0.001	0.001	127.709	40.200	9.807	35.800
2002 WKEW	0.145	0.145	0.145	0.332	0.213	0.001	1.995	0.002	0.001	0.005	51.763	35.800	9.040	34.300
2003 WKEW	0.145	0.332	0.670	0.175	14.377	0.001	2.044	0.003	0.001	0.001	130.725	34.300	9.640	36.400
2004 WKEW	0.670	0.175	18.030	16.944	0.439	1.141	10.133	0.128	0.000	0.001	93.517	36.400	8.020	41.200
2005 WKEW	18.030	16.944	0.601	1.108	2.041	0.001	0.792	0.025	0.010	0.001	106.810	41.200	8.377	42.000
2006 WKEW	0.601	1.108	2.475	2.904	0.145	0.088	1.758	0.001	0.001	0.012	42.000	42.000	8.657	37.000
1979 M14	0.145	0.145	0.145	0.145	1.342	0.091	147.607	0.683	0.017	0.005	138.138	34.800	9.653	39.900
1980 M14	0.145	0.145	0.425	0.277	2.517	0.008	15.153	0.800	0.032	0.004	112.071	39.900	9.003	40.000
1981 M14	0.425	0.277	5.579	0.668		0.032		0.100	0.069	0.018	116.259	40.000	10.033	34.200
1982 M14	5.579	0.668			0.403		103.345	0.124	0.013	0.009	115.828	34.200	11.403	34.900
1983 M14			0.145	0.145	0.823	0.002	159.865	0.581	0.012	0.015	62.764	34.900	9.913	40.300
1984 M14	0.145	0.145	1.949	0.268	11.145	0.108	37.588	0.677	0.000	0.039	135.287	40.300	11.950	42.000
1985 M14	1.949	0.268	28.545	1.226	32.755	0.260	104.528	1.285	0.002	0.114	120.241	42.000	10.473	42.600
1986 M14	28.545	1.226	3.262	33.773	2.461	1.081	203.094	0.575	0.007	0.081	116.998	42.600	11.630	46.300
1987 M14	3.262	33.773	0.610	7.665	1.084	0.085	53.794	0.462	0.017	0.042	37.232	46.300	8.153	39.700
1988 M14	0.610	7.665	0.427	1.037	4.421	0.163	190.787	0.539	0.000	0.113	126.168	36.100	8.693	36.100
1989 M14	0.427	1.037	11.145	4.279	145.932	0.073	183.039	1.239	0.006	0.033	112.703	41.800	8.057	43.200
1990 M14	11.145	4.279	206.535	10.464	1.060	4.693	128.121	0.317	0.004	0.059	114.509	43.200	8.407	36.000
1991 M14	206.535	10.464	28.424	22.395	3.081	0.008	16.910	0.397	0.001	0.035	123.423	36.000	6.943	35.500
1992 M14	28.424	22.395	5.374	58.363	0.281	1.597	22.999	0.257	0.000	0.065	126.503	35.500	6.757	36.900
1993 M14	5.374	58.363	0.216	2.604	0.145	0.450	13.873	0.603	0.004	0.059	132.262	36.900	9.990	33.500
1994 M14	0.216	2.604	0.145	4.922	0.145	0.000	163.342	1.383	0.008	0.280	103.920	33.500	9.100	32.400
1995 M14	0.145	4.922	0.314	4.015	0.145	0.000	31.333	1.011	0.030	0.122	148.727	32.400	8.180	36.100
1996 M14	0.314	4.015	0.577	0.559	0.262	0.125	84.573	0.222	0.001	0.007	122.971	36.100	7.807	44.600
1997 M14	0.577	0.559	0.204	0.145	0.145	0.003	105.322	0.380	0.001	0.061	27.260	44.600	7.700	41.900
1998 M14	0.204	0.145	0.145	0.145	0.145	0.062	9.496	0.027	0.001	0.002	66.036	41.900	8.367	38.300
1999 M14	0.145	0.145	0.731	0.881	0.349	0.015	8.383	0.190	0.000	0.028	84.642	38.300	7.893	40.200
2000 M14	0.731	0.881	0.375	3.678	0.323	0.012	49.370	0.134	0.001	0.016	119.108	40.200	9.807	35.800
2001 M14	0.375	3.678	2.475	0.817	0.189	0.002	27.850	0.095	0.002	0.020	26.032	35.800	9.040	34.300
2002 M14	2.475	0.817	2.297	0.388	0.145	0.009	9.411	0.031	0.001	0.002	144.610	34.300	9.640	36.400
2003 M14	2.297	0.388	5.533	0.341	2.600	0.005	17.658	0.114	0.000	0.004	98.968	36.400	8.020	41.200
2004 M14	5.533	0.341	2.988	0.767	5.184	0.022	66.571	0.171	0.001	0.016	120.195	41.200	8.377	42.000
2005 M14	2.988	0.767	1.823	3.620	1.893	0.100	59.188	0.271	0.000	0.005	42.000	42.000	8.657	37.000
2006 M14	1.823	3.620	1.141	1.570	0.281	0.004	30.687							

1979 MISS	0.145	0.145	0.145	0.145	0.265	0.011	8.392	0.167	0.009	0.000	150.095	37.769	9.653	40.100
1980 MISS	0.145	0.145	0.145	0.145	0.145	0.000	1.260	0.009	0.024	0.002	114.470	40.100	9.003	40.500
1981 MISS	0.145	0.145	0.145	0.145	0.000	0.000		0.004	0.023	0.001	109.435	40.500	10.033	36.600
1982 MISS	0.145	0.145			0.145		20.073		0.003		109.734	36.600	11.403	36.800
1983 MISS			0.145	0.145	0.436	0.000	13.470	0.020		0.001	22.149	36.800	9.913	39.600
1984 MISS	0.145	0.145		0.145	1.509	0.001	43.587	0.025	0.004	0.000	143.094	39.600	11.950	43.200
1985 MISS	0.270	0.145	1.598	0.753	0.587	0.012	27.767	0.174	0.003	0.009	113.857	43.200	10.473	43.500
1986 MISS	1.598	0.753	0.145	0.778	0.775	0.005	49.117	0.073	0.015	0.010	124.162	43.500	11.630	44.900
1987 MISS	0.145	0.778	0.592	0.456	0.702	0.002	9.850	0.088	0.003	0.004	34.726	44.900	8.153	39.000
1988 MISS	0.592	0.456	0.302	0.296	2.288	0.003	41.857	0.022	0.012	0.007	111.065	39.000	8.693	36.700
1989 MISS	0.302	0.296	4.854	0.543	11.910	0.007	8.710	0.077	0.001	0.008	136.118	36.700	6.707	43.500
1990 MISS	4.854	0.543	63.113	2.328	2.219	0.052	15.246	0.041	0.001	0.041	110.594	43.500	8.057	44.000
1991 MISS	63.113	2.328	19.825	4.681	0.878	0.013	15.003	0.045	0.004	0.006	115.741	44.000	8.407	38.200
1992 MISS	19.825	4.681	0.471	0.323	0.336	0.003	2.985	0.034	0.011	0.008	127.207	38.200	6.943	36.500
1993 MISS	0.471	0.323	0.334	0.512	0.145	0.009	2.680	0.010	0.001	0.007	120.530	36.500	6.757	39.500
1994 MISS	0.334	0.512	0.145	1.167	0.145	0.000	16.854	0.008	0.004	0.009	133.525	39.500	9.990	35.300
1995 MISS	0.145	1.167	0.458	0.332	0.145	0.000	24.173	0.037	0.001	0.006	97.755	35.300	9.100	34.500
1996 MISS	0.458	0.332	0.348	0.145	0.217	0.000	8.301	0.036	0.010	0.002	162.122	34.500	8.180	39.600
1997 MISS	0.348	0.145	0.196	0.145	0.193	0.000	26.965	0.008	0.001	0.011	125.062	39.600	7.807	45.400
1998 MISS	0.196	0.145	0.145	0.145	0.145	0.002	3.188	0.059	0.001	0.065	2.693	45.400	7.700	42.000
1999 MISS	0.145	0.145	0.545	0.719	0.199	0.000	7.235	0.006	0.005	0.004	30.704	42.000	8.367	40.200
2000 MISS	0.545	0.719	0.387	0.767	0.145	0.001	8.010	0.021	0.000	0.000	56.249	40.200	7.893	45.900
2001 MISS	0.387	0.767	0.211	0.145	0.199	0.000	1.348	0.010	0.002	0.001	115.877	45.900	9.807	40.500
2002 MISS	0.211	0.145	0.145	0.145	0.193	0.000	1.269	0.005	0.002	0.000	6.181	40.500	9.040	34.900
2003 MISS	0.145	0.145	1.205	0.218	1.333	0.001	7.345	0.002	0.001	0.002	137.458	34.900	9.640	38.300
2004 MISS	1.205	0.218	0.809	0.305	0.266	0.004	13.276	0.016	0.000	0.000	87.598	38.300	8.020	42.400
2005 MISS	0.809	0.305	0.145	0.145	3.013	0.000	26.248	0.019	0.003	0.019	121.145	42.400	8.377	43.800
2006 MISS	0.145	0.145	2.180	0.960	0.145	0.024	1.582	0.070	0.000	0.029	43.800		8.657	38.800
1990 WFBY	0.253	0.324	3.249	1.225	0.292	0.008	99.746	1.085	0.050	0.001	137.585	41.100	8.310	42.900
1991 WFBY	3.249	1.225	1.470	1.089	0.535	0.005	217.616	0.646	0.137	0.001	127.781	42.900	8.133	35.600
1992 WFBY	1.470	1.089	0.330	0.629	0.174	0.102	17.893	1.310	0.189	0.022	145.154	35.600	7.473	36.900
1993 WFBY	0.330	0.629	0.145	0.238	0.145	0.023	45.425	1.605	0.140	0.010	137.039	36.900	8.130	36.300
1994 WFBY	0.145	0.238	0.174	0.322	0.145	0.000	127.174	0.444	0.035	0.042	155.592	36.300	9.560	34.500
1995 WFBY	0.174	0.322	0.301	0.145	0.145	0.001	141.629	0.842	0.093	0.014	124.070	34.500	8.947	32.300
1996 WFBY	0.301	0.145	0.231	0.145	0.353	0.001	47.115	0.836	0.086	0.009	153.676	32.300	6.707	36.700

