Journal of Fish Biology (2007) **71,** 315–345
doi:10.1111/j.1095-8649.2007.01596.x, available online at http://www.blackwell-synergy.com

REVIEW PAPER

Causes and consequences of winter mortality in fishes

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(Received 22 March 2007, Accepted 14 May 2007)

Winter mortality has been documented in a large number of freshwater fish populations, and a smaller, but increasing, number of marine and estuarine fishes. The impacted populations include a number of important North American and European resource species, yet the sources of winter mortality remain unidentified in most populations where it has been documented. Among the potential sources, thermal stress and starvation have received the most research attention. Other sources including predation and pathogens have significant impacts but have received insufficient attention to date. Designs of more recent laboratory experiments have reflected recognition of the potential for interactions among these co-occurring stressors.

Geographic patterns in winter mortality are, in some cases, linked to latitudinal clines in winter severity and variability. However, for many freshwater species in particular, the effects of local community structure (predators and prey) may overwhelm latitudinal patterns. Marine (and estuarine) systems differ from freshwater systems in several aspects important to overwintering fishes, the most important being the lack of isolating barriers in the ocean. While open population boundaries allow fish to adopt migration strategies minimizing exposure to thermal stresses, they may retard rates of evolution to local environments. Geographic patterns in the occurrence and causes of winter mortality are ultimately determined by the interaction of regional and local factors.

Winter mortality impacts population dynamics through episodic depressions in stock size and regulation of annual cohort strength. While the former tends to act in a density-independent manner, the latter can be density dependent, as most sources of mortality tend to select against the smallest members of the cohort and population. Most stock assessment and management regimes have yet to explicitly incorporate the variability in winter mortality. Potential management responses include postponement of cohort evaluation (to after first winter of life), harvest restrictions following mortality events and habitat enhancement.

Future research should place more emphasis on the ecological aspects of winter mortality including the influences of food-web structure on starvation and predation. Beyond illuminating an understudied life-history phase, studies of overwintering ecology are integral to contemporary issues in fisheries ecology including ecosystem management, habitat evaluation, and impacts of climate change.

Key words: predation; recruitment; size-selective mortality; starvation; thermal stress; winter mortality.

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INTRODUCTION AND HISTORY OF DOCUMENTATION

Episodic die-offs of fish and other marine animals due to unusually low winter temperatures, referred to as 'winterkills', have been documented in the scientific literature for over a century (Storey & Gudger, 1936; Horwood & Millner, 1998; Hoag, 2003). Several of the most thoroughly documented events have occurred in the North Sea (Lumby & Atkinson, 1929; Simpson, 1953). For example, a prolonged cold snap in mid-winter 1962–1963, when air temperatures were as much as 6° C below normal for a 2 month period dropped coastal water temperatures to below 0° C, resulting in mass mortalities of fish, shellfish and benthic invertebrates (Crisp, 1964; Woodhead, 1964*b*). Research and fishing vessels reported catching high numbers of dead European conger *Conger conger* L. in nearshore areas and common sole *Solea vulgaris* L., dab *Limanda limanda* L., plaice *Pleuronectes platessa* L. and whiting *Merlangius merlangus* L. in offshore waters.

However, winterkills are not limited to high-latitude environments where severe winter conditions are not unexpected. They occur throughout the oceans and in a wide variety of freshwater lakes, rivers and reservoirs. Early observations of winterkills at Sanibel Island, Florida (Storey, 1937) demonstrated two important aspects of winter mortality episodes: they predominantly affect fishes at the northern edge of their range and they vary dramatically in severity. The link between winter severity and juvenile survival was first made in California brown trout *Salmo trutta* L. (Needham *et al.*, 1945). Despite the recognition that winterkill events of varying magnitude occur with moderate frequency, there has still been little coordinated research on the impact of these events on population dynamics, a deficiency first pointed out by Hubbs & Troutman (1935).

In the 1960s and 1970s, the view that low temperatures and reduced productivity present a chronic stress to overwintering fishes became firmly established in the literature (Reimers, 1963; Bustard & Narver, 1975). In addition, it was recognized that winter mortality rates are sufficiently variable to influence recruitment dynamics in some populations (Hunt, 1969). The observation that winter mortality frequently removes the smallest members of a population (Henderson *et al.*, 1988; Post & Evans, 1989) provided a theoretical framework under which examination of overwintering ecology could be applied to the recruitment dynamics of specific populations, stimulating the pace of research through the 1990s. It also opened the way for exploration of winter's role in shaping the life histories of temperate fishes. The threat of winter mortality has since been indicated to play a dominant role in the evolution of growth rates (Conover, 1992), age at maturity (Fox & Keast, 1991) and spawning times (Conover, 1992; Trexler *et al.*, 1992).

While the early documentation of winterkills was based on observations of marine populations, more recent work on the ecology and mortality patterns of overwintering fishes has largely focused on freshwater species, in particular, salmonids and centrarchids. This focus on freshwater species is likely due to the recognition that insufficient knowledge of the overwintering phase was hindering the ability to construct full life-history models for otherwise well-studied populations (Shuter *et al.*, 1980) as well as the practicality of study (the accessibility of wild populations and familiarity with culture techniques). Problems such as the inability to define population boundaries and poor knowledge of wintering habitats have contributed to the reduced pace of research on marine and estuarine species.

The term 'winter mortality' is now commonly used to refer to all mortality occurring in winter, including, but not limited to episodic mass mortality events ('winterkills'). Unlike the ontogenetically defined 'larval-phase', 'overwintering' is an environmentally defined life stage. Consideration of winter as a separate 'life stage' is based upon the prevailing conditions of low temperatures and reduced productivity that impact most, if not all, aspects of fish physiology and community interactions. However, it is recognized that there are likely to be interactions between environmental variation and ontogeny that determine the impacts of winter. Where possible, this review focuses on juvenile and, in particular, young-of-the-year (age-0) fish due to their generally greater vulnerability to winter stressors and the potential to influence recruitment.

Improved understanding of overwinter mortality will advance the understanding of both life-history evolution and the dynamics of fishery resources. This review synthesizes the research on winter mortality of fishes and organizes it into three major areas: the causes of mortality at the individual level, geographic patterns (including differences between marine and freshwater systems), and the population level effects of winter mortality. It concludes by identifying areas in need of additional research attention.

SOURCES OF MORTALITY

An understanding of the causes of mortality is essential in generating predictive models of population dynamics that account for interannual variation in winter survival. However, where winter mortality has been documented, its causes frequently remain unknown. A retrospective analysis of potential explanations for the winter 1992–1993 collapse of a Pacific herring *Clupea pallasi* (Valenciennes) population highlights a number of difficulties in assigning causes to such events, including insufficient data on biotic and abiotic environmental conditions and evidence supporting multiple or interacting factors (Pearson *et al.*, 1999). Acute thermal stress and starvation have traditionally been assumed responsible for mortalities among overwintering fish, but evidence is accumulating that predation and disease may be significant factors in many populations (Fig. 1). Two other sources, winter hypoxia and physical disturbance from ice flows can be significant sources of mortality in smaller ice-covered ponds and rivers, respectively. The only documented marine case of reduced winter oxygen concentrations involves a large population of Atlantic herring *Clupea harengus* L. overwintering in a Norwegian fjord with restricted water exchange (Dommasnes *et al.*, 1994). Being limited to narrow sets of circumstances and having been more thoroughly discussed in the literature, hypoxia and physical disturbance will not be discussed in detail here (for reviews see Greenbank, 1945; Agbeti & Smol, 1995; Cunjak *et al.*, 1998; Fang & Stefan, 2000; Huusko *et al.*, 2007).

