

Final Project Report to the Hudson River Foundation

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Bioenergetics and habitat requirements of overwintering young-of-the-year striped bass: implications for recruitment

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Final Report Summary

Chapter 1 reviews the literature on winter mortality of fishes. Winter mortality has been implicated in the regulation of populations of Atlantic croaker, steelhead trout and brown trout. In addition, one population of alewife suffered a major winter mortality episode in 1978, from which it has never recovered to previous levels. The most commonly examined aspect of winter mortality is its size-selective pattern. While a few studies have found no size-dependency of winter mortality, most studies have found that it selectively removes smaller individuals from the population. Size-selective winter mortality is believed to be responsible for the evolution of rapid growth rates among northern populations of Atlantic silversides. There has been less research devoted to determining the causes of winter mortality. While a number of causes have been documented, including starvation, predation, disease, osmotic and thermal stress, no framework has yet been developed for evaluating possible sources. Starvation has been cited as the likely source of mortality in most studies, but new research suggests that its importance may have been overemphasized. While most temperate fish suffer from a winter energy deficit, this deficit may not always be the direct cause of mortality. Several studies suggest that the various stresses associated with overwintering acting in concert may be responsible for mortality among wild fish. For example, a study on arctic char found that fish with depleted energy reserves were more vulnerable to pathogens, while another study found that infection by a parasite made bluegill sunfish more vulnerable to winter starvation. We also describe differences between the life histories and the habitats of freshwater, marine and estuarine fishes which may be important in the potential for overwintering.

The second chapter describes the size-selective pattern of overwintering mortality among young-of-the-year (YOY) striped bass in the Hudson River. This chapter was published as a paper in the *Canadian Journal of Fisheries and Aquatic Sciences* in the May 1998 issue. We examined size-distributions of YOY fish captured during five years of the New York Power Authority winter trawl survey. During the winter of 1990, YOY striped bass appeared to suffer

size-selective mortality, as the mean size of fish in the population increased while the variation in size of fish decreased. We conducted a laboratory experiment measuring growth rates of fish at winter temperatures to verify that the changes seen in the population could not be due to growth. In two other years (1986 and 1989), we found indications of size-selective winter mortality but the evidence was not as strong as in 1990. Two years (1987, 1988) showed no evidence of size-selective winter mortality. Winter mortality selecting against smaller individuals in some years, but not others, is a phenomenon which has not been observed in populations where winter mortality has been examined. In a separate analysis, we examined the relationship between the New York State Department of Environmental Conservation's index of abundance for age-1 striped bass and the index of abundance at age-0 and with indices of winter severity. We found that recruitment to age-1 was not strongly correlated with abundance at age-0. Rather, recruitment to age-1 was negatively correlated with measures of winter severity. In addition, recruitment was consistent with a model of winter severity modifying the relationship between yearclass strength at age-0 and strength at age-1. These results suggest that winter mortality may play an important role in the dynamics of the Hudson River population of striped bass affecting both the overall number of recruits as well as their size-distribution.

Our analysis of the seasonal energy dynamics of YOY Hudson River striped bass is presented in chapter 3. This chapter will be published in the January 2000 issue of the *Transactions of the American Fisheries Society*. We captured striped bass from the Hudson River through two winters, measuring lipid levels and caloric content to determine if winter mortality could be due to starvation. Compositional analyses of wild fish showed that YOY striped bass stored energy in the form of lipids prior to winter. During winter fish suffered from a net energy deficit, losing 7 and 16% of total body energy in the two winters examined. We also conducted a laboratory experiment, exposing fish to ambient conditions through winter. Compositional analyses of fish from the laboratory experiment suggested that starvation was probably not the primary source of mortality. Mortality was associated with low energy levels in unfed treatments, but not when food was provided daily. In neither treatment did starvation appear to be the ultimate cause of death, as wild fish were captured with energy levels lower than

those observed among mortalities in the experiment. These results suggest that starvation is not the only source of mortality that produces the observed size-selective patterns among YOY striped bass.