1997 WFBY	0.231	0.145	0.145	0.145	0.222	0.007	24.773	0.592	0.066	0.009	141.563	36.700	7.203	42.496
1998 WFBY	0.145	0.145	0.145	0.145	0.145	0.004	19.001	0.603	0.052	0.014	43.093	42.496	7.165	44.200
1999 WFBY	0.145	0.145	0.380	0.278	0.199	0.001	36.550	0.387	0.052	0.000	108.135	44.200	7.047	40.200
2000 WFBY	0.380	0.278	0.234	0.342	0.145	0.005	42.627	0.290	0.003	0.006	103.556	40.200	7.217	40.700
2001 WFBY	0.234	0.342	0.145	0.199	0.145	0.000	2.521	0.501	0.052	0.001	133.365	40.700	7.940	37.900
2002 WFBY	0.145	0.199	0.145	0.145	0.208	0.002	5.215	0.033	0.071	0.000	125.051	37.900	7.523	37.700
2003 WFBY	0.145	0.145	0.188	0.145	0.145	0.001	6.544	0.033	0.011	0.001	139.063	37.700	7.230	37.600
2004 WFBY	0.188	0.145	0.372	0.229	0.255	0.000	33.256	0.043	0.001	0.000	126.790	37.600	7.783	43.600
2005 WFBY	0.372	0.229	0.255	0.413	0.145	0.032	65.152	2.448	0.017	0.007	125.798	43.600	7.133	43.083
2006 WFBY	0.255	0.413	0.242	0.145	0.296	0.001	25.024	0.382	0.020	0.002	43.083		7.487	38.067
1990 ECAN	1.337	0.145	11.528	0.525	0.825	0.010	80.520	0.146	0.067	0.320	121.582	36.063	6.177	39.453
1991 ECAN	11.528	0.525	15.127	1.505	1.704	0.022	182.891	0.096	0.024	0.168	105.668	39.453	5.883	34.380
1992 ECAN	15.127	1.505	0.267	0.510	0.145	0.081	11.528	0.305	0.012	0.378	124.207	34.380	6.073	34.770
1993 ECAN	0.267	0.510	0.240	0.217	0.145	0.011	83.143	0.059	0.019	0.667	120.585	34.770	7.147	33.237
1994 ECAN	0.240	0.217	0.203	0.554	0.145	0.000	23.890	0.167	0.033	1.230	139.866	33.237	6.213	33.240
1995 ECAN	0.203	0.554	0.249	0.237	0.145	0.000	35.096	0.056	0.024	0.527	22.733	33.240	5.877	31.280
1996 ECAN	0.249	0.237	0.173	0.218	0.145	0.000	2.907	0.106	0.024	1.170	123.230	31.280	6.600	36.237
1997 ECAN	0.173	0.218	0.202	0.145	0.145	0.003	13.934	0.003	0.032	1.022	133.128	36.237	6.507	41.287
1998 ECAN	0.202	0.145	0.145	0.145	0.145	0.039	38.265	0.018	0.007	0.857	0.026	41.287	6.793	42.070
1999 ECAN	0.145	0.145	0.755	0.279	0.145	0.001	9.773	0.108	0.013	0.066	25.040	42.070	6.740	37.447
2000 ECAN	0.755	0.279	0.168	0.223	0.145	0.001	24.040	0.024	0.013	0.209	1.632	37.447	6.800	40.347
2001 ECAN	0.168	0.223	0.194	0.228	0.145	0.001	3.223	0.041	0.005	0.094	117.834	40.347	5.860	35.960
2002 ECAN	0.194	0.228	0.145	0.145	0.145	0.000	24.796	0.004	0.022	0.004	0.222	35.960	6.977	33.337
2003 ECAN	0.145	0.145	0.252	0.145	0.397	0.000	6.818	0.044	0.008	0.301	126.793	33.337	7.513	35.410
2004 ECAN	0.252	0.145	1.919	0.263	0.236	0.003	33.305	0.009	0.001	0.002	89.891	35.410	5.743	42.080
2005 ECAN	1.919	0.263	0.145	0.371	0.289	0.069	68.101	0.049	0.007	1.007	89.543	42.080	6.373	43.767
2006 ECAN	0.145	0.371	0.145	0.476	0.145	0.007	23.767	0.188	0.005	0.347	43.767		5.283	37.250
1990 NIPB	3.739	0.506	2.568	0.572	0.724	0.000	42.786	0.072	0.019	0.002	127.647	35.227	7.467	40.993
1991 NIPB	2.568	0.572	3.637	1.301	1.443	0.004	16.143	0.464	0.008	0.111	125.327	40.993	7.227	33.453
1992 NIPB	3.637	1.301	1.420	0.464	0.145	0.005	58.195	0.333	0.003	0.016	142.091	33.453	7.490	35.563
1993 NIPB	1.420	0.464	0.886	0.439	0.145	0.000	72.866	0.573	0.001	0.073	136.397	35.563	6.863	33.670
1994 NIPB	0.886	0.439	0.529	0.563	0.145	0.000	126.502	0.586	0.008	0.017	140.758	33.670	8.630	34.337
1995 NIPB	0.529	0.563	0.812	0.257	0.145	0.000	36.467	0.811	0.014	0.007	99.451	34.337	7.970	32.480
1996 NIPB	0.812	0.257	0.313	0.182	0.145	0.001	78.621	0.336	0.018	0.000	147.966	32.480	7.847	35.733
1997 NIPB	0.313	0.182	1.122	0.145	0.145	0.000	44.396	0.348	0.011	0.031	140.443	35.733	7.293	42.240