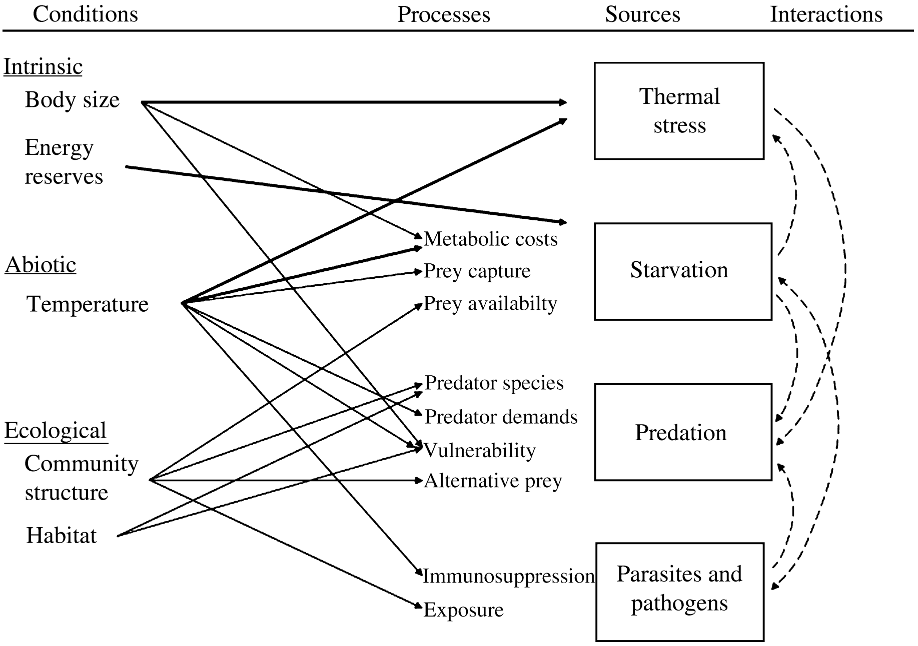


FIG. 1. Schematic representation of factors influencing winter mortality in fishes. Primary Sources of winter mortality (in boxes) are influenced by environmental Conditions (intrinsic, abiotic and ecological) directly or indirectly (indicated by Processes). Heavy lines indicate relationships having received the most research attention to date. Likely Interactions between mortality sources are indicated by dashed lines.

THERMAL STRESS

The direct effects of low-temperature stress appear generally responsible for the episodic mass mortalities in coastal oceans (Storey, 1937; Gunter & Hildebrand, 1951; Holt & Holt, 1983) as other mortality sources are unlikely to affect a wide range of species on similar time scales. Despite clear understanding of the physiological mechanisms involved and the relationship between low-temperature tolerance and risk of winter mortality, measurements of this trait are available for a relatively small number of species (compared to measures of upper lethal temperatures, Beitinger *et al.*, 2000).

Fishes are generally intolerant of freezing, placing a rigid physiological constraint on the evolution of low-temperature tolerance. Among temperate fishes, there is a common assumption that low-temperature tolerance is near 0° C based on the freezing point of blood plasma (−0·5 to −1·0° C). The presence of antifreeze agents in some marine fishes can depress plasma freezing points and lower lethal temperatures to slightly below that of seawater (−1·7° C) (Davies *et al.*, 1988; Goddard & Fletcher, 1994), although the risk of body fluids freezing is significantly increased by direct contact with ice crystals in the water column, a phenomenon know as 'ice crystal seeding' (Templeman, 1965).

For fishes with lower lethal temperatures above the freezing point, the physiological source of mortality is an inability to maintain homeostasis at the cellular and organismal level. The maintenance of ionic gradients across a membrane is dependent upon the balance of down-gradient diffusion, largely temperature-independent and active pumping against the gradient (Hochachka, 1988). The temperature dependence of ion-pumping systems results in the inability of fish to maintain osmotic balance when exposed to low temperatures. Although fish acclimated to low temperatures can compensate by increasing the activity of ion pumps (increase Na^+ and K^+ ATPase activity) or by reducing membrane permeability to ions (slowing down-gradient diffusion) (Schwartzbaum *et al.*, 1991), this compensation is generally incomplete. Many studies have reported that concentrations of ions in the blood approach those in the environment as temperatures approach the lower lethal limits (Woodhead & Woodhead, 1959; Stanley & Colby, 1971; Belkovskiy *et al.*, 1991) supporting the hypothesis that osmoregulatory dysfunction causes death at low temperatures. At the cellular level, inability to maintain ionic gradients affects the central nervous system (and hence all physiological functions) by reducing the effectiveness of synapse transmission (Cossins & Bowler, 1987).

Several authors have suggested, based on allometric relationships between gill surface and body mass, that small fish would be more vulnerable to low temperature-induced osmotic stress than larger fish (Johnson & Evans, 1996). Such a pattern was observed across a wide size range in golden grey mullet *Liza aurata* (Risso) (Shekk *et al.*, 1990), but a number of experiments have observed no size-based pattern of osmotic stress within cohorts (Schultz *et al.*, 1998; Hurst & Conover, 2002; McCollum *et al.*, 2003). Conversely, observations of higher survival of small fish in laboratory experiments led Lankford & Targett (2001) to suggest that higher protein turnover rates among small fish facilitates acclimation to, and tolerance of low-temperature stress.

STARVATION

Starvation has most often been invoked as the cause of mortality among temperate fishes. Several lines of evidence support this hypothesis. Rates of primary and secondary production are greatly reduced in winter due to decreased temperatures and light levels (Cushing, 1975). Because temperature plays a dominant role in regulating consumption rate, many temperate species endure a period of reduced or suspended feeding. While metabolism also decreases with temperature, at some point metabolic expenditures exceed energy intake resulting in an energy deficit (also called negative scope for growth). Declining energy levels through winter have been observed in many temperate fish species (Craig, 1977; Guillemot *et al.*, 1985; Cunjak, 1988*b*). Starvation is consistent with the observed size-selectivity of overwintering mortality: smaller fish tend to have lower energy reserves than larger fish and use up those reserves more rapidly due to the allometry of metabolic rate.

Although there is a strong theoretical basis for expecting winter starvation to be important to overwintering temperate fishes, direct support for this hypothesis is less convincing. The most convincing evidence of winter starvation in a wild population comes from observations during an early-spring mortality episode of gizzard shad *Dorosoma cepedianum* (Lesueur). Comparing the energetic status of dead and severely stressed fish to unaffected fish during the event, 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 with Colorado pikeminnow *Ptychocheilus lucius* (Girard) found that fish dying during the winter had lower somatic energy reserves than surviving fish (Thompson *et al.*, 1991). However, these results were obtained for unfed fish; fed fish did deplete energy reserves, but had significantly lower mortality rates. In these experiments and others obtaining similar results (Oliver *et al.*, 1979; Schultz *et al.*, 1998), food was withheld under the assumption that temperate fish do not generally feed during winter. However, many temperate and warm water fishes continue to feed at temperatures near their lower lethal limit (Foltz & Norden, 1977; Adams *et al.*, 1982; Chilton *et al.*, 1984; Warkentine & Rachlin, 1989). As direct estimates of consumption among overwintering fish are rare, feeding regime in experimental trials should be carefully considered, even for those species generally believed to 'starve' through the winter.

Complicating this picture is evidence that the energy budgets of overwintering fish are more dynamic than previously assumed, with low consumption rates being self-imposed and reversible. Atlantic salmon *Salmo salar* L. increased consumption when levels of internal stores became depleted or insufficient to meet metabolic requirements (Metcalfe & Thorpe, 1992; Bull *et al.*, 1996). Atlantic salmon display a winter energy deficit, despite being physiologically capable of growth at low temperatures (Gardiner & Geddes, 1980). Evidence that such a compensatory response occurs among wild fish is limited to juvenile striped bass *Morone saxatilis* (Walbaum) (Hurst & Conover, 2001). If other species maintain sufficient physiological capacity to delay or prevent starvation with compensatory feeding, it would suggest that prey availability may be as important as thermal regime in determining the risk of overwinter starvation (Ludsin & DeVries, 1997; Garvey *et al.*, 1998).