Chapter 4 describes the results of a five year study of the diets and consumption rates of YOY striped bass overwintering in the Hudson River Estuary. We first conducted laboratory experiments to determine rates of digestion at winter temperatures (2-11°C). Fish were acclimated to test temperature, force-fed a meal of *Crangon septimspinosa* corresponding to 2% of their body weight, and sacrificed to determine extent of digestion at specific time periods following ingestion. The evacuation rates we measured were among the lowest reported for any fish. The diets of wild fish were dominated by Gammarid amphipods and the shrimp species *Crangon septimspinosa*, *Paleomonetes pugio* and *Paleomonetes vulgaris*. Other less common prey were Mysid shrimp, annelids, oligochaetes and the fish species *Anchoa mitchilli*, *Menidia menidia* and *Ammodytes americanus*. We combined gut fullness levels of wild fish with evacuation rate information to estimate consumption rates of wild fish. Estimated consumption rates ranged from 0 to 0.30%/day. Gut fullness levels were not correlated with temperature or body size. On an individual level, maximum gut fullness levels decreased from 3% in fish with lipid levels below 3% body weight to empty ion fish with lipid levels in excess of 25% body weight. Mean gut fullnesses were also higher in early winter than in late winter. These results suggest that fish may increase feeding at times when the potential for energetic stress is high (early in winter and when lipid reserves become depleted).

The final chapter describes the results of experiments on the swimming ability of striped bass at low temperature and how swimming affects the energy budget of overwintering fish. Maximum swimming speeds of individual fish were measured in a Vogul-style flume at temperatures from 2-11°C. Swimming ability increased with body length at all sizes, but relative swimming speed (BL/sec) was independent of body length. Swimming speeds increased from 2.3BL/sec at 2°C to 3.0BL/sec at 5°C. Swimming speeds were 4.5BL/sec at both 8 and 11°C. Swimming speeds at the highest temperature may have been underestimated because of a limited

period of acclimation prior to measurement. Lipid levels of all fish used in the swimming trials were measured, but were not related to swimming ability. In a separate experiment, we measured the cost of activity among YOY striped bass at winter temperatures. Fish were forced to swim at 4 velocities ranging from 0 to 280mm/sec continuously for one month. At each velocity, one group (14 fish) was starved and the other group was allowed to feed to satiation once per day. Energy levels of all fish were measured after they died or at the end of the experiment. A sample of fish at the start of the experiment characterized initial energy levels. Mortality rates in the experiment increased dramatically with velocity, but feeding only resulted in higher survival at one velocity (180mm/sec). As expected, the cost of activity increased as velocity increased, as indicated by energy changes among unfed fish. Energy levels in fish from fed treatments were similar to levels at the start of the experiment, suggesting that fish ate enough to offset the costs of swimming, even at the highest velocity. However, fish at lower velocities did not consume enough to grow even though it appears that they had the ability to do so. These results suggest that YOY striped bass have considerable capacity to increase consumption rates when faced with energetic stress. The observation of a winter energy deficit among wild fish suggests that prey may be insufficient to meet consumption requirements, and in certain cases may lead to starvation.

Table of Contents

Summary.....	i
Table of contents.....	v
List of Figures.....	vii
List of Tables.....	viii
Chapter 1. Review of winter mortality.....	1-1
Introduction.....	1-2
Population level effects.....	1-4
Causes of mortality.....	1-10
Marine vs. freshwater habitats.....	1-18
Chapter 2. Winter mortality of YOY Hudson River striped bass: Size- dependent patterns and effects on recruitment.....	2-1
Introduction.....	2-2
Methods.....	2-4
Results.....	2-9
Discussion.....	2-12
Chapter 3. Seasonal energy dynamics of YOY Hudson River striped bass.....	3-1
Introduction.....	3-2
Methods.....	3-3
Results.....	3-9
Discussion.....	3-11
Chapter 4. Diet and consumption rates of overwintering YOY striped bass in the Hudson River.....	4-1
Introduction.....	4-1
Methods.....	4-3
Results.....	4-8

Table of contents (continued)

Discussion.....	4-10
Chapter 5. Activity costs of overwintering striped bass.....	5-1
Introduction.....	5-1
Methods.....	5-2
Results.....	5-7
Discussion.....	5-8