1998 NIPB	1.122	0.145	0.543	0.195	0.227	0.000	61.280	0.402	0.011	0.001	5.316	42.240	7.320	42.530
1999 NIPB	0.543	0.195	10.242	1.204	0.202	0.000	6.865	1.385	0.002	0.000	11.780	42.530	6.850	35.863
2000 NIPB	10.242	1.204	0.409	0.762	0.145	0.001	36.926	0.214	0.001	0.001	3.669	35.863	7.297	39.053
2001 NIPB	0.409	0.762	0.294	0.559	0.145	0.000	9.567	0.435	0.000	0.000	138.572	39.053	5.680	35.720
2002 NIPB	0.294	0.559	0.145	0.145	0.145	0.000	65.444	0.055	0.003	0.000	9.471	35.720	6.613	33.240
2003 NIPB	0.145	0.145	1.561	0.205	1.052	0.000	8.241	0.115	0.003	0.001	140.097	33.240	7.873	35.693
2004 NIPB	1.561	0.205	8.339	0.407	1.232	0.002	91.529	0.062	0.001	0.000	112.851	35.693	6.703	43.117
2005 NIPB	8.339	0.407	3.882	4.052	0.350	0.011	69.619	0.591	0.001	0.004	123.901	43.117	6.813	43.723
2006 NIPB	3.882	4.052	1.275	0.476	0.145	0.002	20.043	0.457	0.000	0.008	43.723	43.723	6.237	37.610
1990 BLKB	5.205	0.719	3.377	3.663	0.602	0.004	257.085	3.074	0.071	0.000	128.589	37.243	6.617	40.200
1991 BLKB	3.377	3.663	1.199	2.374	0.145	0.004	24.363	6.048	0.102	0.000	130.855	40.200	5.913	34.127
1992 BLKB	1.199	2.374	0.314	0.531	0.145	0.006	350.185	1.553	0.152	0.000	141.516	34.127	6.070	35.007
1993 BLKB	0.314	0.531	1.477	7.659	0.145	0.000	869.315	12.750	0.014	0.000	137.096	35.007	3.697	35.397
1994 BLKB	1.477	7.659	0.314	1.198	0.145	0.000	978.006	19.617	0.115	0.001	139.668	35.397	7.760	33.103
1995 BLKB	0.314	1.198	0.145	0.560	0.145	0.000	384.785	6.293	0.058	0.000	130.192	33.103	6.547	31.930
1996 BLKB	0.145	0.560	0.520	0.267	0.145	0.001	1043.704	3.027	0.103	0.000	156.011	31.930	6.653	35.227
1997 BLKB	0.520	0.267	2.183	0.647	0.145	0.000	962.665	8.778	0.129	0.000	144.921	35.227	6.473	41.933
1998 BLKB	2.183	0.647	0.306	0.260	0.145	0.000	101.017	13.746	0.086	0.006	21.838	41.933	6.767	40.407
1999 BLKB	0.306	0.260	6.976	0.814	0.145	0.000	341.964	1.332	0.006	0.000	98.490	40.407	6.367	35.410
2000 BLKB	6.976	0.814	1.151	5.729	0.145	0.000	1661.948	2.971	0.002	0.000	91.542	35.410	6.467	38.350
2001 BLKB	1.151	5.729	0.145	0.326	0.145	0.000	243.309	3.988	0.000	0.001	140.807	38.350	7.357	35.753
2002 BLKB	0.145	0.326	0.145	0.145	0.145	0.000	79.725	0.869	0.005	0.001	112.247	35.753	6.823	34.807
2003 BLKB	0.145	0.145	1.811	0.145	2.611	0.001	197.683	0.314	0.014	0.007	140.612	34.807	7.913	36.347
2004 BLKB	1.811	0.145	2.353	0.145	1.256	0.012	555.599	0.926	0.000	0.000	130.222	36.347	6.617	40.433
2005 BLKB	2.353	0.145	0.145	5.131	0.794	1.023	611.377	1.530	0.031	0.000	128.990	40.433	6.730	42.483
2006 BLKB	0.145	5.131	4.670	7.554	0.145	0.102	2699.382	1.809	0.001	0.000	42.483	42.483	7.497	36.480
1990 THBY	48.812	4.196	12.830	1.786	1.567	0.006	130.236	0.740	0.006	0.032	120.877	37.243	6.617	40.200
1991 THBY	12.830	1.786	39.988	5.161	0.248	0.007	15.514	0.838	0.009	0.204	123.581	40.200	5.913	34.127
1992 THBY	39.988	5.161	1.433	0.427	0.145	0.001	238.416	0.343	0.039	0.035	129.664	34.127	6.070	35.007
1993 THBY	1.433	0.427	1.664	4.534	0.145	0.000	44.543	1.634	0.012	0.209	130.182	35.007	3.697	35.397
1994 THBY	1.664	4.534	0.145	1.549	0.145	0.006	133.612	0.563	0.003	0.274	131.432	35.397	7.760	33.103
1995 THBY	0.145	1.549	1.364	0.530	0.257	0.000	216.897	0.614	0.008	0.205	119.341	33.103	6.547	31.930
1996 THBY	1.364	0.530	0.677	0.554	0.241	0.002	282.318	1.740	0.039	0.280	148.829	31.930	6.653	35.227
1997 THBY	0.677	0.554	7.163	0.914	0.279	0.005	108.851	1.221	0.020	0.274	139.728	35.227	6.473	41.933
1998 THBY	7.163	0.914	0.476	0.405	0.412	0.003	56.862	1.053	0.025	0.091	21.871	41.933	6.767	40.407

1999 THBY	0.476	0.405	5.322	1.626	0.691	0.003	38.556	1.129	0.012	0.042	86.701	40.407	6.367	35.410
2000 THBY	5.322	1.626	1.058	2.617	0.253	0.005	14.054	0.901	0.001	0.110	88.412	35.410	6.467	38.350
2001 THBY	1.058	2.617	0.326	0.847	0.145	0.004	14.426	0.914	0.000	0.291	132.016	38.350	7.357	35.753
2002 THBY	0.326	0.847	0.145	0.145	0.460	0.001	35.678	0.052	0.006	0.001	66.550	35.753	6.823	34.807
2003 THBY	0.145	0.145	1.561	0.535	3.048	0.004	20.609	0.080	0.003	0.045	132.804	34.807	7.913	36.347
2004 THBY	1.561	0.535	15.367	2.984	2.916	0.062	87.231	0.116	0.000	0.024	118.797	36.347	6.617	40.433
2005 THBY	15.367	2.984	0.746	8.692	0.264	0.070	567.856	0.594	0.011	2.302	124.209	40.433	6.730	42.483
2006 THBY	0.746	8.692	0.597	0.498	0.145	0.000	48.011	1.603	0.001	0.040	42.483	42.483	7.497	36.480

**APPENDIX C**  
**ADDITIONAL TABLES – CHAPTERS 1 AND 2**

Table 1. Data used for stock-recruitment analysis. Spawner (ST) and recruit (RT) densities (fish/ha) estimated from bottom-trawls, spawner CPUE (fish/km) estimated from fishery-independent gill-net surveys or targeted commercial fisheries (SA), combined spawner density (fish/ha) estimated from bottom-trawls and fishery-independent gill-net surveys or targeted commercial fisheries (AST), and the logarithm of recruits per spawner (LNRAST) are provided for each spatial unit and year. The coefficient of variation (CV) and relative standard error (RSE) are provided for bottom-trawl densities and fishery-independent gill-net or targeted commercial fishery CPUE. Years provided correspond to year of hatching for year-classes produced during 1979–2006. Spawning stock sizes provided correspond to spawning stock sizes that produced the 1979–2006 year-classes. Shaded cells indicate CV and RSE values too large to be displayed.

Year	Spatial Unit	LNRAST	ST	CV	RSE	RT	CV	RSE	SA	CV	RSE	AST
1979	MINN		0.145	1.29	0.49	0.145	0.00	0.00				
1980	MINN		0.145	0.00	0.00	0.585	2.11	0.67				
1981	MINN		0.145	0.00	0.00	0.145	0.00	0.00				
1982	MINN		0.145	0.00	0.00	0.145	0.00	0.00				
1983	MINN		0.145	0.00	0.00	0.236	1.27	0.40				
1984	MINN		0.145	0.00	0.00	0.777	3.76	1.19				
1985	MINN	1.871	0.145	0.00	0.00	0.942	3.25	1.03	1.472	0.95	0.32	0.145
1986	MINN	1.931	0.145	0.00	0.00	1.000	3.82	1.21	1.560	0.90	0.29	0.145
1987	MINN	-0.169	0.193	1.11	0.35	0.145	0.00	0.00	3.212	2.30	0.73	0.172
1988	MINN	1.188	0.193	1.11	0.35	0.575	7.01	2.22	4.634	1.77	0.53	0.176
1989	MINN	4.604	0.145	0.00	0.00	14.766	4.91	1.55	2.905	1.33	0.38	0.148
1990	MINN	1.117	0.145	0.00	0.00	0.500	3.90	1.23	16.382	1.94	0.58	0.164
1991	MINN	0.553	0.145	0.00	0.00	0.291	3.64	1.15	23.503	1.69	0.49	0.167
1992	MINN	1.325	0.145	0.00	0.00	0.614	2.14	0.68	15.783	2.28	0.63	0.163
1993	MINN	0.225	0.145	0.00	0.00	0.209	1.47	0.47	23.718	1.66	0.46	0.167
1994	MINN	0.797	0.145	0.00	0.00	0.340	1.82	0.58	5.459	1.42	0.39	0.153
1995	MINN	-0.012	0.145	0.00	0.00	0.145	0.00	0.00	2.577	1.15	0.32	0.147
1996	MINN	0.829	0.145	0.00	0.00	0.332	2.90	0.92	1.102	0.38	0.11	0.145
1997	MINN	0.806	0.145	0.00	0.00	0.325	1.91	0.61	1.394	0.72	0.20	0.145
1998	MINN	1.180	0.145	0.00	0.00	0.472	5.43	1.72	1.433	0.75	0.22	0.145
1999	MINN	0.484	0.221	1.75	0.55	0.281	3.37	1.07	1.214	0.52	0.15	0.173
2000	MINN	0.222	0.145	0.00	0.00	0.181	0.83	0.26	1.397	0.94	0.26	0.145
2001	MINN	0.000	0.145	0.00	0.00	0.145	0.00	0.00	1.515	0.92	0.26	0.145
2002	MINN	-0.165	0.197	1.18	0.37	0.145	0.00	0.00	2.565	1.21	0.33	0.171
2003	MINN	2.822	0.145	0.00	0.00	2.458	7.02	2.48	2.418	1.28	0.35	0.146