PREDATION

While most fish species are subject to predation risk year-round, there are circumstances under which the risk is greater in winter than at other times of the year. The reduced swimming ability of fishes at low temperatures (Bennett, 1990; Guderley & Blier, 1988) can make them more vulnerable to predators, especially if the predators are less sensitive to low temperatures. Distributional overlap of fish from different thermal guilds would enhance this risk (for example exposing temperate prey to active cold-water predators). Woodhead (1964*a*,*b*) reported that during the exceptionally cold winter of 1963, sole were far more common in the stomachs of Atlantic cod *Gadus morhua* L. than in previous winters. These observations (and trawl catches) suggested that at low temperatures, sole are sluggish and do not exhibit the normal behaviour of burrowing during the day, making them more vulnerable to cod predation. Similarly, McLean *et al.* (1985) suggested that the reduced schooling behaviour of threadfin shad *Dorosoma petenense* (Günther) below 12° C increases vulnerability to predation by sauger *Stizostedion canadense* (Smith) and skipjack herring *Alosa chrysochloris* (Rafinesque). As low temperatures increase the metabolic requirements of endothermic avian and mammalian predators, they may represent a substantial, but unevaluated, risk to some overwintering fishes (Winship *et al.*, 2002).

Seasonal migrations may expose fish to a varying suite of predators. For example, many estuarine fishes migrate offshore in winter, where large-bodied predators may be more common (Able & Fahay, 1998). Variation in thermal regime may determine the degree of distributional overlap between predator and prey in marine systems. Murawski (1993) found that species in the north-west Atlantic varied in their distributional response to interannual temperature variation, with small-bodied prey species displaying greater shifts than larger-bodied predators. Although this analysis was based on spring and autumn distributions, similar patterns are likely to exist in winter. Several studies suggest that warm winters allow fish to occupy areas unsuitable during colder winters (Wyllie Echeverria, 1995; Corten & van de Kamp, 1996; Wyllie-Echeverria & Wooster, 1998), but the implications of these movements have not yet been resolved for any specific predator–prey pair.

DISEASE AND PARASITES

Several studies have suggested that pathogens may play an important role in determining survival of overwintering fishes. Horning & Pearson (1973) found that smallmouth bass *Micropterus dolomieui* (Lacepède) exposed to low temperatures died as a result of fungal infection but were unaffected at higher temperatures. Gilthead sea bream *Sparus aurata* L. in aquaculture settings suffer from a condition known as 'winter syndrome' in which cultured fish die from *Pseudomonas anguilliseptica* infection during cold periods (Doménech *et al.*, 1997). At low temperatures, sea bream appear to suffer from a general immunosuppression, making them vulnerable to a wide variety of pathogens (Tort *et al.*, 1998). An increased susceptibility to pathogens has similarly been documented in overwintering channel catfish *Ictalurus punctatus* (Rafinesque) (Bly & Clem, 1991; Bly *et al.*, 1993). While studies of disease mortality in laboratory and cultured stocks are difficult to apply to natural populations, the reduced ability of fish to fend off infections may be a common result of the energetic and thermal stresses of overwintering.

Parasites may also have more severe effects on host survival at low temperatures (Doménech *et al.*, 1997). A thorough study of the effects of a trematode parasite *Uvulifer amblopitis* on juvenile bluegill *Lepomis macrochirus* (Rafinesque) demonstrated that parasite infection substantially reduced overwinter survival (Lemly & Esch, 1984). The parasite increased metabolic rate in the host, depleting energy reserves. When infection occurred prior to the overwintering period, parasitized fish had insufficient energy reserves to meet metabolic needs. Overwinter survival was directly related to the level of parasitism with complete mortality among the most heavily parasitized individuals. Similar patterns of mortality among parasitized hosts have been observed in several other species. In both sheepshead minnow *Cyprinodon variegatus* (Lacepède) and Atlantic salmon, the abundance of heavily parasitized individuals decreased during winter (Cunjak & McGladdery, 1991; Coleman & Travis, 1998) suggesting mortality of fish with the highest levels of parasitism. In both of these cases, as in bluegills, mortality appeared to be an indirect result of increased metabolic requirements in parasitized individuals.

COMBINED FACTORS

In several species, there is evidence to support multiple mechanisms of winter mortality. Largemouth bass *Micropterus salmoides* (Lacepède) represent one such example (described in Miranda and Hubbard, 1994*a*,*b*). The higher mortality rates and rapid depletion of energy reserves of small fish compared to larger fish indicate starvation as the source of mortality. However, in a caging study, survival rates of small fish were high (>75%) in the absence of predators and when provided with submerged cover suggesting predation as the primary source of mortality. Evidence supporting both the starvation and lethal exposure hypotheses has been found in the Atlantic silversides (Schultz *et al.*, 1998; Schultz & Conover, 1999) and striped bass (Hurst and Conover, 2002 & 2003).

The lack of evidence pointing to a singular cause of winter mortality also results from the fact that the mortality agent or primary stressor may differ among years, between times of the overwintering period or among individuals within a population (Fig. 2). In addition, because most laboratory and field

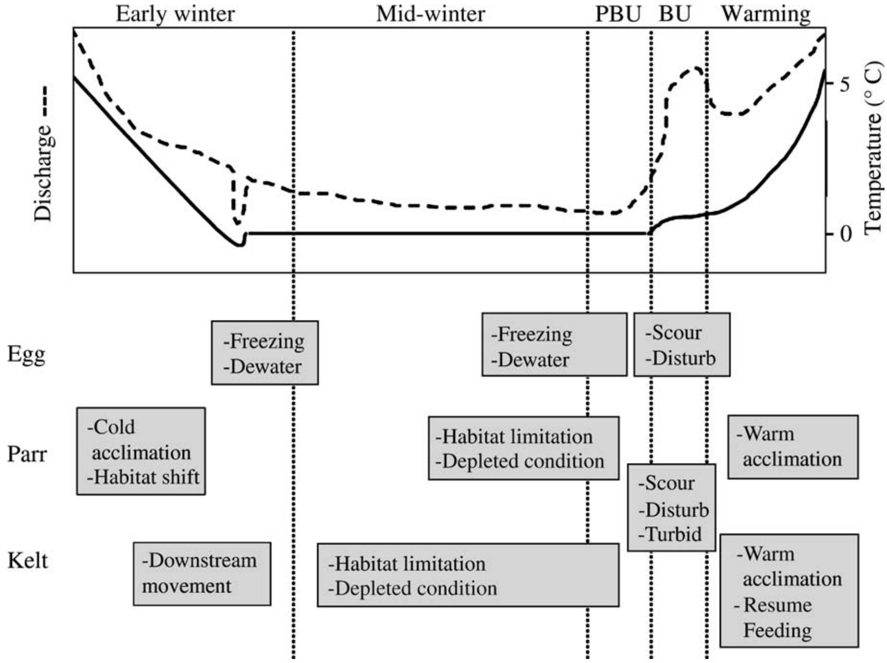


FIG. 2. Conceptual representation of biophysical phases of winter depicting generalized pattern of discharge and water temperature in relation to freshwater life stages (egg, parr, kelt) of Atlantic salmon (*Salmo salar*) in ice-covered rivers. PBU = pre-break-up and BU = break-up. Sizes and placement of boxes corresponds to timing and duration of the described events. Abbreviations: scour = ice scour; disturb = disturbance; dewater = dewatering; turbid = elevated turbidity. Reproduced with permission from Cunjak *et al.* (1998, Fig. 1).

studies have focused on evaluating a single source of mortality potentially important interactions among stressors have likely been overlooked. Johnson & Evans (1996) attempted to discriminate among possible causes of mortality among overwintering white perch *Morone americana* (Gmelin) in earlier laboratory experiments (Johnson & Evans, 1990, 1991) by comparing observed relationships between body size and mortality rates to theoretically derived relationships based on the allometries of energy storage, metabolic rate and gill surface area. The results suggested starvation as the cause at 4·0° C but osmoregulatory failure at 2·5° C. While this approach can offer some insight, it does not consider possible interactions between stressors. For example, low-temperature stress may elevate metabolism above levels predicted from experiments at higher temperatures, hence shortening the time to starvation (Hoss *et al.*, 1988).