List of Figures

Pre- and post winter size-distributions of YOY striped bass.....	2-24
Mean length and CV of YOY striped bass through 5 winters.....	2-25
Growth rates (mm/day and %dry weight/day) of striped bass.....	2-26
Lengths of fish dying in lab experiment against date of death.....	2-27
Correlations between Age-1 survey and YOY survey and winter severity.....	2-28
Seasonal patterns in length, lipids and caloric content of YOY striped bass.....	3-24
Temperature record at Ambrose Channel through 2 winters.....	3-25
Condition indices of fish from laboratory experiment.....	3-26
Growth rates (kcal %/day) of YOY striped bass.....	3-27
Energy content of laboratory mortalities and wild striped bass.....	3-28
Gastric evacuation patterns of YOY striped bass.....	4-22
Consumption estimates of striped bass in 5 winters with temperatures.....	4-23
Gut fullness values of striped bass against lipid level and date.....	4-24
Design of flume for energy use experiment.....	5-17
Survival rates in flume experiment.....	5-18
Consumption rates in flume experiment.....	5-19
Energy use in flume experiment.....	5-20
Swimming speeds of YOY striped bass.....	5-21

List of Tables

Summary of winter characteristics, 1996-1990..... 2-29

Sampling dates of striped bass for lipid analyses..... 3-29

Diets of YOY striped bass in Hudson River through 5 winters..... 4-25

Chapter 1. Influence of winter mortality on recruitment and life history evolution of marine and estuarine fishes.

Abstract:

The effects of winter mortality on recruitment dynamics and life histories of temperate fish populations has received little attention, especially in marine and estuarine species. However, several studies have shown winter mortality to be a major determinant of year class strength and a strong selective force in the evolution of life history. Here we summarize current knowledge and provide a conceptual framework for evaluating the mechanisms of mortality, implications for recruitment, and differences between freshwater, marine, and estuarine systems. Winter mortality is often size-dependent, selecting against smaller individuals. Hence, young-of-the-year fish are most susceptible to winter mortality. Energy depletion is often assumed to be the cause of size-dependent winter mortality but the 'starvation hypothesis' has rarely been evaluated rigorously. Other possible mechanisms include predation and loss of homeostasis. These alternative explanations may be particularly applicable to marine and estuarine species. In marine systems, cold-water predators may migrate into the overwintering grounds of temperate species and the minimum temperatures experienced are likely to be substantially lower and more variable than in freshwater systems. Estuarine fishes are further exposed to variations in salinity, amplifying osmoregulatory stress. Interannual variability in winter severity combined with variation in the size and energy reserves of YOY fish could lead to highly varying and density-dependent rates of recruitment. Evidence suggests that long winters at high latitudes exert selection for increased growth rates and may ultimately determine species range, but episodic mortality due to rapid temperature declines may occur anywhere and influence recruitment.

Introduction

Episodic die-offs of fish and other marine animals due to unusually low winter temperatures, commonly referred to as winterkills, have been documented in the scientific literature for nearly a century (Horwood and Millner 1998). The most thoroughly documented winter mortality episodes have occurred in the North Sea (Lumby and Atkinson 1929; Simpson 1953). A prolonged cold snap in mid-winter 1962-63 with air temperatures up to 6°C below average for a two month period dropped coastal temperatures to below 0°C resulting in mass mortalities of fish, shellfish and benthic invertebrates (Crisp 1964; Woodhead 1964). Research and fishing vessels reported catching high numbers of dead conger eels (*Conger vulgaris*) in nearshore areas and soles (*Solea vulgaris*), dabs (*Pleuronectes limanda*), plaice (*P. platessa*) and whiting (*Gadus merlangus*) in offshore areas.

Despite the notion that winters are more severe in high latitude environments, these events have occurred throughout the oceans, from the North Sea to Texas and Florida. Early observations on winterkills at Solomons Island, Florida demonstrated two important aspects of winter mortality episodes; they predominantly affect fishes at the northern edge of their range and that these events vary dramatically in severity. Fish described as having tropical distributions were always or often affected during winterkills whereas only several 'temperate' species were ever killed during these events (Storey 1937). Storey and Gudger (1936) ranked nine winterkills between 1886 and 1934, in terms of the severity of damage to fish populations. They concluded that winterkill severity was dependent on several factors, including the minimum temperature, the rate of temperature decline and duration of the cold spell. Despite the recognition that winterkill events of varying magnitude occur with relative frequency there has still been little coordinated research on the impact of these events on population dynamics.