2004 MINN	0.328	0.145	0.00	0.00	0.201	1.71	0.77	1.355	0.64	0.18	0.145
2005 MINN	-0.003	0.145	1.04	0.37	0.145	1.82	0.81	2.223	0.94	0.26	0.145
2006 MINN	-0.029	0.145	1.82	0.81	0.145	1.82	0.81	3.423	1.52	0.42	0.149
1980 W11	4.370	0.145	4.73	2.73	23.891	23.24	13.42	1.801	1.45	0.40	0.302
1981 W11		1.555	62.70	36.20	0.339	2.30	1.15				
1982 W11	-3.036	19.494	30.96	17.87	0.233	2.14	1.07	3.420	1.47	0.29	4.843
1983 W11		4.422	19.65	9.83	0.526	5.96	2.98				
1984 W11	2.885	1.085	5.02	2.51	45.900	2.98	1.49	16.997	2.15	0.41	2.564
1985 W11		3.881	0.88	0.44	8.359	48.39	24.19				
1986 W11	-1.619	3.621	1.37	0.69	0.797	3.13	1.57	12.573	1.96	0.38	4.023
1987 W11		3.621	4.56	2.28	0.145	0.00	0.00				
1988 W11	-0.377	37.170	3.04	1.52	10.550	8.28	4.14	17.845	2.55	0.49	15.378
1989 W11		8.055	60.11	30.06	305.438	2.58	1.29				
1990 W11	1.466	3.043	20.36	10.18	38.057	18.93	9.47	70.364	2.97	0.57	8.787
1991 W11		21.161	7.47	3.74	0.470	5.39	2.70				
1992 W11	-3.724	16.092	3.02	1.51	0.401	12.69	6.35	47.686	2.15	0.43	16.607
1993 W11		15.181	96.08	48.04	0.145	0.00	0.00				
1994 W11	-3.973	86.800	1.06	0.53	0.680	2.92	1.46	41.932	2.28	0.44	36.149
1995 W11		28.246	3.81	1.90	0.145	0.00	0.00				
1996 W11	-3.132	4.015	31.15	15.57	0.325	2.19	1.10	38.572	3.32	0.64	7.454
1997 W11		4.190	25.06	12.53	0.575	6.37	3.18				
1998 W11	0.328	2.507	10.41	5.21	9.795	44.96	22.48	55.178	2.91	0.56	7.055
1999 W11		9.910	49.32	24.66	1.949	8.15	4.08				
2000 W11	-2.808	3.376	1.62	0.81	0.324	2.09	1.05	23.868	2.57	0.50	5.367
2001 W11		1.217	65.42	32.71	0.145	0.00	0.00				
2002 W11	1.598	1.352	55.19	27.60	17.299	162.02	81.01	25.314	2.19	0.42	3.499
2003 W11		3.016	17.37	8.68	356.555	3748.04	2163.93				
2004 W11	0.237	5.216	27.33	13.67	6.850	1238.60	715.10	15.713	2.69	0.62	5.403
2005 W11		7.260	56.33	32.52	0.268	6.46	3.73				
2006 W11	-1.089	1.599	79.04	45.64	0.922	20.17	11.64	13.191	3.25	0.75	2.739
1979 W12	-0.086	0.175	0.71	0.21	0.145	0.00	0.00	1.634	0.91	0.21	0.158
1980 W12	2.396	0.210	0.97	0.29	1.889	3.46	1.10	1.611	1.31	0.30	0.172
1981 W12	-0.236	0.260	1.21	0.37	0.215	1.07	0.32	3.278	1.63	0.21	0.272
1982 W12	-0.651	0.257	1.71	0.54	0.145	0.00	0.00	3.464			0.278
1983 W12	0.766	0.535	2.04	0.61	1.225	3.37	1.02	7.013	1.67	0.21	0.570

1984 W12	6.334	0.450	2.87	0.86	272.411	8.98	2.71	6.001	1.97	0.27	0.483
1985 W12	4.894	0.675	3.76	1.13	113.961	2.34	0.71	12.548			0.854
1986 W12	1.528	0.610	3.22	0.97	3.006	2.42	0.73	8.081			0.652
1987 W12	-2.148	3.259	3.74	1.13	0.186	0.97	0.29	9.029	1.49	0.19	1.593
1988 W12	3.051	2.915	9.69	2.92	64.428	7.38	2.23	37.401			3.049
1989 W12	5.508	0.708	4.99	1.51	431.307	2.89	0.87	50.791	2.28	0.31	1.748
1990 W12	3.899	0.777	5.70	1.72	40.873	7.08	2.14	10.246			0.828
1991 W12	0.851	0.409	3.74	1.13	2.515	2.18	0.66	33.043	2.22	0.31	1.074
1992 W12	1.441	0.508	3.96	1.19	2.301	2.06	0.62	6.755			0.545
1993 W12	-1.793	1.821	6.12	1.85	0.328	2.14	0.65	24.939	2.00	0.27	1.971
1994 W12	-2.365	4.816	5.35	1.61	0.470	2.25	0.68	61.152			5.000
1995 W12	-3.124	17.134	5.02	1.51	0.355	1.64	0.50	44.701	2.21	0.30	8.074
1996 W12	-0.683	1.366	5.39	1.62	0.729	2.11	0.64	17.797			1.444
1997 W12	-0.398	0.552	3.99	1.20	0.397	1.85	0.56	7.328			0.591
1998 W12	3.770	1.796	5.29	1.60	82.046	5.58	1.76	23.265			1.891
1999 W12	-1.778	2.945	6.14	1.85	0.575	2.97	0.90	46.238	2.22	0.30	3.404
2000 W12	-1.897	0.909	4.50	1.42	0.145	0.00	0.00	11.944			0.967
2001 W12	-2.096	6.258	4.90	1.48	0.385	2.34	0.71	18.309	1.98	0.27	3.134
2002 W12	0.448	3.303	5.68	1.71	5.395	3.82	1.15	42.259			3.447
2003 W12	2.568	3.426	8.32	2.51	37.056	7.54	2.27	27.572	2.11	0.34	2.841
2004 W12	0.491	1.358	3.92	1.18	2.346	2.73	0.91	17.701			1.436
2005 W12	0.202	0.348	2.18	0.66	1.202	5.41	1.80	32.554	1.99	0.32	0.983
2006 W12	-2.871	4.131	5.22	1.74	0.243	1.42	0.47	52.615			4.298
1979 WKEW		0.145	0.00	0.00	0.145	0.00	0.00				
1980 WKEW		0.145	0.00	0.00	0.807	3.69	1.40				
1981 WKEW		0.252	1.31	0.50	0.197	1.09	0.41				
1982 WKEW		0.145	0.00	0.00	0.190	0.94	0.36				
1983 WKEW		0.145	0.00	0.00	1.710	2.23	0.84				
1984 WKEW		0.200	1.15	0.43	74.294	5.46	2.06				
1985 WKEW		0.272	1.57	0.59	4.019	5.12	1.93				
1986 WKEW		0.219	1.57	0.59	0.607	2.21	0.84				
1987 WKEW		0.293	3.57	1.35	0.145	0.00	0.00				
1988 WKEW		0.145	0.00	0.00	5.538	8.14	3.08				
1989 WKEW		0.224	1.68	0.63	37.346	9.09	3.43				
1990 WKEW	4.848	0.275	1.58	0.60	22.920	7.95	3.01	13.074	3.30	0.95	0.180
1991 WKEW	1.709	0.145	0.00	0.00	0.822	3.59	1.36	15.849	2.67	0.77	0.149

1992 WKEW	1.962	0.362	2.66	1.00	1.667	2.45	0.93	15.750	1.71	0.49	0.234
1993 WKEW	-1.793	0.562	2.30	0.87	0.145	0.00	0.00	76.612	1.72	0.50	0.871
1994 WKEW	-2.048	19.463	5.55	2.10	0.351	1.68	0.63	30.574	1.07	0.31	2.717
1995 WKEW	-0.130	0.207	1.31	0.50	0.351	1.70	0.64	51.046	1.88	0.54	0.400
1996 WKEW	0.053	0.262	2.66	1.01	0.400	1.44	0.54	40.014	2.54	0.73	0.380
1997 WKEW	-1.445	0.422	2.13	0.80	0.342	1.09	0.41	197.074	1.04	0.30	1.449
1998 WKEW		0.214	1.45	0.55	1.125	17.66	6.67				
1999 WKEW	0.246	0.145	0.00	0.00	0.185	0.85	0.32	9.890	1.97	0.57	0.145
2000 WKEW	-0.120	0.209	1.36	0.51	0.145	0.00	0.00	13.899	2.15	0.62	0.163
2001 WKEW	-0.382	0.145	0.00	0.00	0.145	0.00	0.00	26.493	0.76	0.22	0.212
2002 WKEW	1.374	0.365	6.28	2.37	0.670	3.38	1.28	9.800	2.81	0.85	0.170
2003 WKEW	3.596	0.683	5.11	1.93	18.030	45.19	26.09	29.330	1.45	0.42	0.494
2004 WKEW	0.676	0.247	1.37	0.52	0.601	4.55	2.04	30.475	2.07	0.60	0.306
2005 WKEW	2.501	0.255	4.25	2.45	2.475	9.19	4.11	16.467	2.34	0.68	0.203
2006 WKEW	-0.192	0.198	1.71	0.76	0.183	1.60	0.72	22.497	1.51	0.44	0.222
1979 M14	1.076	0.145	1.63	0.73	0.425	2.78	1.24	2.093			0.145
1980 M14	3.650	0.145	1.63	0.73	5.579	7.67	3.43	2.093			0.145
1981 M14		0.196	1.69	0.75				2.696			0.175
1982 M14	0.000	0.145	1.63	0.73	0.145	1.63	0.73	2.093			0.145
1983 M14					1.949	18.42	6.96				
1984 M14	5.130	0.190	1.64	0.73	28.545	8.47	3.20	2.624			0.169
1985 M14	1.249	0.956	3.87	1.46	3.262	6.86	2.59	10.297			0.935
1986 M14	-0.023	0.916	5.49	2.08	0.610	6.96	2.63	5.763	2.08	0.79	0.624
1987 M14	-0.614	2.147	7.83	2.96	0.427	3.58	1.35	4.308	2.98	1.05	0.788
1988 M14	1.129	6.750	19.67	7.43	11.145	16.38	6.19	18.077	1.95	0.69	3.604
1989 M14	4.289	3.899	14.44	5.46	206.535	8.01	3.03	19.017	1.10	0.42	2.833
1990 M14	1.978	3.289	14.06	5.31	28.424	14.40	5.44	35.568	3.06	1.08	3.934
1991 M14	-0.219	5.046	28.64	10.83	5.374	9.01	3.41	57.484	1.04	0.37	6.691
1992 M14	-3.081	6.066	49.36	18.66	0.216	1.52	0.57	29.417	2.08	0.74	4.713
1993 M14	-4.197	8.529	22.59	8.54	0.145	0.00	0.00	67.204	3.31	1.17	9.644
1994 M14	-3.548	16.393	26.33	9.95	0.314	2.22	0.84	49.509	1.38	0.49	10.927
1995 M14	-3.100	18.008	44.04	16.65	0.577	3.68	1.39	58.658	1.52	0.54	12.810
1996 M14	-4.204	18.309	27.57	10.42	0.204	1.48	0.60	63.812	1.32	0.47	13.655
1997 M14	-3.662	3.993	6.64	2.51	0.145	0.00	0.00	53.075	4.00	1.41	5.647
1998 M14	0.454	0.493	3.75	1.53	0.731	5.11	1.93	5.884			0.464
1999 M14	-1.383	0.931	7.32	2.77	0.375	2.88	1.09	21.386	1.67	0.59	1.496