The most thorough attempt to examine interactions between potential mortality sources in an overwintering fish was conducted on coho salmon *Oncorhynchus kisutch* (Walbaum) by Moles *et al.* (1997). They reared YOY fish at three representative winter temperatures (0·2, 2·0, 4·0° C) for 150 days under both fed and starved conditions. After 150 days, fish from each group were subject to tests of salinity tolerance, critical swimming speed and disease resistance. In general, all aspects of fitness appeared compromised among unfed fish compared to fed fish, but contrary to expectations, there was little effect of overwintering temperature. Data from this type of experiment can be used to estimate the risk of various mortality sources among wild fish by comparing the condition levels of wild fish through the winter to those in the laboratory experiments.

GEOGRAPHIC PATTERNS

The occurrence of winter mortality is being documented in an ever-increasing number of fish populations. However, it should not be expected in each new population examined. Both its occurrence and its causes in different populations are likely to have discernable geographic patterns. Unfortunately, few species have been studied over a broad enough geographic range to be instructive in this regard. The most widely held belief is that winter mortality will be most severe at the northern limits of a species' distribution. While this pattern is almost certain to hold true for some causes in most species, the degree of local adaptation and food-web structure are likely to be as important as thermal regime in explaining patterns of winter mortality among temperate fishes. In the following sections, the Atlantic silverside *Menidia menidia* L. and largemouth bass are used to illustrate such patterns of latitudinal and localized effects.

DIFFERENCES BETWEEN FRESHWATER AND MARINE SYSTEMS

There are differences between marine and freshwater systems that have significant influences on the ecology and survival of overwintering fishes. However, these do not appear directly related to the physiology of osmoregulation in different osmotic environments. Fish in both environments are faced with the problem of having to overcome the diffusive processes between their blood and the environment with the breakdown of ion transport systems at low temperatures having equally lethal implications (see above – Thermal stress). Rather, the differences between marine and freshwater systems as related to the risk of winter mortality are related to thermal characteristics and the scales of habitat variation and population structure.

The lack of a density maximum of salt water allows the entire water column to cool uniformly, and bottom waters can reach temperatures as low as –1·5° C when wind aids in mixing the water column (Koutitonsky & Bugden, 1991). Streams resemble oceans in that water temperatures in winter may approach 0° C, with water movement retarding ice formation, allowing continued cooling of water through contact with overlying air. Hence, while high latitude populations of lacustrine fish may not be exposed to temperatures substantially below 4° C, stream and coastal marine fishes are often exposed to freezing temperatures. At lower latitudes, oceanic waters are often warmer than lakes, but the systems may display similar temperature patterns with annual minima being of short duration, associated with the passage of low-pressure systems.

The potential for migration to favourable overwintering habitats represents a major difference between freshwater and marine systems. Although small gradients in temperature exist in freshwater systems, the range of temperatures available in an isolated lake is narrower than in the ocean. Riverine fish may have some opportunity to move into connected lakes or local thermal refuges for overwintering (West *et al.*, 1992). Marine systems that lack geographic barriers to migration allow fish to migrate to avoid cold temperatures. Many marine fish migrate from the coastal zone to warmer offshore areas, while others avoid the stress of low temperatures by migrating to warmer waters at lower latitudes (Able & Fahay, 1998). While alleviating thermal stress, these migrations can incur significant energetic costs and may expose fish to a new predator fields.

In contrast to the reduced levels of large-scale thermal variation, inland waters may offer a wider variety of microhabitats utilized for overwintering. Freshwater fish display small-scale winter habitat selection based on avoiding low oxygen levels, minimizing energy expenditures, taking advantage of small temperature changes or predator refuges (Magnuson *et al.*, 1985; Knights *et al.*, 1995). The microhabitats of stream dwelling salmonids have been investigated more than any other group of fishes (Cunjak, 1988*a*; Huusko *et al.*, 2007), but the habitat requirements of other freshwater fish may be similarly narrow (Kynard *et al.*, 2000). It is possible that overwintering marine and estuarine fishes have specific habitat requirements analogous to freshwater species, but this question has rarely been addressed and the microhabitats of overwintering marine and estuarine fishes are largely unknown (Winslade, 1974; Smith & Able, 1994).

Estuarine residency presents an interesting set of circumstances for overwintering fish. While fluctuating salinities may exacerbate osmoregulatory stress, mesohaline regions may provide optimal habitat, minimizing osmoregulatory costs. It has been speculated that intermediate salinities near iso-osmotic to the blood of fishes should offer the greatest chance for survival by alleviating osmotic stress (Allanson *et al.*, 1971). Such a response has been demonstrated in juvenile striped bass (Hurst & Conover, 2002). It is also important to recognize that in addition to the salinity gradient through the estuary, there is often a corresponding temperature gradient. Hence, the combination of salinity and temperature gradients through the estuary may present a trade-off between factors beneficial to survival. Overwintering habitat requirements of estuarine fish would appear to be a very interesting area for future research.