In the 1960's and 70's a broader understanding of the effects of winter began to appear, as the view that the low temperatures and reduced productivity present a chronic stress to overwintering fishes became established in the fish ecology literature (Reimers 1963; Bustard and Narver 1975). In addition, it was recognised that mortality rates during winter could fluctuate sufficiently to influence recruitment dynamics in some populations (Hunt 1969). The term 'winter mortality' now is commonly used to refer to all mortality occurring in winter, it

includes, but is not limited to the episodic mortality events. While most of the early documentation of winterkills occurred on marine populations, the majority of recent work on winter mortality and other aspects of the ecology of overwintering fishes has been conducted on freshwater species, in particular salmonids and centrarchids. This focus on freshwater fish is likely due to the feasibility of field work in freshwater systems, and the recognition that a lack of knowledge on overwintering fishes was hindering our ability to construct full life-history population models for otherwise well studied populations (Shuter et al. 1980). The ecology of most marine species was not known to the same extent as many freshwater species, so the role of winter in the ecology of individual species was not appreciated. Other problems such as the inability to define population boundaries, poor knowledge of wintering habitats, and the difficulty of working at sea in winter also likely contributed to the reduced pace of research on marine species.

More recently the role of winter in shaping the life histories of temperate fishes has become apparent. The threat of winter mortality has been suggested to play a dominant role in the evolution of growth rates (Conover 1990), age at maturity (Fox and Keast 1991), and spawning times (Trexler et al. 1992).

Most studies of winter mortality have not actually defined winter. This apparently semantic issue is particularly important when examining size-distributions for evidence of size-selective mortality. Any potential growth during the winter can bias analyses (Post and Evans 1989; Miller 1997), therefore it is important to restrict these analyses to periods of no growth. Based on this consideration, we suggest that investigators determine *a priori* the "overwintering period" during which populations are examined. For many species the "overwintering period" could be defined as the period of the year during which fish experience a net energy deficit due to physiological limitations at low temperatures or reduced prey production. For fishes which grow year-round (eg: cod), this definition would not apply, rather the "overwintering period" might be defined as the period when temperatures approach the species lethal limit. This view of winter explicitly reflects the notion that winter duration is not fixed, varying with thermal regime and species biology and provides a straightforward way of comparing winters of differing severity.

Based on the preceding definition of winter, in this review, we consider winter mortality

to be a seasonal phenomenon, directly or indirectly the result of low temperatures and primary production. Predation that occurs during the winter will not be considered, except in cases where exposure to winter conditions makes prey substantially more vulnerable to predators, or when anomalies in environmental conditions alter the distributions of predator and prey, allowing predatory interactions not observed under average conditions. In addition, we will not consider in detail mortality events that occur during the larval period of winter spawning fishes, as the factors that regulate larval survival are likely to be similar for fish spawning at all times of the year (temperature, salinity, and prey availability).

Where possible we will focus on juvenile, and in particular young-of-the-year fish for several reasons. As most studies have found mortality during the winter to select against smaller individuals in the population, or to have no size-selective pattern. If mortality is biased against smaller individuals, its greatest impacts will be observed when fish are the smallest (ie. youngest). Winter mortality that is not inherently related to body-size will also disproportionately affect YOY fish, as they will be encountering these conditions for the first time. In addition, winter mortality of juveniles will have a much greater impact on recruitment dynamics than will die-offs of older fish.

In this review we synthesize the research on winter mortality of fishes, focusing on the population level effects of winter mortality, the causes of mortality at the individual level, differences between marine and freshwater systems, and the life history consequences of winter mortality.

Population level effects

Recruitment Effects

Although winter mortality episodes have been documented for over a century, there have been relatively few attempts to assess their importance in determining recruitment to local fish populations. This is likely due to the evolution of ideas on factors affecting recruitment in fish populations. The vast majority of research effort has been placed on uncovering factors which regulate survival of larval fishes (Frank and Leggett 1994). The demonstration that small changes in growth and mortality rates of larval fish can generate tremendous variation in survival

(Houde 1987) supported the importance of the larval stage in determining recruitment. However, it is unlikely that recruitment to a population is determined at a single life stage. There is increasing evidence that variations in the mortality rate of juvenile fish can play an important role in recruitment regulation, and that all life history stages and the relationships between stages need be examined in attempting to explain recruitment variability (Bradford 1992; Myers and Cadigan 1993a,b; Bailey et al. 1996). Bradford and Campana (1992) demonstrated that our ability to predict abundance at later life stages increases after the larval stage. One reason for this may be that our estimates of juvenile abundances are more accurate than those of eggs and larvae, but it is also recognized that mortality of all life stages is variable, and assessing abundances at later life stages prevents more of this variability from altering recruitment levels after the assessment. We take the view that the first winter of life may be an important episode in the life history, regulating recruitment to the population. As most studies of the size-selective nature of winter mortality have suggested that small fish are more vulnerable than larger fish, it likely affects YOY fish most. In addition, fish in seasonal habitats are subject to a variety of environments through the year, each imposing different stresses which likely take their greatest toll during the first encounter. Finally, the severity of winter can vary significantly from year to year, and it is this variability that could determine winter mortality rates, and hence recruitment.