2000 M14	0.310	0.837	6.46	2.44	2.475	4.00	1.51	31.092	3.25	1.15	1.816
2001 M14	0.424	1.698	11.36	4.29	2.297	2.85	1.16	13.668	2.45	0.87	1.503
2002 M14	0.972	1.057	7.77	2.94	5.533	10.56	3.99	32.311	1.59	0.56	2.093
2003 M14	1.253	0.567	2.76	1.13	2.988	17.64	7.89	13.316	2.85	1.01	0.854
2004 M14	0.819	0.347	1.62	0.61	1.823	12.17	7.02	17.611	1.02	0.36	0.804
2005 M14	0.178	0.979	8.01	3.58	1.141	73.03	42.17	10.430	2.37	0.84	0.955
2006 M14	-1.132	0.527	11.90	6.87	0.243	4.17	2.41	11.690	1.77	0.63	0.755
1979 MISS		0.145	0.00	0.00	0.145	0.00	0.00				
1980 MISS		0.145	0.00	0.00	0.145	0.00	0.00				
1981 MISS		0.145	0.00	0.00							
1982 MISS		0.145	0.00	0.00	0.145	0.00	0.00				
1983 MISS					0.270	2.89	1.18				
1984 MISS		0.145	0.00	0.00	1.598	11.10	4.53				
1985 MISS		0.145	0.00	0.00	0.145	0.00	0.00				
1986 MISS	0.977	0.613	6.38	2.60	0.592	6.42	2.62	2.793	2.23	0.79	0.223
1987 MISS	0.734	0.331	5.05	2.06	0.302	3.95	1.61	1.935	0.74	0.26	0.145
1988 MISS	2.766	0.351	5.90	2.41	4.854	16.61	6.78	9.735	2.02	0.71	0.305
1989 MISS	5.348	0.446	10.98	4.48	63.113	12.64	5.16	7.305	2.97	1.05	0.300
1990 MISS	4.044	0.536	17.64	7.20	19.825	19.04	7.77	8.195	3.77	1.33	0.348
1991 MISS	-0.192	0.980	23.29	9.51	0.471	4.06	1.66	12.296	3.20	1.13	0.570
1992 MISS	0.052	0.361	6.31	2.58	0.334	2.55	1.04	10.270	3.69	1.30	0.317
1993 MISS	-1.436	0.602	8.66	3.53	0.145	0.00	0.00	23.616	2.93	1.04	0.609
1994 MISS	-0.406	1.100	11.54	4.71	0.458	2.32	0.95	16.152	2.01	0.71	0.687
1995 MISS	-0.894	1.064	20.51	8.37	0.348	2.45	1.00	26.148	2.69	0.95	0.850
1996 MISS	-0.875	0.445	10.91	4.46	0.196	1.04	0.43	18.753	2.90	1.03	0.469
1997 MISS	-1.158	0.257	2.54	1.04	0.145	0.00	0.00	32.202	2.46	0.87	0.461
1998 MISS		0.145	0.00	0.00	0.545	22.03	9.85				
1999 MISS	0.749	0.145	0.00	0.00	0.387	3.45	1.41	8.427	1.10	0.39	0.183
2000 MISS	-0.409	0.145	0.00	0.00	0.211	1.39	0.62	26.812	2.74	0.97	0.317
2001 MISS	-0.711	0.275	3.06	1.25	0.145	0.00	0.00	11.733	2.53	0.89	0.295
2002 MISS	1.918	0.145	0.00	0.00	1.205	10.46	4.27	7.843	2.33	0.82	0.177
2003 MISS	1.526	0.145	0.00	0.00	0.809	12.41	5.55	7.742	2.76	0.98	0.176
2004 MISS	-0.287	0.145	0.00	0.00	0.145	0.00	0.00	9.428	1.41	0.50	0.193
2005 MISS	2.092	0.145	0.00	0.00	2.180	12.83	5.74	18.931	1.82	0.64	0.269
2006 MISS	0.652	0.145	0.00	0.00	0.285	4.25	2.12	5.428	0.88	0.31	0.149



1990 WFBY	0.874	0.581	3.80	1.34	1.470	1.39	0.46	67.965	3.21	1.44	0.613
1991 WFBY	-1.266	2.121	3.70	1.23	0.330	1.74	0.58	67.104	2.01	0.48	1.168
1992 WFBY	-1.424	0.567	3.68	1.23	0.145	0.00	0.00	66.284	1.62	0.59	0.603
1993 WFBY	-1.364	0.718	5.93	1.98	0.174	0.64	0.21	66.748	1.02	0.22	0.679
1994 WFBY	-0.811	0.456	1.46	0.49	0.301	1.49	0.50	189.719	2.18	1.02	0.678
1995 WFBY	-0.647	1.417	4.26	1.42	0.231	1.18	0.39	1.893	56.76	40.13	0.442
1996 WFBY		0.494	3.18	1.06	0.145	0.00	0.00				
1997 WFBY	-1.284	1.058	2.93	0.98	0.145	0.00	0.00	8.173	21.17	14.72	0.524
1998 WFBY		0.327	2.46	0.87	0.380	3.12	1.04				
1999 WFBY		0.244	1.37	0.46	0.234	0.88	0.29				
2000 WFBY		0.219	1.66	0.55	0.145	0.00	0.00				
2001 WFBY	-0.340	0.232	1.22	0.41	0.145	0.00	0.00	3.455	757.10	535.35	0.204
2002 WFBY		0.257	1.43	0.51	0.188	0.96	0.32				
2003 WFBY	0.828	0.145	0.00	0.00	0.372	2.98	0.99	3.600	1.82	0.82	0.162
2004 WFBY	0.563	0.170	0.56	0.19	0.255	4.84	2.80	1.109	1.14	0.51	0.145
2005 WFBY	0.360	0.145	0.00	0.00	0.242	3.91	2.26	4.351	2.06	0.60	0.169
2006 WFBY		0.351	19.52	11.27	0.145	0.00	0.00				
1990 ECAN	3.928	0.145	1.55	0.63	15.127	3.12	0.94	123.097	0.39	0.19	0.298
1991 ECAN	-0.884	0.572	4.15	1.47	0.267	1.27	0.38	183.353	2.36	0.73	0.645
1992 ECAN	-1.096	0.767	5.94	1.79	0.240	1.39	0.42	152.341	1.16	0.33	0.717
1993 ECAN	-1.096	0.397	2.74	0.83	0.203	1.36	0.41	319.365	1.38	0.45	0.607
1994 ECAN	-0.832	0.290	2.39	0.72	0.249	1.11	0.33	501.892	86.33	60.87	0.572
1995 ECAN	-1.134	1.887	6.88	2.08	0.173	0.66	0.20	5.147	56.76	40.13	0.536
1996 ECAN		0.697	4.94	1.49	0.202	0.86	0.26				
1997 ECAN	-1.552	1.849	6.15	1.86	0.145	0.00	0.00	16.509	1.86	0.93	0.685
1998 ECAN		0.175	0.71	0.21	0.755	2.27	0.69				
1999 ECAN	-0.624	0.336	2.69	0.81	0.168	0.56	0.17	22.960	428.80	303.21	0.314
2000 ECAN		0.255	1.61	0.49	0.194	0.76	0.23				
2001 ECAN	-0.467	0.309	1.93	0.58	0.145	0.00	0.00	6.898	757.10	535.35	0.231
2002 ECAN		0.278	2.05	0.62	0.252	1.68	0.51				
2003 ECAN	2.176	0.235	0.99	0.30	1.919	4.36	1.38	9.789	1.82	0.82	0.218
2004 ECAN	0.000	0.145	0.00	0.00	0.145	1.80	0.80	3.015	1.14	0.51	0.145
2005 ECAN	-0.588	0.311	2.55	0.81	0.145	1.55	0.63	11.834	2.06	0.60	0.261
2006 ECAN		0.422	1.92	0.86	0.145	1.55	0.63				
1990 NIPB	1.255	1.261	8.64	3.86	3.637	29.49	12.04	1000.350			1.037