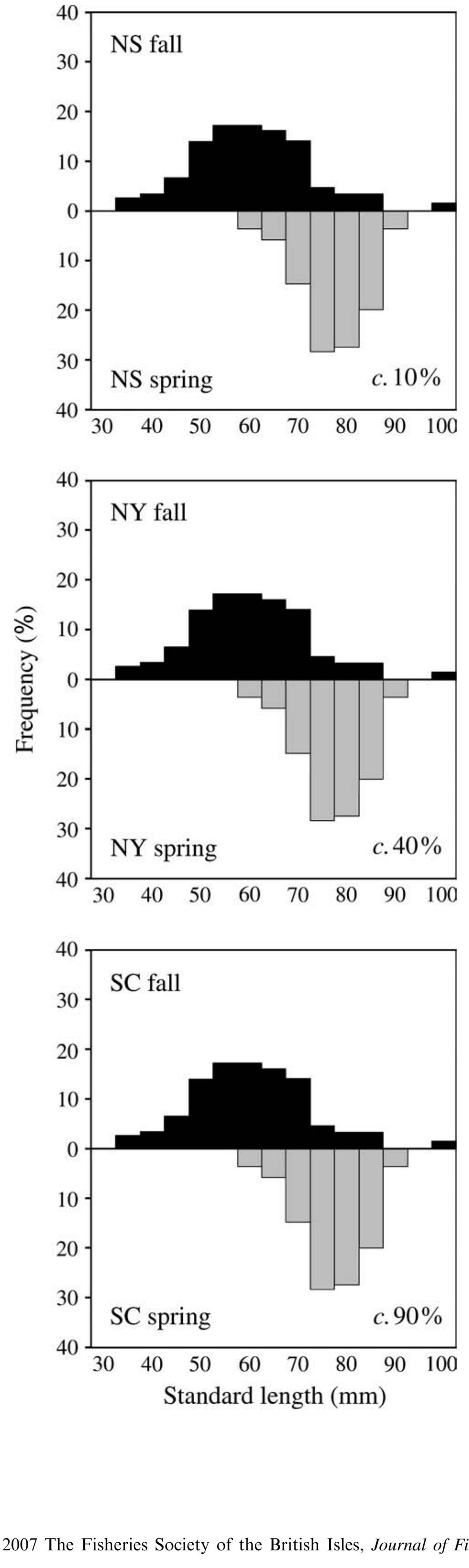
LATITUDINAL PATTERNS

Climate is believed to be the primary factor in limiting species distributions at the high-latitude boundary, with species interactions more commonly defining the low-latitude boundary (MacArthur, 1972). Consistent with this theory, several models of recruitment dynamics have been developed which directly link winter mortality to the distribution limits of temperate fish populations (Johnson & Evans, 1990; Shuter & Post, 1990). These models are based upon increasing winter severity as well as decreasing length of the growing season with increases in latitude. Predicted latitudinal patterns in winter mortality are evident in Atlantic silversides where the rate and size-selectivity of winter mortality increase from low- to high-latitude populations (Fig. 3) (Billerbeck *et al.*, 1997). However, the predicted latitudinal pattern in size-dependence of winter mortality was not observed among wild populations of largemouth bass (Garvey *et al.*, 1998). Rather, they suggest that variation in the primary source of mortality resulted in size-dependent mortality being more common at lower latitudes than at high latitudes. While starvation-induced mortality appears to be common in southern parts of the range, size-dependent winter mortality in northern parts of the range is restricted to those populations co-occurring with cold-water predators.

From another perspective, there are geographic patterns in the degree of intra- and interannual thermal variation that may define the nature and risk of winter mortality in local populations. At high latitudes, the potential for freezing may define the severity of winter. In boreal and sub-arctic coastal habitats (and some temperate ponds and streams), water temperatures may fall below the freezing point, creating a critical constraint on fishes. The presence of antifreeze agents can reduce, but not eliminate this risk for fishes in shallow coastal waters. In addition, the presence of ice in the environment poses other risks including scouring disturbance and oxygen limitation. At the extreme, freshwater ponds and marshes that freeze to the bottom are uninhabitable by fishes (Power & Power, 1995).

In the temperate regions, where most documentation of winter mortality has occurred, seasonality is the dominant characteristic of thermal regimes. In marine waters, seasonal temperature variation is most extreme at western ocean margins in the mid-latitudes (Levitus, 1987). Such seasonal environments may pose challenges for fishes, as the physiological adaptations necessary for growth and survival at high temperatures may compromise survival ability at low temperatures.

At lower, subtropical latitudes, winters are characterized by warmer average temperatures but are subject to infrequent rapid cooling events. These events result in the well-documented winterkills of sub-tropical species in Florida and Texas (see below – Winterkill depletions). In these regions, the critical characteristic of winter is the unpredictability of extreme conditions. For example,


NS fall
NS spring
c. 10%
NY fall
NY spring
c. 40%
SC fall
SC spring
c. 90%
Frequency (%)
Standard length (mm)
40
30
20
10
0
10
20
30
40
30
40
50
60
70
80
90
100

spotted sea trout *Cynoscion nebulosus* (Cuvier) are common in nearshore waters from the Chesapeake Bay to the Gulf of Mexico, but winterkills appear more common in Florida and Texas than in Chesapeake Bay (VanderKooy & Muller, 2003). In the northern part of the range, seasonal southward migrations appear to protect fish from predictably harsh winter conditions.

LOCAL ADAPTATION

The potential for populations to adapt to local conditions can add significant complexity to geographic patterns in the potential for winter mortality. Largemouth bass in North America display significant levels of genetic differentiation, including two recognized sub-species ('northern' *Micropterous salmoides salmoides* and 'Florida' *M. s. floridanus*) and an extensive intergrade zone (Philipp *et al.*, 1981). Several studies have demonstrated a greater tolerance to low temperatures in the 'northern' than 'Florida' sub-species (Cichra *et al.*, 1981; Carmichael *et al.*, 1988; Philipp & Whitt, 1991) with one more recent study (Fullerton *et al.*, 2000) suggesting a finer degree of adaptation occurring with the northern sub-species. Fish from three latitudes (Alabama, Ohio, Wisconsin) were exposed to simulated winter conditions. Population of origin had a significant effect on survival under severe winter conditions (Wisconsin fish performed best), consistent with local adaptation to the latitudinal cline in winter severity.

The lack of geographic barriers to population mixing has been predicted to hamper local adaptation in marine fishes, but such local adaptation appears to be common (Conover *et al.*, 2006). Several examples of local adaptation to winter conditions have been documented among marine fishes in both low-temperature tolerance (Malloy & Targett, 1994; Schultz *et al.*, 1998) and energetic requirements for overwintering (Schultz & Conover, 1997). A latitudinal gradient in growth rates of Atlantic silversides is believed to be a direct evolutionary response to winter mortality at high latitudes (Conover & Present, 1990). The maintenance of intraspecific genetic variation in thermal tolerance and growth rate in a species with high levels of gene flow suggests trade-offs between these traits and other traits required for survival in warmer climates and that the variation is maintained by continuing natural selection in each habitat (Conover *et al.*, 2006). Even with these adaptations to winter severity, Atlantic silversides suffer high rates of winter mortality in northern populations (Fig. 3).

LOCAL ENVIRONMENTAL VARIATION

A further factor complicating latitudinal patterns is the tremendous variation in non-climate aspects of local environments (both biotic and abiotic). This variation is most clearly expressed through the diversity of communities found

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FIG. 3. Latitudinal patterns in size-selectivity and rates of winter mortality in Atlantic silversides (*Menidia menidia*). In each panel, upper and lower histograms represent the size-distributions of fish at the onset of and end of winter, respectively. Populations sampled from north to south are NS: Nova Scotia (latitude 44° N), NY: New York (41° N), SC: South Carolina (33° N). The number in the lower right of each panel is the approximate relative population density between fall and spring sampling (D. Conover, unpublished data). Redrawn with permission from Billerbeck *et al.* (1997) (Fig. 3).

inhabiting lakes within a climatic region. The structures of inland fish (and invertebrate) communities vary markedly over small spatial scales as a result of colonization history, basin or habitat characteristics and management activities (stocking or harvesting). Further, local food-web structure can change dramatically in response to fluctuations in the abundance of any member (Mittelbach *et al.*, 1988; Elser *et al.*, 1995; Brönmark & Weisner, 1996). The size that fish attain before facing winter stresses can be an important regulator of winter survival and may be directly related to the presence or abundance of a particular prey or competitor species (Micucci *et al.*, 2003; Garvey *et al.*, 2000; Ostrand *et al.*, 2005). Similarly, the threat of overwinter predation may depend on the abundances of predators and availability of alternative prey (Ridgway *et al.*, 1990; Fitzgerald *et al.*, 2006). Hence, the contributions of biotic interactions to winter mortality can vary on a small spatial scale and may not be effectively predicted by climate descriptions.

Studies of largemouth bass demonstrate that these impacts of local community structure rival those of latitudinal climate patterns. Several studies have documented that survival of small fish is dependent on availability of winter prey (Oliver *et al.*, 1979; Fullerton *et al.*, 2000), despite the expectation of minimal activity and metabolic expenditures at low temperatures (Lemons & Crawshaw, 1985). Furthermore, in experimental pond systems, Micucci *et al.* (2003) and Ostrand *et al.* (2005) demonstrated that co-occurring bluegill may serve as either prey or competitor for overwintering largemouth bass, depending on the availability of alternative invertebrate prey. In a review of the literature on wild populations, Garvey *et al.* (1998) found inconsistent geographic patterns, concluding that where size-selective winter mortality occurred in northern populations, it was frequently attributable to predation by a co-occurring cold-water species; where size-selective winter mortality occurred in southern populations, it was attributable to starvation (Ludsin & DeVries, 1997).