The first attempts to determine the effects of winter kills on fish populations involved estimating the number of fish of each species killed during such episodes (Gunter 1941; Moore 1976). Storey and Gudger (1936) examined accounts of winterkills over a 50 year period at Sanibel Island, Florida. Through these reports they ranked the nine winterkills in terms their effect on local fish populations by reports of the number of fish washing ashore following the events. Gunter (1941) observed reduced catches in a local fishery for several months following a cold spell which led to a winterkill. It was believed though that the reduced catches were due to fish moving away from the affected area, as anecdotal information suggested that catches returned to normal levels several months following the winterkill episode. However, these events may have more long-term consequences for some populations. A severe winterkill in Lake Ontario in 1978 dramatically reduced the abundance of alewife and white perch, from which neither population recovered for at least several years (Minns and Hurley 1986; Ridgway

et al. 1990).

The idea that winter mortality could regulate the recruitment of early life stages into the population was not adopted until much later. Hunt (1969) observed that juvenile survival in a population of brook trout was positively related to January temperatures. Two decades later, Seelbach (1987) demonstrated that return rates of steelhead trout (*Oncorhynchus mykiss*) were positively correlated with the severity of winter prior to smoltification, and others have documented interannual variability in overwinter survival of other salmonid populations (Schmidt et al. 1994; Quinn and Peterson 1996). These observations changed our views on winter mortality from an episodic phenomenon which may reduce the size of a local population to viewing winter as an annual occurrence during which mortality of juvenile fish may regulate future abundance. In addition to those freshwater examples, there have been several marine populations in which winter mortality of juveniles appears to play a role in regulating recruitment. Northern populations of Atlantic croaker appear to suffer recruitment failure following years when winter water temperatures fall below 3°C (Lankford 1997). We have observed that the abundance of age-1 striped bass from the Hudson River was more tightly correlated with the severity of winter which YOY fish experience than it was with the abundance of YOY fish (Hurst and Conover 1998).

A number of studies have attempted to correlate a broad suite of environmental variables with recruitment indices. Based on this approach, recruitment to the Bearing Sea population of walleye pollock appears correlated to winter temperatures at age-1 (Ohtani and Azumaya 1995; Quinn and Niebauer 1995). Other studies have compared recruitment time series to annual temperature changes, several of which have found higher recruitment of multiple species during warm years (Holmes and Henderson 1990; Zebdi and Collie 1995; Corten and van de Kamp 1996). While these studies did not set out to assess the role of winter in determining recruitment, correlations with environmental information may point to winter as an important regulator for some species (Friedland et al. 1993).

Size-dependence of winter mortality

Anderson (1988) assessed how size-dependent mortality among early life stages of fish fit into existing theories concerning major influence on recruitment. Although he did not address

winter mortality specifically, the size-dependent nature of mortality has been the most extensively studied aspect of overwintering ecology in recent years. The general pattern emerging is one in which larger fish tend to have greater survival rates than smaller individuals, but several exceptions have been reported (Sogard 1997). The question of size-dependence has been addressed with two general methods. The first involves laboratory experiments exposing fish to simulated winter conditions and comparing the survival rates of fish in different size-classes (also conducted with field enclosures). Alternatively, the size-distributions of natural populations have been followed through the winter to determine if certain size-classes become markedly less abundant following winter. The evidence gathered through these techniques and their strengths and weaknesses will be discussed below.