1991 NIPB	1.112	0.439	4.26	1.74	1.420	6.57	2.48	567.227	0.59	0.26	0.467
1992 NIPB	-0.244	1.461	9.03	3.69	0.886	4.86	1.62	1028.281	0.51	0.23	1.131
1993 NIPB	0.314	0.346	2.74	1.04	0.529	3.42	1.14	490.083	0.33	0.19	0.387
1994 NIPB	0.426	0.436	3.92	1.31	0.812	3.98	1.33	746.799	46.26	32.71	0.530
1995 NIPB	-1.334	1.465	4.61	1.54	0.313	2.19	0.73	1137.920			1.188
1996 NIPB	1.335	0.239	2.15	0.72	1.122	4.91	1.64	409.326			0.295
1997 NIPB	0.732	0.204	1.30	0.43	0.543	2.51	0.84	375.248			0.261
1998 NIPB	3.407	0.288	2.06	0.69	10.242	7.25	2.56	452.299			0.340
1999 NIPB	0.377	0.242	1.32	0.44	0.409	2.17	0.77	363.949	3.27	1.64	0.280
2000 NIPB	-0.184	0.407	3.54	1.25	0.294	1.96	0.69	341.480	0.56	0.16	0.353
2001 NIPB	-1.456	0.929	4.12	1.46	0.145	0.00	0.00	472.130	0.58	0.08	0.622
2002 NIPB	0.861	0.536	6.95	2.46	1.561	4.07	1.44	950.831	0.40	0.11	0.660
2003 NIPB	3.920	0.145	0.00	0.00	8.339	11.80	4.17	205.859	1.40	0.12	0.166
2004 NIPB	2.453	0.276	1.70	0.60	3.882	6.46	2.89	456.808	0.63	0.07	0.334
2005 NIPB	1.036	0.305	2.16	0.76	1.275	2.59	1.16	778.909	1.06	0.21	0.452
2006 NIPB	-0.674	0.470	14.64	6.55	0.246	2.30	1.03	567.809	0.53	0.07	0.483
1990 BLKB	1.654	0.615	8.96	4.48	1.199	57.63	28.82	100.729	1.45	0.22	0.229
1991 BLKB	-1.394	7.499	1.53	0.76	0.314	5.83	2.92	164.225	1.51	0.24	1.267
1992 BLKB	1.303	0.340	7.53	3.76	1.477	6.25	3.13	250.199	1.92	0.25	0.401
1993 BLKB	-1.015	0.947	19.18	9.59	0.314	5.83	2.92	329.755	1.52	0.12	0.867
1994 BLKB	-1.653	0.749	10.40	5.20	0.145	0.00	0.00	323.222	1.45	0.15	0.757
1995 BLKB	-1.153	1.660	8.31	4.16	0.520	5.75	2.88	484.491	1.21	0.13	1.648
1996 BLKB	0.958	0.372	9.98	4.99	2.183	102.37	51.18	522.568	0.94	0.11	0.838
1997 BLKB	-1.192	0.806	19.25	9.63	0.306	5.32	2.66	421.224	0.83	0.09	1.007
1998 BLKB	1.752	0.557	6.30	3.15	6.976	34.34	17.17	623.260	0.65	0.08	1.210
1999 BLKB	-0.243	0.617	7.37	3.69	1.151	25.76	12.88	724.863	0.77	0.10	1.468
2000 BLKB	-2.781	2.891	14.48	7.24	0.145	0.00	0.00	523.521	0.78	0.10	2.339
2001 BLKB	-1.866	0.727	10.09	5.04	0.145	0.00	0.00	411.859	1.04	0.16	0.937
2002 BLKB	0.143	1.450	7.45	3.72	1.811	9.91	4.95	494.190	1.25	0.14	1.569
2003 BLKB	1.696	0.300	4.99	2.49	2.353	149.28	74.64	289.448	2.28	0.23	0.432
2004 BLKB	-1.736	0.346	7.92	3.96	0.145	0.00	0.00	533.184	1.34	0.16	0.823
2005 BLKB	1.731	0.305	5.31	2.65	4.670	302.91	151.45	572.111	0.75	0.12	0.827
2006 BLKB	-2.288	3.032			0.385	11.19	5.60	854.216	0.72	0.09	3.796
1990 THBY	5.620	0.286	4.27	2.14	39.988	11.28	5.05	312.481	0.97	0.13	0.145
1991 THBY	0.981	0.868	12.46	5.57	1.433	4.82	2.16	535.331	0.78	0.18	0.537

1992 THBY	0.914	1.348	24.76	11.07	1.664	11.99	5.36	534.064	1.30	0.29	0.667
1993 THBY	-1.549	0.842	14.73	6.59	0.145	0.00	0.00	631.148	0.65	0.12	0.683
1994 THBY	-0.504	4.971	8.78	3.93	1.364	9.36	4.19	770.332	0.77	0.15	2.258
1995 THBY	-1.327	6.188	57.98	25.93	0.677	10.94	4.89	776.862	1.15	0.19	2.552
1996 THBY	2.657	0.212	1.40	0.63	7.163	23.69	10.59	809.108	0.58	0.10	0.503
1997 THBY	-0.290	0.553	7.64	3.42	0.476	15.14	6.77	691.006	0.79	0.13	0.636
1998 THBY	2.080	0.410	10.00	4.47	5.322	44.81	20.04	782.754	0.56	0.09	0.665
1999 THBY	-0.244	0.357	2.47	1.10	1.058	21.94	9.81	1293.446	0.46	0.08	1.350
2000 THBY	-1.706	2.527	5.10	2.28	0.326	2.47	1.10	826.188	0.76	0.14	1.794
2001 THBY	-2.553	1.612	11.64	5.21	0.145	0.00	0.00	978.573	0.81	0.20	1.862
2002 THBY	-0.333	2.341	17.41	7.79	1.561	50.73	22.69	959.772	0.48	0.08	2.178
2003 THBY	3.601	0.361	2.86	1.28	15.367	34.77	15.55	605.587	2.26	0.29	0.419
2004 THBY	0.303	0.321	5.01	2.24	0.746	11.99	5.99	750.566	0.53	0.07	0.551
2005 THBY	0.795	0.208	1.32	0.59	0.597	6.24	2.79	544.115	0.64	0.13	0.270
2006 THBY	-2.894	2.584	15.72	7.86	0.224	1.70	0.76	1386.532	0.46	0.08	4.044

## REFERENCES

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64(4):912–923.
- Anderson, E. D., and L. L. Smith Jr. 1971. Factors affecting the abundance of lake herring (*Coregonus artedii* Lesueur) in western Lake Superior. *Transactions of the American Fisheries Society* 100(4):691–707.
- Assel, R. A. 2005. Great Lakes ice cover climatology update: winters 2003, 2004, and 2005. NOAA Technical Memorandum GLERL-135. National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.
- Assel, R. A., D. C. Norton, and K. C. Cronk. 2002. A Great Lakes ice cover digital data set for winters 1973–2000. NOAA Technical Memorandum GLERL-121. National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.
- Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. *Mar. Ecol. Prog. Ser.* Vol. 6:1–9.
- Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. National Oceanic and Atmospheric Administration, California Sea Grant College System, La Jolla, California.
- Baldwin, N. A., R. W. Saalfeld, M. R. Dochoda, H. J. Buettner, and R. L. Eshenroder. 2006. Commercial fish production in the Great Lakes 1867–2000. <http://www.glf.org/databases/commercial/commerc.php>.

- Becker, G. C. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin.
- Bennett, E. B. 1978. Characteristics of the thermal regime of Lake Superior. *Journal of Great Lakes Research* 4:310–319.
- Berst, A. H., and G. R. Spangler. 1973. Lake Huron: the ecology of the fish community and man's effects on it. Great Lakes Fishery Commission, Technical Report No. 21, Ann Arbor, Michigan.
- Bowen, S. H., D. J. D'Angelo, S. H. Arnold, M. J. Keniry, and R. J. Albrecht. 1991. Density-dependent maturation, growth, and female dominance in Lake Superior lake herring (*Coregonus artedii*). *Can. J. Fish. Aquat. Sci.* 48:569–576.
- Bronte, C. R., M. P. Ebener, D. R. Schreiner, D. S. DeVault, M. M. Petzold, D. A. Jensen, C. Richards, and S. J. Lozano. 2003. Fish community changes in Lake Superior 1970–2000. *Can. J. Fish. Aquat. Sci.* 60:1552–1574.
- Brown, R. W., W. W. Taylor, and R. A. Assel. 1993. Factors affecting the recruitment of lake whitefish in two areas of northern Lake Michigan. *Journal of Great Lakes Research* 19(2):418–428.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York.
- Busiahn, T. R., editor. 1990. Fish community objectives for Lake Superior. Great Lakes Fishery Commission, Special Publication 90-1, Ann Arbor, Michigan.
- Coffin, A. B., D. L. Pereira, and G. R. Spangler. 2003. Stock-specific growth rates of lake herring, *Coregonus artedii*, in western Lake Superior.