POPULATION LEVEL EFFECTS

Winter mortality has the potential to impact the population dynamics through two general mechanisms. Winterkills can cause severe reductions in standing stock size that cut across age-classes. These events occur in response to short-term environmental conditions and represent a density-independent mortality source (Pearson *et al.*, 1999). The impact of such declines on fish communities and fisheries is a function of the severity of the decline as well as the population response to such a decline. Conversely, winter mortality of early life stages can play a significant role in regulating cohort strength and may act as a density-dependent regulator, where mortality is strongly size-selective.

WINTERKILL DEPLETIONS

Early attempts to determine the effects of winterkills on fish populations involved estimating the numbers of fish killed (Storey & Gudger, 1936; Gunter, 1941; Moore, 1976). A severe winterkill along the Texas coast in 1941 appeared to reduce harvest rates by one-third to one-half of those during the same period in previous years (Gunter, 1941), prompting managers to institute more rigorous winterkill evaluations. The subsequent winterkill, in early 1951, killed an estimated 60–90 million pounds of fish along the Texas coast (Gunter & Hildebrand, 1951). Although efforts to enumerate the number of fish lost to such events continue (Economidis & Vogiatzis, 1992; McEachron *et al.*, 1994), when winter mortality episodes occur in routinely assessed populations, the significance of these losses can be evaluated relative to stock size. The 1992–1993 winter die off of Prince William Sound Pacific herring reduced spawning biomass by *c.* 80% (Pearson *et al.*, 1999), while the spawning stock biomass of the North Sea population of sole was reduced by 67 and 27% during the severe winters of 1962–1963 and 1995–1996, respectively (Fig. 4; Millner & Whiting, 1996; ICES, 2006).

While severe winter conditions cause well-documented die offs of adult sole in the North Sea, they also tend to produce spring flow regimes that are favourable for transport of sole larvae to inshore nursery grounds. As a result, adult winterkills are routinely followed by strong recruitment of events of juvenile sole. Hence, yield in the sole fishery is closely related to winter conditions: harvest falls in response to a winter die off, but recovers within 2–3 years when the subsequent strong year-class enters the fishery (Fig. 4) (de Veen, 1978; Millner & Whiting, 1996).

Unfortunately, such rapid population recovery does not occur in all populations. The most persistent effects of winterkills (and other episodic climate events) result from an alteration of trophic structure and biotic controls on recruitment (Bond & Overland, 2005). For example, abundance of alewife *Alosa pseudoharengus* (Wilson) in the Upper Bay of Quinte, Lake Ontario, remained depressed for at least a decade following a 1978 winterkill (Ridgway *et al.*, 1990). The inability to recover in this embayment was potentially due to high abundances of predatory walleye *Stizostedion vitreum* (Mitchill; alewife recovered rapidly in the Lower Bay where walleye abundances were lower). Interestingly, a related outcome may have been the recovery of lake whitefish *Coregonus clupeaformis* (Mitchill). Alewife are predators on larval whitefish and the 1978 winterkill appears to have played a large role in the rapid recovery of the long-depressed whitefish population (Casselman *et al.*, 1996).

ANNUAL RECRUITMENT

The first winter of life is frequently marked by dramatic changes in physiology, energy budgeting and habitat requirements, such that variation in environmental conditions may regulate survival. As such, winter may represent a recruitment bottleneck, through which new cohorts must pass for production of a strong cohort. These effects on recruitment of early life stages are hypothesized to result in both density-dependent and density-independent population regulation (Cunjak *et al.*, 1998), depending on the sources of mortality.

The first confirmation (to author's knowledge) of the role of winter in the annual recruitment dynamics of a fish population was produced by Hunt (1969). The author observed that survival of juvenile brook trout *Salvelinus fontinalis* (Mitchill) was positively related to January water temperatures and overwintering body size. Two decades later, Seelbach (1987) demonstrated that return rates of steelhead (rainbow trout) *Oncorhynchus mykiss* (Walbaum) were

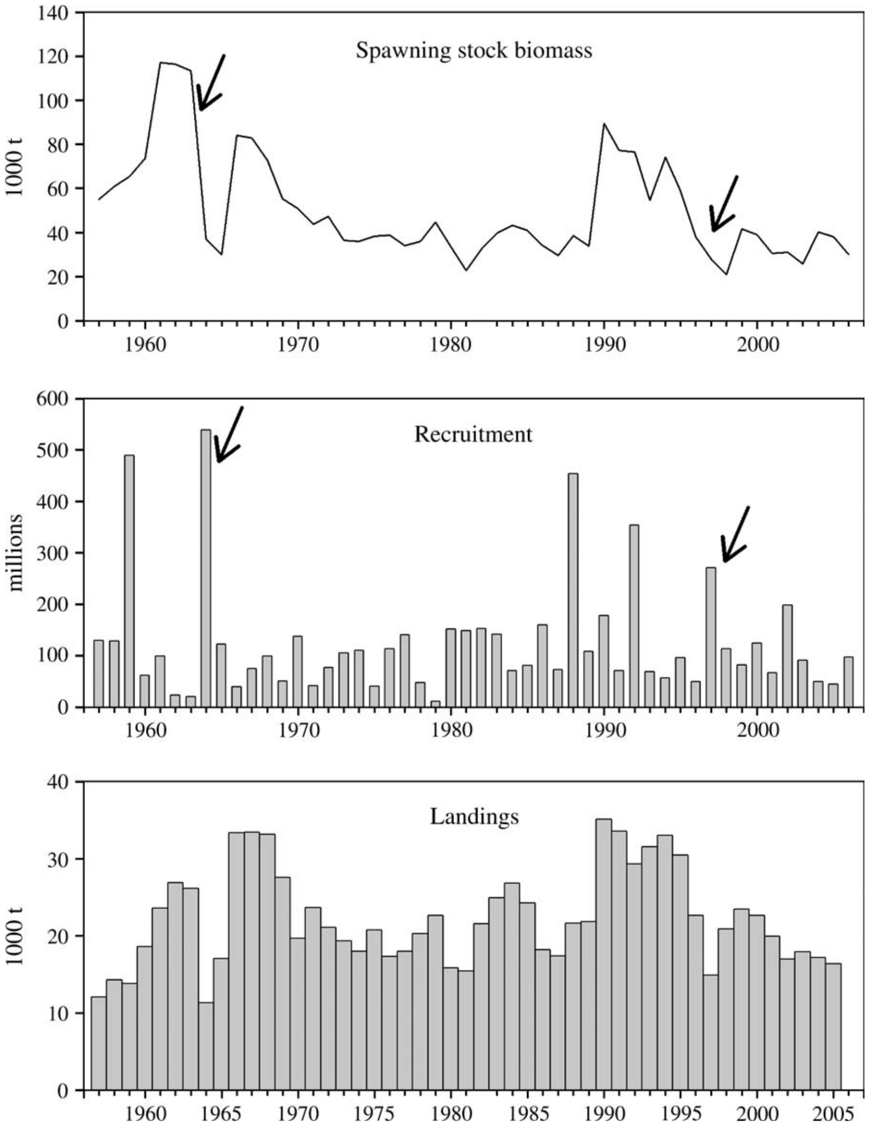

FIG. 4. Dynamics of sole (*Solea solea*) in the North Sea (ICES subarea IV). Significant winter mortality events depressed spawning stock biomass (panel a) by 67% and 27% during the winters of 1962–1963 and 1995–1996, respectively (indicated by arrows). However, strong recruitment (panel b) of the 1963 and 1996 cohorts (indicated by arrows) allowed fishery landings (panel c) to recover within three years of the winterkill. Figure redrawn with permission from data in ICES (2006).

positively correlated with the severity of winter prior to smoltification. Inter-annual variability in overwinter survival of early life stages has been demonstrated in numerous other freshwater populations (Schmidt *et al.*, 1994; Quinn & Peterson, 1996; O'Gorman *et al.*, 2004; Fitzgerald *et al.*, 2006).

There are several examples of marine and estuarine populations for which winter mortality of juveniles appears to play a role in regulating recruitment.

Northern populations of Atlantic croaker *Micropogonias undulatus* L. appear to suffer recruitment failure following years when winter water temperatures fall below 3° C (Lankford & Targett, 2001) and the abundance of age-1 Hudson River striped bass is correlated with the severity of winter experienced by age-0 fish (Hurst & Conover, 1998). Several studies have linked survival of juvenile walleye pollock *Theragra chalcogramma* (Pallas) in the Bering Sea to temperature conditions during the first year of life (Ohtani & Azumaya, 1995; Quinn & Niebauer, 1995; Mueter *et al.*, 2006). Cannibalism by older age classes of pollock is believed to be largely responsible for mortality of juveniles in the Bering Sea, with colder winters increasing the spatial overlap between juveniles and predatory adults (Francis & Bailey, 1983; Wepestad *et al.*, 2000). Interestingly, these studies relied upon summertime temperature observations reflective of winter forcing. The development of the sub-surface Bering Sea cold pool is related to the formation of sea ice in winter, with summertime bottom water temperatures functionally linked to severity of the previous winter (Luchin *et al.*, 1999).

Other studies have compared recruitment time series to annual patterns of temperature variation, several of which have found higher recruitment of multiple species during warm years (Holmes & Henderson, 1990; Zebdi & Collie, 1995; Corten & van de Kamp, 1996). While these studies did not set out to assess the role of winter in recruitment regulation, correlations with environmental conditions may suggest the need for further consideration of the role of winter in recruitment dynamics (Friedland *et al.*, 1993).

Where overwinter survival varies as a function of body size (see below), there is the potential for winter to act as a density-dependent regulator of population size, through competition and depression of first year growth rates. Overwinter survival was negatively correlated with density in experimental populations of largemouth bass (Ludsin & DeVries, 1997) and among cohorts in a natural population of creek chub *Semotilus atromaculatus* (Mitchill) (Schlosser, 1998). While these clearest examples of regulation come from small freshwater systems, such regulation is also believed to occur in larger coastal systems (Henderson *et al.*, 1988). Competition for suitable overwintering habitat has been suggested as an alternative mechanism inducing density-dependent regulation of recruitment in some stream fish populations (Chapman, 1966; Armstrong & Griffiths, 2001). Lacking knowledge of the microhabitat requirements of overwintering marine fishes, it is unknown if such constraints might apply to some coastal species as well.

SIZE-DEPENDENCE

Considerable effort has been directed towards determining the size-dependence of mortality among juvenile fishes (see reviews by Anderson, 1988; Sogard, 1997). This question has been addressed more than any other in the ecology of overwintering fishes as it links traits such as birth date and growth rate to survival and may provide a mechanistic explanation for density-dependent population regulation (Mills & Mann, 1985; Carngelli & Gross, 1996; Jackson & Noble, 2000). Until recently, the idea that winter mortality, if selective, would select against smaller fish (positive size-dependence) was almost universally accepted. However, continued research has suggested that the observed selectivity of winter mortality may be related to factors such as the mechanism of mortality and local trophic links.

Evidence for the positive size-dependence of winter mortality comes from both laboratory experiments and field surveys. Laboratory experiments exposing fish to simulated winter conditions have frequently found higher mortality rates among small fish or have observed small fish dying before larger conspecifics (Oliver *et al.*, 1979; Post & Evans, 1989; Johnson & Evans, 1990; Malloy & Targett, 1991; Thompson *et al.*, 1991; Hurst & Conover, 1998). These experiments offer the advantage of environmental control but may suffer from a lack of ecological realism. As the overwintering habits of many marine species remain unknown, design of representative experiments remains problematic (Sogard & Olla, 2000; Hales & Able, 2001). Initially, these experiments were limited to examining internal physiological constraints on overwintering, starvation and thermal stress. However, several researchers have adopted creative designs to simultaneously assess external mortality sources such as predation and disease susceptibility (Miranda & Hubbard, 1994*b*; Moles *et al.*, 1997).

Comparison of fish sizes in wild populations at the beginning and end of winter has also suggested that mortality is size-dependent, selecting against smaller individuals (Toneys & Coble, 1979; Henderson *et al.*, 1988; Miranda & Hubbard, 1994*a*). A few studies have not found any size-dependent pattern of overwinter survival (Toneys & Coble, 1979; Kohler *et al.*, 1993), and there have been no reports of selection against larger fish. The value of the field approach is that all potentially important sources of mortality are expressed and captivity artefacts are removed. However, the conditions in a given year may not represent average conditions, may vary substantially during the winter and may not be closely monitored by the researcher. Further, interpreting size-selective mortality from an increase in mean size should be done with caution, as it is based on the assumption that growth does not occur during the sampling interval, or that it can be reliably differentiated from selective mortality. While techniques for differentiation have been suggested by Post & Evans (1989) and Munch *et al.* (2003), where possible the temperature threshold for growth should be experimentally determined. At temperatures below this threshold, changes in the size-distribution can be more confidently attributed to mortality (Hurst & Conover, 1998). It has also been suggested that samples should be taken throughout the winter in order to reduce the probability of sampling error and to determine the timing of mortality in winter (Miranda & Hubbard, 1994*a*). Unfortunately, in many cases the fish are unavailable to sampling due to ice cover or migration patterns.

The clearest examples of negative size-selective winter mortality (selecting against larger individuals) comes from laboratory studies of two fish species with subtropical origins, Atlantic croaker (Lankford & Targett, 2001) and bluefish *Pomatomus saltatrix* (L.) (Slater *et al.*, 2007). In both cases, mortality appeared related to thermal stress (see above – Sources of mortality). Field evidence for negative size-selection of winter mortality is scarce, but has been suggested for several marine species, including Atlantic croaker (Hildebrand & Cable, 1930; Gunter, 1947). To the author's knowledge, negative size-selective mortality has not been observed among overwintering freshwater fishes, despite its expectation in ice-covered, hypoxic ponds. Whether negative size-selection is limited to subtropical fishes or is more common among fishes suffering low-temperature stress remains to be clarified.

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 only one or two winters (Lappalainen *et al.*, 2000; Jackson & Noble, 2000). However, Quinn & Peterson (1996) and Hurst & Conover (1998) found that winter mortality was size selective in some years, but independent of body size in others. Adams *et al.* (1982) found that the mean size of stressed gizzard shad and threadfin shad (captured in a power plant intake) varied with temperature, presenting a clear mechanism through which the size-selectivity of winter mortality would vary among years. Interannual variation in pre-winter body size or lipid reserves could also result in qualitative differences in the size-selective pattern of winter mortality (Post *et al.*, 1998; Cooney *et al.*, 2001; Fitzgerald *et al.*, 2006). Future research should include extended field studies evaluating the potential for, and consequences of, variation in the selective pattern of winter mortality.

MANAGEMENT CONSIDERATIONS

Despite evidence that winter mortality can influence population dynamics through reductions in adult density and regulation of juvenile recruitment, these effects have rarely been incorporated into fisheries models or management decisions (North Sea sole and Texas spotted sea trout being notable exceptions). The demonstration that slight changes in growth and mortality rates of larval fish can generate tremendous variation in survival (Houde, 1987) supports the importance of the larval stage in determining recruitment. Hence, abundance surveys of a wide variety of species are conducted during the first summer of life as indices of recruitment. However, it is unlikely that recruitment to most populations is determined at a single life stage, and there is increasing evidence that variation in the mortality rates of juveniles can play an important role in recruitment regulation (Bradford, 1992; Myers & Cadigan, 1993; Bailey *et al.*, 1996). As winter mortality may have its greatest impact during the first winter of life, indices of recruitment measured prior to this stage should be used cautiously (Hurst & Conover, 1998). Of particular importance is the determination of the density-dependence of winter mortality, a question that, unfortunately, will be difficult to resolve in many stocks. For example, recruitment of Bering Sea walleye pollock appears to be correlated with winter severity (Ohtani & Azumaya, 1995; Quinn & Niebauer, 1995), implying a direct density-independent regulation. However, winter mortality is believed to result from increased inter-cohort cannibalism in cold winters due to increased spatial overlap between age classes, a mechanism likely to act, at least in part, in a density-dependent manner (Ciannelli *et al.*, 2004).

Several models of population dynamics that incorporate size-dependent winter mortality have been developed (Johnson & Evans, 1990; Shuter & Post, 1990). These models assume that winter mortality is due to starvation, inherently selecting against smaller fish, and that all variation results from temperature regime differences. Assuming that all winter mortality is due to starvation, and that starvation occurs when fish have lost a certain proportion of pre-winter body mass, these models do not take into account observed interannual differences in body size and energy storage (Foy & Paul, 1999; Hurst & Conover, 2003) or predation pressure (Fitzgerald *et al.*, 2006). While these models have proven useful for predicting species ranges, the ability to describe patterns of recruitment in specific populations would be improved by incorporating information on the size-dependence of all sources of mortality.

One place where an understanding of winter mortality has led to direct management activities is the improvement of overwintering habitats for early life stages of salmonids (Solazzi *et al.*, 2000; Giannico & Hinch, 2003). Another is the harvest restrictions placed on spotted seatrout in Texas following winterkills in 1983 and 1989 intended to promote population recovery from the winterkill depletions (McEachron *et al.*, 1994; Rebecca Hensley, pers. comm.).

CONCLUSIONS AND RECOMMENDATIONS

The pace of research in the ecology of overwintering fishes has increased rapidly during the last two decades, resulting in marked improvements in our understanding of winter mortality. However, there is presently a danger of a plateau in our understanding of this phase. The next suite of major advances will require adoption of new approaches integrating ecological and demographic processes in fish populations. It will also require recognition that ecological processes are equally, if not more important than physiological processes in the winter mortality of many species. However, there is strong motivation for pursuing winter mortality research as it represents an integral, yet understudied component of the primary initiatives in contemporary fisheries science (ecosystem management, habitat evaluation and impacts of climate change).

Logistical impediments to some research questions are continuously being resolved. The increasing ubiquity of remote and *in situ* sensors will provide ever more refined observations of the overwintering environment. These will provide data for evaluation of habitat suitability and describe changes in the location or extent of preferred habitats (Hurst & Conover, 2002) and aid in retrospective analyses of winterkills (Pearson *et al.*, 1999). Active and passive acoustic tracking approaches are beginning to be applied in overwintering studies, aiding in identifying overwintering habitats and improving our understanding of movement patterns and activity levels. Advances in *in situ* physiological sensors will provide much needed information on field metabolic rates and stress levels (Briggs & Post, 1997; Cooke *et al.*, 2004).

In order to incorporate winter mortality into models of recruitment dynamics, it is imperative that the cause(s) of mortality operating in populations of interest be identified. Recognizing the difficulties in accomplishing this, researchers (including myself) have been content to interpret seasonal energy cycles as consistent with potential winter starvation. Future work requires rigorous examination of whether significant numbers of fish die from starvation (or as an indirect result) or if most fish are able to offset starvation through low levels of compensatory feeding. As winter represents a period of co-occurring stressors, more studies need to adopt creative experimental designs that evaluate the potential interactions among these stressors. Specifically, the relationship between energetic condition and other stressors is frequently assumed but rarely tested. The studies of Lemly & Esch (1984) and Moles *et al.* (1997) provide particularly useful models in this regard, the former integrating field and laboratory experiments.

Evaluation of the size-selectivity of mortality remains a critical question in evaluating the potential role of winter in the dynamics of populations, but represents only the first step in understanding. For only a few populations has the relative variation in winter mortality rate been determined, and for almost none have actual rates been measured (but see Cunjak & Therrien, 1998; Letcher *et al.*, 2002). In evaluating the recruitment implications of winter mortality, particular emphasis should be placed on discriminating between density-dependent and density-independent effects. A difficult question to resolve (involving detailed analysis of pre-winter growth and density measurements or long time series of recruitment), resolution of the density-dependence is central to incorporating winter mortality into population forecasts and determining appropriate management responses.

Determining the levels of winter predation has received insufficient attention to date. Although low temperatures reduce the consumption rates of ectothermic piscivores, winter may still represent the primary period of influence by some predators on some prey (Winship *et al.*, 2002). Increased predation pressure could be caused by changes in distribution associated with seasonal migration of the predator, prey or an alternative prey (Murawski, 1993; Cooney *et al.*, 2001). Changes in behaviour and swimming performance at low temperatures may also result in increased vulnerability to predators (Woodhead, 1964*a*; McLean *et al.*, 1985). In addition to enhanced field sampling to describe diets and distributions, this field would benefit from better characterization of behavioural responses of fish to low temperatures (Lemons and Crawshaw, 1985; Hurst & Duffy, 2005; Hurst, 2007). Poor characterization of the seasonal changes in strengths of trophic links is a recognized weakness of existing ecosystem models (Aydin *et al.*, 2005). Hence, the outcome of these studies will feed directly into initiatives to apply effective ecosystem management.

The critical role of habitat on the survival and recruitment of fishes is reflected in the widespread adoption (in both the science and policy arenas) of the 'essential fish habitat' concept. Winter represents a critical period in the life history of some species, yet understanding of the role of habitat is largely limited to studies of salmonids (Cunjak *et al.*, 1998; Huusko *et al.*, 2007). The factors that determine habitat suitability for most overwintering marine and estuarine fishes have yet to be considered. Winter habitat studies should strive to determine the specificity of habitat requirements for overwintering fishes and evaluate the links between habitat availability and recruitment.

Climate change will undoubtedly impact many aspects of fish life history and recruitment dynamics. Evaluating the effects of climate warming (and other long-term climate cycling) on overwintering fishes will not be straightforward. Environmental changes always result in both winners and losers (Reist *et al.*, 2006) depending on the source of mortality and population-specific ecological conditions (Blenckner, 2005). Warmer average winters may reduce the frequency of episodic winterkills in some species (as has been observed for Texas spotted seatrout). Conversely, warmer water resulting in increased metabolic demands of predators may well increase predation risk. The threat of winter starvation will be exacerbated or relieved depending upon the productivity responses of lower trophic levels (McDonald *et al.*, 1996). Modelling efforts to predict such changes will need to go well beyond the direct physiological responses to temperature variation, and include quantitative predictions of the abundance and distribution of predator and prey fields.

I would like to thank my graduate advisor David Conover, under whose guidance much of the early work on this paper was conducted. Thanks also to J. Buckel, S. Munch, T. Lankford, M. Davis, A. Stoner and B. Laurel for many thoughtful discussions of fisheries ecology relevant to this review and for reviewing various portions of this manuscript. I would also like to acknowledge the assistance of library staffs at Stony Brook and Oregon State Universities for tracking down literature. Financial support for my research on the overwintering ecology of striped bass was provided by the Hudson River Foundation for Science (graduate fellowship and research grant #OCE 9217025 to D. Conover), Stony Brook University, and a Fellowship in Population Biology from the Electric Power Research Institute.

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