Evidence of size-dependent winter mortality in laboratory experiments comes from the overall survival rates of different size classes (Oliver et al. 1979; Malloy and Targett 1991; Thompson et al. 1991; Hurst and Conover 1998), and the relationship between the timing of mortality and body-size (Oliver et al. 1979; Post and Evans 1989; Johnson and Evans 1990; Hurst and Conover 1998). In all of these cases larger fish had higher survival than smaller fish. In at least one case (yellow perch; Post and Evans 1989) there was little apparent size-benefit to survival after 174 days of winter conditions, but small fish which died, did so before larger fish which died, indicating an interaction between body-size and exposure duration. The only case we are aware of in which size-dependent overwinter mortality favored survival of small fish over large fish is in Atlantic croaker. Small Atlantic croaker exposed to temperatures below 7°C survived longer than larger fish (Lankford 1997).

There have been no reported studies in which the size-dependence of winter mortality was evaluated in an experiment which did not yield differential survival among size classes. This lack of examples is likely due, at least in part, to under-reporting of such occurrences, as well as the selection of species and populations for which investigators had other indications that winter mortality would be acting in a selective manner. For example, Conover (1990) suggested that apparent growth rate differences between populations of striped bass, American shad and mummichog could represent an evolutionary response to size-dependent winter mortality. Such selective mortality was later confirmed for the Hudson River population of striped bass (Hurst

and Conover 1998).

By conducting laboratory experiments, the investigator has the ability to monitor and control environmental factors to which the fish are exposed. In addition, there is the potential design experiments which directly test hypotheses about factors which regulate winter survival. Initially, these experiments were limited to investigating the internal physiological constraints to winter survival (lower lethal temperatures, starvation), but more recent designs have attempted to assess risk of external mortality sources such as predation and disease susceptibility (Moles et al. 1997). When field populations are examined, all potentially important mortality factors are included, and artifacts of captivity are removed. However, the conditions that fish are exposed to may not represent average conditions, may vary substantially during the experiment, and may not be as closely monitored by the researcher.

Comparison of fish sizes from the beginning and end of winter has also suggested that mortality is size-dependent, selecting against smaller individuals (Tonys and Coble 1979; Henderson et al. 1988; Miranda and Hubbard 1994; Hurst and Conover 1998). A few studies have not found any size-dependent pattern of overwinter survival (Tonys and Coble 1979; Kohler et al. 1993), and there have been no reported observations of selection against larger fish in the field. Interpreting size-selective mortality from an increase in mean size of fish in the population should be done with caution, as it is based on the assumption that fish did not grow during the sampling interval. Post and Evans (1989) suggest the use of quantile plots to discriminate among various size-dependent patterns in growth and mortality, but this technique may not clearly rule out growth. The best approach, we feel is to experimentally determine the minimum temperature at which fish can maintain increases in length. At temperatures below this threshold, changes in the size-distribution can be more confidently attributed to selective removal (Hurst and Conover 1998). It has also been suggested that where possible samples be taken throughout the winter in order to reduce the probability of sampling error affecting the outcome or to determine the timing of mortality in winter (Miranda and Hubbard 1994; Hurst and Conover 1998). Unfortunately, in many cases the fish are unavailable for sampling due to ice cover (Post and Evans 1989, Tonys and Coble 1979), or migration patterns (Conover and Ross 1982). Several studies have used passive sampling gear to collect fish which have died or become

severely stressed due to exposure to winter conditions. McLean et al. (1985) found that larger fish became impinged at a power plant intake as temperatures declined, and that nearly all fish captured were young-of-the-year. Similarly Bodensteiner and Lewis (1992) found that few adults, but high numbers of juveniles of several species of fish were impinged at a dam on the Mississippi River when temperatures were lower. While this approach may provide a continuous sampling effort, a conclusion of size-selective mortality should be based on comparisons with independent collections describing the size-structure of the surviving population.

Interannual variability in the size-dependent pattern of winter mortality has been largely ignored to date, in part because most field studies have followed a population through one or two winters. We (Hurst and Conover 1998) examined the size-distributions of YOY striped bass in the Hudson River through five winters. Strong evidence of size-dependent winter mortality was observed in only one of five winters, with some evidence in two others. Size-dependent mortality was observed in one of two winters among juvenile coho salmon, and may have been related to differences in flow patterns (Quinn and Peterson 1996). Adams et al. (1982) found that the mean size of shad impinged at a power plant intake varied with temperature, and that differences in winter temperatures during the two years led to different sizes of shad being impinged. This represents a clear mechanism through which the size-selectivity of winter mortality may vary interannually. Even when investigators have information over multiple winters, it has not generally been examined with an eye toward looking for variability in the pattern of mortality. Kohler et al. (1993) examined winter mortality of largemouth bass in two Illinois reservoirs over three winters, and found evidence of a shift in mean size in one of the six cases. They attributed the one case of apparent size-selective mortality to sampling error, as opposed to interannual variability in the pattern of mortality, concluding that there was little evidence for size-dependent winter mortality. We suggest that although size-dependent winter mortality has been observed in a population, it may not be an annual occurrence in that population. Furthermore, this interannual variability has implications for applying results of studies, where it has been observed, as well as those where it was found to be absent in a short study.

Several models of population dynamics have been developed incorporating size-

dependent winter mortality (Johnson and Evans 1990; Shuter and Post 1990). These models assume that winter mortality is due to starvation, inherently selecting against smaller fish, and all variation results from temperature regime differences. However, for most species, the causes of winter mortality are still unknown (including the species modeled above) and for white perch there is a suggestion that mortality has two sources with unique size-selective patterns (Johnson and Evans 1996). By assuming that all winter mortality is due to starvation, and that starvation occurs when fish have lost a certain proportion of their body weight, these models also do not take into account observed interannual differences in body size and levels of energy storage fish have to rely upon for overwintering (Hurst et al. in press). While these models have proven useful for predicting species ranges, by incorporating information on the size-dependence of all sources of mortality they may better explain patterns of recruitment in specific populations.

Sources of mortality

Knowledge of the causes of mortality is essential in generating predictive models of recruitment incorporating the interannual variation of the impacts of winter mortality. While there is a substantial literature describing the physiological effects of low temperature on fish, these studies have not, in general, been linked to field observations of mortality among overwintering fishes. Hence, the cause of winter mortality in many populations where it has been documented remains unknown. Most laboratory work has focused on the acute response of fish to low temperatures, while most field work has focused on the potential for starvation among overwintering fishes. In addition to these causes, we will discuss the less studied sources of winter mortality of predation and disease. Given that the latter mortality sources are not exclusive to winter, we only consider aspects of them directly related to the low temperatures or reduced production associated with overwintering. Hypoxia rarely occurs during winter in marine or estuarine systems, and will not be discussed here. At the end of this section we describe the importance of interrelationships among stressors which co-occur during winter.

Starvation

The "starvation hypothesis" has most often been invoked as the cause of mortality among temperate fishes, especially in cases where mortality selects against smaller individuals. There

are several lines of evidence which suggest that starvation as an important source of winter mortality. Rates of primary and secondary production are greatly reduced due to the decreased temperatures and light levels in winter (Cushing 1975). Because temperature plays a dominant role in regulating consumption rate, many species annually face periods during which feeding is dramatically reduced or ceases completely. While metabolism also decreases with temperature, it cannot reach zero, and at some point metabolic rate will exceed energy intake from feeding, forcing fish into a net energy deficit (also called negative scope for growth). Such a pattern of declining energy levels through winter has been observed in many temperate fish species, freshwater and marine (Craig 1977; Guillemot et al. 1985; Cunjak 1988; Hurst et al. 2000). Starvation as the source of mortality fits well with the observation that winter mortality often tends to select against smaller individuals, as smaller fish tend to have less energy reserves than larger fish, and because of the allometry of metabolic rate, they use up those reserves more rapidly. Further implicating starvation as an important source of winter mortality, Schultz and Conover (1997) have found that northern populations of Atlantic silversides deposit greater energy reserves in autumn than do fish from southern populations. This genetically based latitudinal pattern in energy storage is believed to be an adaptive response to the greater threat of winter starvation at high latitudes.

Given the strong theoretical basis for expecting winter starvation to be important to overwintering temperate fishes, there is relatively little direct support for the hypothesis. The most convincing evidence of winter starvation of wild fish comes from observations during a spring mortality episode of gizzard shad. Comparing the energetic status of dead or severely stressed fish to unaffected fish during the episode, Adams et al. (1985) found that stressed fish had significantly lower condition factors and lipid levels than unaffected fish. They estimated that at least 10% of the population died from starvation as a result of unusual winter and spring conditions.

Laboratory experiments on smallmouth bass and Colorado squawfish have shown that fish dying during the winter had less body energy than surviving fish (Oliver et al. 1979; Thompson et al. 1991). These results were obtained for fish which were not fed during the overwintering period; fed Colorado squawfish depleted energy reserves during the experiment,

but had negligible mortality rates (Thompson et al. 1991). In both of these experiments and others examining winter mortality patterns, fish are often not fed during the overwintering period under the assumption that temperate fish do not generally feed during winter. As direct estimates of consumption among overwintering fish are rare, feeding regime in experimental trials should be carefully considered, even for species which are generally believed to "starve" through the winter. Schultz et al. (in press) observed that energy levels among wild Atlantic silversides more closely resembled unfed laboratory treatments than fed treatments. The reduced activity related metabolic expenditures of laboratory fish appeared to offset the effect of withholding food among starved fish. Laboratory fish offered food depleted energy more slowly than wild fish.

In addition, recent work suggests that the view that temperature alone drives consumption rates with starvation being unavoidable at low temperatures may be too simplistic. Work on Atlantic salmon has shown that the low consumption rates of overwintering fish are self-imposed and reversible; fish increased consumption rates when levels of internal stores became depleted or insufficient to meet metabolic requirements (Metcalf and Thorpe 1992; Bull et al. 1996). This cold water species has been observed to suffer a winter energy deficit, despite being physiologically capable of growth at winter temperatures (Gardiner and Geddes 1980). Whether other species display similar control of their energy budget has yet to be examined in detail. Many temperate and warm water fishes have been observed with food in their stomachs at temperatures near their lower lethal limit including Atlantic silversides, smelt, channel catfish, largemouth bass, and striped bass (Warkentine and Rach 1989; Chilton et al. 1984; Foltz and Norden 1977; Adams et al. 1982; Hurst unpublished observations), but the importance of this consumption to preventing starvation has not been determined. The reduced metabolic requirements and potentially plastic consumption rates of overwintering fish could indicate that starvation may be avoided with small amounts of energy consumed to supplement internal energy stores. If minimal levels of consumption provide protection for most fish from starvation, food availability may be the determining factor in the survival of overwintering fish facing starvation.

Lethal exposure

Direct physiological effects due to exposure to low temperatures limiting the ability of fish to maintain homeostasis at both the organismal and cellular level can also be responsible for

mortality of overwintering fishes. These direct effects of low temperature are likely to be the mechanism of mortality in winterkills of multiple species common in coastal ocean areas (ex: Storey 1936; Gunter and Hildebrand 1951; Holt and Holt 1983). It is unlikely that starvation would affect a wide range of species on similar time scales, oxygen is not limiting in oceanic environments, and the observation of dead fish at the surface or along shorelines means that they are not being preyed upon by less sensitive species.

Exposure to low temperature affects the central nervous system by reducing the effectiveness of synapse transmission and disrupting ionic regulation (Cossins and Bowler 1987). The maintenance of an ionic gradient across a membrane is dependent upon the balance of diffusion down the gradient and active pumping against the diffusional gradient. Down-gradient diffusion is relatively insensitive to temperature, whereas maintenance of the gradient with ion pumps is dependent upon ATP production which declines with temperature, (generally having Q_{10} values in the range of 2-4) (Hochachka 1988). The temperature dependence of ion pumping systems results in the inability of fish to maintain osmotic balance when exposed to temperatures below those for which the ionic balance is optimized. Schwartzbaum et al. (1991) have shown that fish acclimated to low temperatures can maintain ionic balance by increasing the activity of ion pumps (increase Na^+ and K^+ ATPase activity) or by reducing membrane permeability to ions (slowing down-gradient diffusion).

Due to the allometry between gill surface area and body size, small fish with high gill surface areas will be at higher risk of mortality than larger fish from ionic imbalance when ion regulation breaks down at low temperatures. As the need for ionic regulation is common to both freshwater and marine species, differences between the groups is likely to be the result of physical differences in the environment, described below. As fish plasma freezes at temperatures of -0.5 to -1.0°C , in the absence of antifreeze agents, marine fish residing in waters below 0°C face extreme risk from the formation of ice crystals within the body (Davies et al. 1988). Many studies have reported that concentrations of ions in the blood approach those in the environment as temperatures approach the lower lethal limits (Woodhead and Woodhead 1959; Stanley and Colby 1971; Belkovskiy et al. 1991) supporting the hypothesis of osmoregulatory dysfunction as the cause of death at low temperatures. Conversely, the increased concentration of solutes in the