- Colby, P. J., and L. T. Brooke. 1969. Cisco (*Coregonus artedii*) mortalities in a southern Michigan lake. *Limnology and Oceanography* 14:958–960.
- Colby, P. J., and L. T. Brooke. 1970. Survival and development of lake herring (*Coregonus artedii*) eggs at various incubation temperatures. Pages 417–428 *In* *Biology of Coregonid Fishes*, *Edited* by C. C. Lindsey and C. S. Woods. University of Manitoba Press, Winnipeg, Manitoba.
- Conner, D. J., C. R. Bronte, J. H. Selgeby, and H. L. Collins. 1993. Food of salmonine predators in Lake Superior, 1981–1987. Great Lakes Fishery Commission, Technical Report No. 59, Ann Arbor, Michigan.
- Corradin, L. M., M. J. Hansen, D. R. Schreiner, and M. J. Seider. 2008. Recruitment dynamics of lake trout in western Lake Superior during 1988–1995. *North American Journal of Fisheries Management* 28:663–677.
- Cox, S. P., and J. F. Kitchell. 2004. Lake Superior ecosystem, 1929–1998: simulating alternative hypotheses for recruitment failure of lake herring (*Coregonus artedii*). *Bulletin of Marine Science* 74(3):671–683.
- Davis, B. M., and T. N. Todd. 1992. Diet overlap in larval lake herring (*Coregonus artedii*) and bloaters (*Coregonus hoyi*). *Pol. Arch. Hydrobiol.* 39(3–4):279–287.
- Dorr Jr., J. A., and D. F. Eschman. 1970. *Geology of Michigan*. The University of Michigan Press, Ann Arbor, Michigan.
- Dryer, W. R., and J. Beil. 1964. Life history of lake herring in Lake Superior. U.S. Fish and Wildlife Service Bulletin 63(3):493–530.
- Dryer, W. R., L. F. Erkkila, and C. L. Tetzloff. 1965. Food of lake trout in Lake Superior. *Transactions of the American Fisheries Society* 94(2):169–176.

- Ebener, M. P., J. D. Stockwell, D. L. Yule, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, D. R. Schreiner, S. Geving, K. Scribner, S. T. Schram, M. J. Seider, and S. P. Sitar. 2008. Status of cisco (*Coregonus artedii*) in Lake Superior during 1970–2006 and management and research considerations. Great Lakes Fishery Commission, Lake Superior Technical Report 1, Ann Arbor, Michigan.
- Edsall, T. A., and P. J. Colby. 1970. Temperature tolerance of young-of-the-year cisco, *Coregonus artedii*. Transactions of the American Fisheries Society 99(3):526–531.
- Edsall, T. A., and T. J. DeSorcie. 2002. The growth-temperature relation and preferred temperatures of juvenile lake herring. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 57:335–342.
- Fechhelm, R. G., and D. B. Fissel. 1988. Wind-aided recruitment of Canadian arctic cisco (*Coregonus autumnalis*) into Alaskan waters. Can. J. Fish. Aquat. Sci. 45:906–910.
- Fechhelm, R. G., and W. B. Griffiths. 1990. Effect of wind on the recruitment of Canadian arctic cisco (*Coregonus autumnalis*) into the central Alaskan Beaufort Sea. Can. J. Fish. Aquat. Sci. 47:2164–2171.
- Fisher, S. J., and D. G. Fielder. 1998. A standard weight equation to assess the condition of North American lake herring (*Coregonus artedii*). Journal of Freshwater Ecology 13(3):269–277.
- Fitzsimons, J. D., and R. O’Gorman. 2006. Status and assessment, research, and

- restoration needs for lake herring in the Great Lakes. Can. Tech. Rep. Fish. Aquat. Sci. 2638:v+55p.
- Freeberg, M. H., W. W. Taylor, and R. W. Brown. 1990. Effect of egg and larval survival on the year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. Transactions of the American Fisheries Society 119:92–100.
- Frey, D. G. 1955. Distributional ecology of the cisco (*Croegonus artedii*) in Indiana. Invest. Indiana Lakes and Streams 4(7):177–228.
- Fuller, W. A. 1987. Measurement error models. John Wiley and Sons Inc., New York, New York.
- Goodyear, C. D., T. A. Edsall, D. M. Ormsby-Dempsey, G. D. Moss, and P. E. Polanski. 1981. Atlas of the spawning and nursery areas of Great Lakes fishes, Volume No. 2: Lake Superior. U.S. Fish and Wildlife Service, Washington, D.C. FWS/OBS-82–52.
- Gorman, O. T. 2007. Changes in a population of exotic rainbow smelt in Lake Superior: boom to bust, 1974–2005. Journal of Great Lakes Research 33(Supplement 1):75–90.
- Hansen, M. J., editor. 1990. Lake Superior: the state of the lake in 1989. Great Lakes Fishery Commission, Special Publication 90-3, Ann Arbor, Michigan.
- Hansen, M. J., editor. 1996. Causes of declining survival of lake trout stocked in U.S. waters of Lake Superior in 1963–1986. Transactions of the American Fisheries Society 125:831–843.
- Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958–



1995. North American Journal of Fisheries Management 18:764–774.
- Hartman, W. L. 1973. Effects of exploitation, environmental change, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fishery Commission, Technical Report No. 22, Ann Arbor, Michigan.
- Hatch, J. T., and J. C. Underhill. 1988. Abundance, distribution, growth, and mortality of larval lake herring in western Lake Superior. American Fisheries Society Symposium 5:96–103.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, New York.
- Hile, R. 1936. Age and growth of the cisco *Leucichthys artedi* (LeSueur), in the lakes of the northeastern highlands, Wisconsin. U.S. Bur. Fish., Bull. 48:211–317.
- Hinrichs, M. A., and H. E. Brooke. 1975. Egg development and larval feeding of the lake herring, *Coregonus artedii* (LeSueur). Museum of Natural History, University of Wisconsin, Reports on Fauna and Flora of Wisconsin 10(4):75–86.
- Hoff, M. H. 2004. Biotic and abiotic factors related to lake herring recruitment in the Wisconsin waters of Lake Superior, 1984–1998. Journal of Great Lakes Research 30(Supplement 1):423–433.
- Hoff, M. H., J. Link, and C. Haskell. 1997. Piscivory by Lake Superior lake herring (*Coregonus artedi*) on rainbow smelt (*Osmerus mordax*) in winter, 1993–1995. Journal of Great Lakes Research 23(2):210–211.
- Horns, W. H., editor. 2003. Fish-community objectives for Lake Superior. Great Lakes Fishery Commission, Special Publication 03-01, Ann Arbor, Michigan.
- Hrabik, T. R., J. J. Magnuson, and A. S. McLain. 1998. Predicting the effects of

- rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes. *Can. J. Fish. Aquat. Sci.* 55:1364–1371.
- Hubbs, C. L., and K. F. Lagler. 2004. *Fishes of the Great Lakes region*. Revised edition. The University of Michigan Press, Ann Arbor, Michigan.
- Hurst, T. P., and D. O. Conover. 1998. Winter mortality of young-of-the-year Hudson River striped bass (*Morone saxatilis*): size-dependent patterns and effects on recruitment. *Can. J. Fish. Aquat. Sci.* 55:1122–1130.
- Jensen, E. T. 1996. The effect of surface temperature and population biomass on lake herring (*Coregonus artedii*) year class strength in Lake Superior. M.S. Thesis, Michigan Technological University, Houghton, Michigan.
- John, K. R., and A. D. Hasler. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallow water cisco (*Leucichthys artedii* LeSueur) in Lake Mendota, Wisconsin. *Limnology and Oceanography* 1:176–194.
- Johnson, T. B., and D. O. Evans. 1990. Size-dependent winter mortality of young-of-the-year white perch: climate warming and invasion of the Laurentian Great Lakes. *Transactions of the American Fisheries Society* 119:301–313.
- Kinnunen, R. E. 1997. The effect of Lake Superior surface water temperature on lake herring (*Coregonus artedii*) length and year-class strength. Ph.D. Thesis, Michigan Technological University, Houghton, Michigan.
- Kirjasniemi, M., and T. Valtonen. 1997. Size-dependent over-wintering mortality of young-of-the-year roach, *Rutilus rutilus*. *Environmental Biology of Fishes* 50:451–456.

- Koelz, W. 1931. The coregonid fishes of northeastern America. Pap. Mich. Acad. Sci. Arts Lett. 13:303–432.
- Koslow, J. A. 1991. Fecundity and the stock-recruitment relationship. Can. J. Fish. Aquat. Sci. 49:210–217.
- Latta, W. C. 1995. Distribution and abundance of lake herring (*Coregonus artedii*) in Michigan. Michigan Department of Natural Resources, Fisheries Research Report No. 2014, Lansing, Michigan.
- Lawrie, A. H. 1978. The fish community of Lake Superior. Journal of Great Lakes Research 4:513–549.
- Lawrie, A. H., and J. F. Rahrer. 1973. Lake Superior: a case history of the lake and its fisheries. Great Lakes Fishery Commission, Technical Report No. 19, Ann Arbor, Michigan.
- Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer Jr. 1980. Atlas of North American freshwater fishes. North Carolina Biological Survey 1980-12, Raleigh, North Carolina.
- Lee, T. R., and A. Beaulieu. 1971. Great Lakes water use. Canada Department of Fisheries and Forests, Map No. JN 359, Ottawa, Ontario.
- Link, J., J. H. Selgeby, M. H. Hoff, and C. Haskell. 1995. Winter diet of lake herring (*Coregonus artedii*) in western Lake Superior. Journal of Great Lakes Research 21(3):395–399.
- MacCallum, W. R., and J. H. Selgeby. 1987. Lake Superior revisited 1984. Can. J. Fish. Aquat. Sci. 44(Suppl. 2):23–36.
- Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996.

- First year growth, recruitment, and maturity of walleyes in western Lake Erie. Transactions of the American Fisheries Society 125(6):821–830.
- Madenjian, C. P., T. O. Hook, E. S. Rutherford, D. M. Mason, T. E. Croley II, E. B. Szalai, and J. R. Bence. 2005. Recruitment variability of alewives in Lake Michigan. Transactions of the American Fisheries Society 134:218–230.
- Marshall, E. W. 1967. Lake Superior ice characteristics. Int. Ass. Great Lakes Res., Proc. 10<sup>th</sup> Conf. Great Lakes Res.:214–220.
- McCormick, J. H., B. R. Jones, and R. F. Syrett. 1971. Temperature requirements for growth and survival of larval ciscoes (*Coregonus artedii*). Journal of the Fisheries Research Board of Canada 28:924–927.
- McLain, A. S., and J. J. Magnuson. 1988. Analysis of recent declines in cisco (*Coregonus artedii*) populations in several northern Wisconsin lakes. Finnish Fisheries Research 9:155–164.
- McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada, Ottawa, Ontario. 38 pp.
- Myers, J. T. 2008. A re-assessment of rainbow smelt (*Osmerus mordax*) predation on cisco (*Coregonus artedii*) in Lake Superior. M.S. Thesis, Michigan State University, East Lansing, Michigan.
- Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability. ICES J. of Mar. Science 58:937–951.
- Myers, R. A., G. Mertz, and J. M. Bridson. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can. J. Fish.

- Aquat. Sci. 54:1400–1407.
- Myers, R. A., G. Mertz, and N. J. Barrowman. 1995. Spatial scales of variability in cod recruitment in the North Atlantic. *Can. J. Fish. Aquat. Sci.* 52:1849–1862.
- Myers, R. A., G. Mertz, and N. J. Barrowman. 1996. Invariants of spawner-recruitment relationships for marine, anadromous, and freshwater species. ICES CM 1996/D: 11.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. The maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* 56:2404–2419.
- Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. *Fish. Bull. (U.S.)* 75:23–41.
- O’Gorman, R., B. F. Lantry, and C. P. Schneider. 2004. Effect of stock size, climate, predation, and trophic status on recruitment of alewives in Lake Ontario, 1978–2000. *Transactions of the American Fisheries Society* 133:855–867.
- Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperatures. *Transactions of the American Fisheries Society* 108:130–136.
- Oyadomari, J. K. 2005. Ecology of larval fishes and large zooplankton in the Keweenaw Current region of Lake Superior, with special focus on lake herring, *Coregonus artedii*. Ph.D. Thesis, Michigan Technological University, Houghton, MI.
- Oyadomari, J. K., and N. A. Auer. 2004. Inshore-offshore distribution of larval fishes of Lake Superior off the coast of the Keweenaw Peninsula, Michigan. *Journal of Great Lakes Research* 30(Supplement 1):369–384.
- Pangle, K. L., T. M. Sutton, R. E. Kinnunen, and M. H. Hoff. 2004. Overwinter survival

- of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. Transactions of the American Fisheries Society 133(5):1235–1246.
- Peterman, R. M. 1981. Form of random variation in salmon smolt-to-smolt relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38:1113–1119.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, *in situ* enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46:1958–1968.
- Powers, C. F., D. L. Jones, P. C. Munding, and J. C. Ayers. 1959. Exploration of *collateral* data potentially applicable to Great Lakes hydrography and fisheries. University of Michigan, Great Lakes Research Institute, Final Report for U.S. Fish and Wildlife Service Contract No. 14-19-008-9381, Ann Arbor, Michigan.
- Pritchard, A. L. 1930. Spawning habits and fry of the cisco (*Leucichthys artedi*) in Lake Ontario. Contrib. Can. Biol. Fish. N.S. 6(9):227–240.
- Pritchard, A. L. 1931. Taxonomic and life history studies of the ciscoes of Lake Ontario. Univ. Toronto Stud., Biol. Ser. 35, Pub. Ont. Fish. Res. Lab. 41:1–78.
- Richards, J. M., M. J. Hansen, C. R. Bronte, and S. P. Sitar. 2004. Recruitment dynamics of the 1971–1991 year-classes of lake trout in Michigan waters of Lake Superior. North American Journal of Fisheries Management 24:475–489.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191 of the Fisheries Research Board of Canada.
- Ridgway, M. S., D. A. Hurley, and K. A. Scott. 1990. Effects of winter temperature and predation on the abundance of alewife (*Alosa pseudoharengus*) in the Bay of

- Quinte, Lake Ontario. *Journal of Great Lakes Research* 16:11–20.
- Rothschild, B. J., and T. R. Osborn. 1988. Small-scale turbulence and plankton contact rates. *Journal of Plankton Research* 10:465–74.
- Rudstam, L. G., R. C. Lathrop, and S. R. Carpenter. 1993. The rise and fall of a dominant planktivore: direct and indirect effects on zooplankton. *Ecology* 74(2):303–319.
- Scott, W. B. 1951. Fluctuations in abundance of the Lake Erie cisco (*Leucichthys artedi*) population. *Contr. Royal Ontario Museum of Zoology* 32:1–41.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa, Ontario.
- Selgeby, J. H. 1982. Decline of lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin herring fishery, 1936–78. *Can. J. Fish. Aquat. Sci.* 39:554–563.
- Selgeby, J. H., and M. H. Hoff. 1996. Seasonal bathymetric distributions of 16 fishes in Lake Superior, 1958–75. National Biological Service, Biological Science Report 7. 14pp.
- Selgeby, J. H., W. R. MacCallum, and D. V. Swedberg. 1978. Predation by rainbow smelt (*Osmerus mordax*) on lake herring (*Coregonus artedii*) in western Lake Superior. *Journal of the Fisheries Research Board of Canada* 35:1457–1463.
- Selgeby, J. H., W. R. MacCallum, and M. H. Hoff. 1994. Rainbow smelt – larval lake herring interactions: competitors or casual acquaintances? U.S. Department of the Interior, National Biological Survey, Biological Report 25.
- Smith, O. B., and J. VanOosten. 1940. Tagging experiments with lake trout, whitefish,

- and other species of fish from Lake Michigan. Transactions of the American Fisheries Society 69:63–84.
- Smith, S. H. 1956. Life history of lake herring of Green Bay, Lake Michigan. U.S. Fish and Wildlife Service Bulletin 109(57):87–138.
- Smith, S. H. 1995. Early changes in the fish community of Lake Ontario. Great Lakes Fishery Commission, Technical Report No. 60, Ann Arbor, Michigan.
- Stockwell, J. D., M. P. Ebener, J. A. Black, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, S. T. Schram, D. R. Schreiner, M. J. Seider, S. P. Sitar, and D. L. Yule. 2009. A synthesis of cisco recovery in Lake Superior: implications for native fish rehabilitation in the laurentian Great Lakes. North American Journal of Fisheries Management 29:626–652.
- Swenson, W. A., and B. Heist. 1981. Optimizing yield from western Lake Superior commercial fisheries through smelt stock assessment. University of Wisconsin, Sea Grant Institute, Final Report R/LR-8, Madison, Wisconsin.
- SYSTAT. 2004. SYSTAT 11: Statistics. SYSTAT Software Inc., Richmond, California.
- Taylor, W. W., M. A. Smale, and M. H. Freeberg. 1987. Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 44(Supp. II):313–323.
- Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. Transactions of the American Fisheries Society 120:346–353.
- Toneys, M. L., and D. W. Coble. 1979. Size-related first winter mortality of freshwater



- fishes. Transactions of the American Fisheries Society 108:415–419.
- Walter, G., and W. J. Hoagman. 1975. A method for estimating year class strength from abundance data with application to the fishery of Green Bay, Lake Michigan. Transactions of the American Fisheries Society 104(2):245–255.
- Walters, C. J., M. Stocker, A. V. Tyler, and S. J. Westrheim. 1986. Interactions between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasii*) in the Hecate Strait, British Columbia. Can. J. Fish. Aquat. Sci. 43:830–837.
- Warlen, S. M. 1994. Spawning time and recruitment dynamics of larval Atlantic menhaden, *Brevoortia tyrannus*, into a North Carolina estuary. Fish. Bull. (U.S.) 92:420–433.
- Weiler, R. R. 1978. Chemistry of Lake Superior. Journal of Great Lakes Research 4:370–385.
- Wells, L., and A. L. McLain. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fishery Commission, Technical Report No. 20, Ann Arbor, Michigan.
- Yule, D., J. Stockwell, L. Evrard, G. Cholwek, K. Cullis, and J. Black. 2006a. Comparison of commercial landings of cisco to acoustic estimates of abundance in Thunder Bay and Black Bay, Ontario. U.S. Geological Survey Technical Report.
- Yule, D. L., J. D. Stockwell, G. A. Cholwek, L. M. Evrard, S. Schram, M. Seider, and M. Symbal. 2006b. Evaluation of methods to estimate lake herring spawner abundance in Lake Superior. Transactions of the American Fisheries Society 135(3):680–694.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey.