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Time modelled as an explicit feature to quantify habitat quality and preference of chinook salmon (Oncorhynchus tshawyscha) in western Lake Ontario at two time scales: The relative importance of environmental conditions and some implications.

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Time modelled as an explicit feature to quantify habitat quality and preference of chinook salmon (*Oncorhynchus tshawyscha*) in western Lake Ontario at two time scales: The relative importance of environmental conditions and some implications.

by
Denis Roy
B.Sc. (Honours), Queen's University, 1996

A Thesis
Submitted to the College of Graduate Studies and Research
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apply to other time periods and could not be extrapolated to other temporal scales.

In Chapter III, I examined actual chinook distribution collected acoustically to quantify chinook salmon habitat preference at both the seasonal and diel time scales. Predicted chinook habitat preference was determined using three habitat preference models, namely; behavioural thermoregulation, prey-taxis or optimal foraging, and behavioural bioenergetics. Each model's predicted distribution was compared with actual chinook distributions over time. The degree of overlap between predicted and actual chinook distributions quantified the relative importance of monitored environmental conditions to chinook habitat preference at both time scales. I know of no other study capable of assessing the relative importance of monitored environmental conditions to habitat preference at such a high temporal resolution. I found that chinook habitat preference at both the seasonal and diel time scales was variable. This was attributed to both changing environmental conditions, and to changes in chinook habitat requirements at both scales. Overall, I demonstrated that chinook habitat preference assessments made at a particular time scale and period, cannot be applied to other time periods or extrapolated to other time scales. These results have important implications in terms of the trophic cascade theory and predator-prey interactions within large lake ecosystem. A predators ability to control and deplete its prey base within dynamic systems is not only limited by how much prey the system contains, but also by a variety of environmental constraints which effectively limit the amount of prey available.

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For Walace

TABLE OF CONTENTS

List of Tables

List of Figures

CHAPTER I

Background

Processes in aquatic ecology deterministic of fish distribution are legion and attempting to describe each of their influences is beyond the scope of present fisheries understanding (Crowder and Magnuson 1983; Brett 1952). Still, as Brett (1971) stated: " there is something to be said for knowing where and when fish cannot be found." Although this statement may seem plain and pedantic, it nevertheless points to two fundamental concepts in the study of fish distribution. The first is that of the fish distribution itself, and the underlying mechanisms regulating it. The second is that of the spatial and temporal scales at which these mechanisms operate.

Organism abundance and distribution measurements have diverse applications in ecology (Dodson 1998; Holling 1992). Estimates of distribution and abundance are used extensively: as indices of trophic dynamics within systems; to describe the influence of both natural and anthropogenic processes; and to show patterns giving insight into organism behaviour. For example, Carpenter et al., (1985), revealed that high piscivore density can impose strict top-down control over planktivore abundance within a lake system, allowing overall diversity to increase. Warwick (1996) used the distribution and occurrence of deformities in chironomid larvae at different sites along the St-Clair river to assess its chemical contamination. His results indicated deterioration of the aquatic habitat in a downstream progression. Brett (1952), demonstrated that salmonid species exposed to temperature gradients aggregate at specific temperatures that maximize physiological efficiency, indicating a preference for this temperature. Common to all of the studies cited above is the use of distribution and abundance indices in making logical inferences about organisms and their interactions within their biological, chemical, and physical environments.

Most distributions and mechanisms causing those distributions are scale dependent. The importance of scale is often overlooked in ecology (Turner 1998; Holt 1997; Holling 1992; Levin 1992; Lawton 1987; Harris 1980). It has been demonstrated that scale, or the size of the 'space-time window' through which observations are made, can impose or obscure patterns in collected data (Hondorp 1998; Holling 1992; Levin 1992; Lawton 1987; Legendre and Demers 1984; Harris 1980; Stommel 1963). Thomas (1991) found that yearly estimates of variation among butterfly (*Plebejus argus*) sub-populations fluctuated in synchrony. Such synchronous patterns were not observed, however, when the same estimates were made at 3-year intervals.

Certain patterns observed at one particular scale, may be driven by mechanisms operating on a variety of different scales (Levin 1992; Legendre and Demers 1984; Harris 1980). Stommel (1963) contends that a description of the surface temperature of the sea would require the consideration of factors ranging in scale from unitary measures of vertical heat transfer (fine scale), to shifts in continental currents and meteorological events (course scale).

Other processes occurring at very specific scales have the power to entrain patterns observed over much larger scales (Holling 1992). For example, Legendre and Demers (1984) and Harris (1980) describe how phytoplankton density throughout the growing season can be predicated by the size of production blooms occurring within approximately 3-7 days in early spring. These blooms coincide with the emergence of zooplankton which use the phytoplankton as food. This is followed quickly by emerging larval fish which feed on the abundant zooplankton (Legendre and Demers 1984). Failure of the early season plankton blooms to realize themselves within a critical period can have enormous impact on the higher trophic levels. Plankton bloom failures can lead to decreased abundance of zooplankton and ultimately to a poor year class of fish, the consequences of which are evident over several generations (Carpenter and Kitchell 1987; Frank and Leggett 1982).

Another important scaling principle is that individual processes can have varying degrees of influence at different scales of observation (Hondorp 1998; Turner 1998; Holling 1992; Levin 1992; Legendre and Demers 1984; Harris 1980). For instance, in boreal forests, when the crown foliage of spruce and balsam-fir trees is sparse, insectivorous birds impose strong predation pressure on the spruce-budworm (*Choristoneura fumiferana*). As the density of the crown foliage increases however, the predation pressure on the worms decreases (Holling 1992). The increasing density of the crown foliage provides better refuge for the worms, thus decreasing the foraging efficiency of the birds. The relaxation of the predation pressure allows for increases in budworm density and distribution which can reach outbreak proportions (Holling 1992). Initially the budworm population within the spruce-balsam-fir forest is controlled by heavy predation pressure. However, this pressure diminishes with time, allowing the expansion of budworm density and distribution. Thus, inferences made about the control of budworm populations by insectivorous birds in times of sparse crown foliage are not necessarily applicable when the foliage increases density (Holling 1992). The above examples suggest that studies quantifying species distribution are intimately related with time/space scales of observation. It is therefore unlikely that mechanisms or processes regulating these distributions are immune to scaling principles (Turner 1998; Holt 1997).

In aquatic ecology, and especially in fisheries ecology, studies of distribution focus largely on the influence of temperature, food, and bioenergetic combinations of these latter on the distribution of fish within the pelagic environment of different systems (Filbert and Hawkins 1995; Ryer and Olla 1995; Perry and Smith 1994; Bevelhimer and Adams 1993; Brandt and Kirsch 1993; Levy 1991; Levy 1990; Wildhaber and Crowder 1990; Clark and Levy 1988; Christie and Regier 1988; Olson et al., 1988; Crowder and Magnuson 1983; Brandt et al., 1980; Brett 1971; Wells 1968). Many studies however, fail to consider the dynamic aspect of the environment through time. In many cases, the particular distributional process under scrutiny is considered to be the sole factor determining distribution in a static environment. Specific distributional processes are considered to be relatively constant through time based on instantaneous 'snapshots' of a continuously changing environment (e.g. Bevelhimer and Adams 1993; Christie and Regier 1988; Brandt et al., 1980; Wells 1968; Foltz and Norden 1977).

More contemporary study designs incorporate the notion of spatial heterogeneity of the environment, but continue to treat the environment as static where processes describing distributions are also static (e.g. Mason and Brandt 1996; Brandt and Kirsch 1993; Goyke and Brandt 1993). Although these studies help elucidate important spatial relationships between the organisms under study and their environment, they create the conception of temporal homogeneity between sampling events. Yet, as mentioned above, there are numerous examples that show that the environments, and the processes operating on species distribution within these environments, also have inherent temporal dynamics.

I assert that distributional processes operating on fish in a dynamic aquatic environment, are themselves dynamic with time, and that their relative importance in describing fish distribution are also temporally dependent. The purpose of this chapter is four-fold: First, it serves to describe 3 processes traditionally used to characterize fish distribution within pelagic environments. Second, it demonstrates that each of these processes may vary in its relative importance to fish distribution over time. Third, it serves to outline certain limitations of different sampling techniques used to acquire temporal measurements of fish distribution. Finally, it outlines the strategies I used to evaluate the above hypothesis.

Behavioural thermoregulation

Temperature has long been identified as an important determinant of fish distribution (Brandt et al., 1980; Magnuson et al 1979; Brett 1971; 1952). As fish are ectotherms, most of their physiological processes including digestion, respiration, growth, and activity levels are temperature dependent (Moyle and Cech 1996; Schmidt-Neilsen 1990; Eckert 1988). While studying lethal thermal tolerance of several salmonid species, Brett (1952) found that physiological rates and metabolic processes were more efficient at certain temperatures than at others. Such temperature optima were described for all salmonid species used in Brett's (1952) study. Brett also found that different salmonid species, exhibited different thermal tolerances and were much more resilient to thermal stress than others.

Wells (1968) used depth directed trawling in different thermal strata to describe the depth and thermal distribution of pelagic species in Lake Michigan, and showed that although most species were rarely found at their laboratory determined optimal temperatures, they did track a range of temperatures that were closely correspondent. Changes in depth and near shore-offshore distribution of pelagic species in this system followed changes in the thermal structure of the water column. Wells (1968) also emphasized within species thermal preference differences depending on the age structure of the population. For example, young alewives (*Alosa pseudoharengus*) were much more abundant in mid-water at temperatures between 6 - 12 °C than were adults. Wells' (1968) study supports the concept of regulating thermal experience by behaviour, and that this type of behaviour could separate species, and indeed individuals within a species, based on thermal requirements (Moyle and Cech 1996; Brett 1971; Wells 1968).

Magnuson et al., (1979), extended this concept to consider temperature as an ecological resource, supporting the notion of a temperature niche. Species typically aggregate at a range of temperatures (±2°C) centered around a preferred optimum, and different species prefer different temperature ranges segregating them from each other in the pelagic habitat (Magnuson et al., 1979). Brandt et al., (1980) supported this concept by demonstrating that species once thought to have overlapping distributions are actually segregated within the pelagia based on the thermal niche concept. Moreover, certain species exhibit ontogenetic shifts in thermal niche which decreased the amount of overlap and intraspecific interaction within this species (Brandt et al., 1980). The aggregation of fish species at their preferred temperature, and the segregation of these species based on thermal niche can thus provide structure to an apparently homogenous habitat (Brandt 1993; Brandt et al., 1980; Magnuson et al., 1979; Wells 1968).

Brandt (1980) also indicated that the temperature range of a given species year-class can vary over much wider ranges than that suggested by Magnuson et al., (1979). For example, adult rainbow smelt (*Osmerus mordax*) distributions exhibit a total range from 7-18°C. During the day, adult smelt are found mostly at temperatures of 7-8 °C, very close to their laboratory determined preference (Brandt et al., 1980). Their nighttime distribution, on the other hand, is clustered at temperatures ranging from 11-16°C. This inconsistency was also encountered by Brett (1952) who discussed how fish aggregated in a thermally preferred temperature periodically migrated to thermally hostile environments to feed. This demonstrates that although fish distributions may be well characterized by temperature, different processes may override this influence—even if only periodically.

Distributional assessments of fish made at large time intervals may determine temperature as the distributional process and fail to characterize periodic events occurring at smaller, yet ecologically important time scales. The assumption that fish segregate based on thermal preference, however, continues to have merit. This is certainly the assumption used by Christie and Regier (1988) who show that the sustained yield of four commercially important species in northern-temperate lake systems is highly correlated with their distinct thermal habitat area and thermal habitat volumes. Thermal habitat area and volumes were calculated as a function of the total area and volume of these lakes which were characterized by species' specific preferred temperature ranges as described by Magnuson et al., (1979) (Christie and Regier 1988). Brett (1971) and Magnuson et al., (1979) conceded separately, however, that characterizing distributions in terms of a single process or mechanisms may generate misleading assumptions about ecological interactions between species and their environment (Crowder and Magnuson 1983; Magnuson and et al., 1979; Brett 1971; Janssen and Brandt 1980).

Optimal Foraging

The theory of optimal foraging is quite intricate, and involves a degree of complexity beyond the scope of this study. For the purposes of this study we describe the theory in its rudimentary form as it relates to fish distributional processes. The central tenant of the optimal foraging theory is that fish (or any species) aggregate in areas of high food abundance. In terms of predator-prey interactions, predators will be attracted to areas of high prey densities (Ryer and Olla 1995; Brandt 1993; Wildhaber and Crowder 1991; Crowder and Magnuson 1983; Kareiva and Odell 1987). Optimal foraging is a strategy adopted by predators to maximize food and energy intake while minimizing energetic costs associated with finding and capturing prey (Brandt 1993; Alcock 1988; Crowder and Magnuson 1983). Kareiva and Odell (1987) suggest that the process of predator aggregation in areas of high prey density may be a function of the encounter rate between a predator and its prey, and that prey-taxis is a direct consequence of the number of prey encountered in a specified area over time. In terms of fish predator-prey encounters, Brandt (1993) breaks the foraging process into two quantitative steps. The first describes predator consumption C as a function of encounter rate E, and probability of prey consumption P_c.

$$C = EP_c \tag{1}$$

The second, developed by Gerritsen and Strickler (1977), is a formula defining encounter rate E (above) as a function of predator search radius R (ability to perceive prey), the predator and prey swimming speeds v, and u respectively, and the prey density D, in the following manner:

$$E = \frac{\pi R^2}{3} . \frac{3v^2 + u^2}{v} D \tag{2}$$

According to optimal foraging as described here, if predators are aggregated in areas of high prey density (D), the encounter rate (E) increases, ultimately leading to increased consumption (C) and energy intake (Brandt 1993; Brandt and Kirsch 1993; Brandt et al., 1992). Sih (1980) indicated that sensitivity of certain predators to encounter rates may be so finely tuned that, in times of abundant prey, predators may take a limited number of "big juicy bites" from a prey item before resuming its search for more prey. Sih (1980) contended that certain portions of prey items are more energetically valuable then others, and thus when prey is abundant, only high energy parts are targeted for consumption.

Wildhaber and Crowder (1991) suggested that predators will remain aggregated in areas of high prey densities until prey encounter rates within that specified area equals, or falls below that of the remaining environment. This has been termed the "matching rule" for optimal foraging. There are two implicit assumptions to the matching rule. The first is that a predator has the ability to evaluate its environment as to the nature of prey density. This assumption is reasonable as it has been demonstrated that certain species continue to periodically sample their environment even when in patches where food intake reaches its maximum (Ryer and Olla 1995; Krebs and Kacelnik 1993; Wildhaber and Crowder 1991; Kareiva and Odell 1987; Sih 1980). The second assumption is that areas of high prey density are only recognized as they compare to other areas within that environment. This assumption implies that prey are heterogeneously distributed within the environment (Levin 1994; Gaston and Lawton 1990; Legendre and Fortin 1989; Legendre and Demers 1984; Mc Eadie and Keast 1983; Harris 1980; Levandowsky and White 1977). The manner in which prey is distributed within the environment can be critical in determining predator foraging behaviour (Ryer and Olla 1995). For example, certain predators are known to form groups foraging together in search of clustered prey. When prey are not clustered, group foraging is not observed (Ryer and Olla 1995). The matching rule and the group foraging theory are not necessarily relevant to this study, but are good examples of the numerous associated postulates of optimal foraging. For this study, it is sufficient to state that if predators distribute themselves in terms of optimal foraging, they will be located in areas of highest prey density.

This theory of optimal foraging, in concert with more complex relationships (described above), is applied in several studies (Brandt 1993; Levy 1991, 1990; Wildhaber and Crowder 1991, 1990; Clark and Levy 1988; Olson et al., 1988; Crowder and Magnuson 1983; Janssen and Brandt 1980; Foltz and Norden 1977). However, even the most convincing of these studies shows that optimal foraging and prey-taxis, is at best an ephemeral descriptor of fish distribution. Wildhaber and Crowder (1990), demonstrate under laboratory conditions that bluegill (*Lepomis macrochirus*) distributions are more highly associated with areas of high food concentration during feeding periods. When not feeding, however, bluegills spend a greater proportion of time in patches containing their optimal temperature. Moreover, shifts in bluegill distribution from areas of low to high food density during feeding bouts is obscured when the disparity between the food densities is marginal (Wildhaber and Crowder 1990).

Clark and Levy (1988) demonstrate that although there is strong coherence between juvenile sockeye salmon (*Oncorhynchus nerka*) and their zooplankton prey in British Columbia lakes, this overlap is only temporary, and restricted to crepuscular periods. These authors submit that the limited overlap observed is attributable to the predation pressure on juvenile sockeye by larger piscivores. This submission is supported by a number of studies demonstrating that predation pressure can substantially alter distribution patterns in prey (Levy 1991, 1990, Janssen and Brandt 1980). Crowder and Magnuson (1983), and Brett (1971), however, both suggest that the changes in the sockeye-zooplankton distribution overlap is the result of a metabolic strategy of the sockeye maintaining itself in ready states for consumption. Sockeye migrate up through the water column at dusk following their zooplankton prey (Levy 1990; Clark and Levy 1988; Brett 1971). After a certain time feeding, the sockeye are satiated and must digest their prey before feeding can resume. Remaining in the warmer, shallow water, however, decreases efficient energy extraction from the consumed food (Brett 1971; 1952). Likewise, deep, cold hypolimnetic waters decrease the rate of digestion (Mac 1985; Brett

1971; Javaid and Anderson 1967). Thus, after their dusk feeding period, juvenile sockeye migrate down to temperatures which maximizes the efficiency and speed of digestion. After the night hours are spent at digestion conducive temperatures, the sockeye migrate back toward their prey and feed once again (Brett 1971). These last examples show that, although foraging is a well-accepted distributional process in fish, it is deficient for characterizing distributions over more than brief time intervals.

Behavioural Bioenergetics

Recent studies suggest that the judicious combination of several distributional processes is likely more important when considering fish distributions within their environment (Hondorp and Brandt 1996; Tyler and Rose 1996; Tyler and Gilliam 1995; Dolloff et al., 1994; Goyke and Brandt 1993; Bevelhimer and Adams 1993; Brandt 1993; Luo and Brandt 1993; Brandt et al., 1992; Stewart and Iberra 1991; Wildhaber and Crowder 1990; Clark and Levy 1988; Crowder and Magnuson 1983; Kitchell et al., 1977). Several studies indicate that a better descriptor of *in situ* fish distribution is one which incorporates the effects of both food and temperature (Kelsch 1996; Filbert and Hawkins 1995; Wildhaber and Crowder 1990; Crowder and Magnuson 1983; Brett 1971). This is a reasonable postulate, as both factors have been shown to influence fish growth and activity rates (Ney 1993; Hewett and Johnson 1992; Crowder and Magnuson 1983; Brett 1971; Kitchell et al.,1977).

The relationship between growth rate and the factors mentioned above however, is not linear (Brandt 1993; Brandt and Kirsch 1993; Hewett and Johnson 1992). Rather, similar growth rates can be achieved from a variety of temperature and food density combinations. Such relationships are distinct among species, and the distinction can be extended to within species depending on individual size, sex, or ontogenetic shifts in life history stages (Brandt 1993; Brandt and Kirsch 1993; Brandt et al., 1992). Bioenergetics models elucidate the nature of these complex relationships, and are essentially mass/energy balance equations that relate growth and consumption of fish to both fish physiology and environmental conditions (Hewett and Johnson 1992; Stewart and Iberra 1991; Stewart et al., 1983; Kitchell et al., 1977). Bioenergetics models are typically used to estimate trophic demand of predators on existing prey populations (Rand and Stewart 1998; Rand et al., 1994; Ney 1993; Hansen et al., 1993; Stewart and Iberra 1991; Ney 1990; Stewart et al., 1983). Several bioenergetics models exist, but for the sake of brevity, I describe only that which is applicable to this study (for review see Ney 1993; Hansen et al., 1993). I apply the Wisconsin bioenergetic model, originally devised by Kitchell et al., (1977), and later modified by Hewett and Johnson (1992) to estimate species specific growth rates (G in g g^{-1} day^{-1}) in a habitat characterized by a particular temperature and prey density, according to the following formula:

$$G=C-(R+F+U) \tag{3}$$

Where C = consumption,
R = metabolism and respiration,
F = egestion, and,
U= excretion.

Consumption in terms of growth can be expressed as;

$$C = a_c W^{b_c} \cdot f(T) \cdot P \tag{4}$$

Where a_c = maximum rate of consumption achieved at optimal temperature,
W= wet weight of the fish,
b_c = exponent describing the weight dependent consumption (certain sized fish can consume only a finite amount of prey),
T = the ambient temperature, and,
P = the proportion(ranging form 0 - 1) of maximum consumption (C_{max}) possible for a given species at a given temperature and prey density,
C_{max} = the ceiling value of consumption for a particular sized predator at its optimal temperature, where C_{max} is defined as:

$$C_{max} = a_c W^{b_c} \tag{5}$$

Prey density will only contribute to growth as long as P in the consumption equation (equation 4) remains < 1. When P = 1, further increase in the prey density no longer contribute to predator growth (see Brandt 1993).

Similarly, respiration in terms of growth can be calculated as a function of fish weight, ambient temperature and prey density.

$$R = a_r W^{b_r} \cdot f(T) \cdot A \ + S(C - F) \tag{6}$$

Prey density in this case however, is related to respiration only through its influence on consumption C.

Where a_r = the standard respiration rate achieved at optimal temperature for respiration,
b_r = the exponent relating weight dependent respiration,
W= the wet weight of the fish,

T = the ambient temperature,
A = the activity index of respiration rates above standard level,
S = a coefficient related to the cost of digestion, absorption and assimilation of energy, and,
F = the egestion term of the growth equation (equation 3).

F is defined by the following formula:

$$F=C\cdot a_f\, T^{b_f}\cdot e^{(g_f\cdot P)} \tag{7}$$

Where C = consumption as detailed in equation (4),
T = the ambient water temperature,
a_f = the proportion of consumption egested when the fish is at 1°C (Brandt 1993),
b_f = the exponent relating temperature to egestion,
g_f = a coefficient relating the feeding level P to the egestion rate.

Excretion U can be derived as per egestion (equation 7), by substituting (C-F) for C, and replacing the subscripts *f* with u (see Brandt 1993).

In a heterogenous environment where temperature and prey are nonuniformly distributed, this model can partition the environment into areas of varying growth rates. This creates an environment represented by a mosaic of sub-environments, each characterized by a different growth rate potential (Hondorp and Brandt 1996; Brandt and Kirsch 1993; Brandt et al., 1992). Potential is an adequate term because this model delimits the environment only in terms of how well a particular fish would grow if placed within this environment, and is completely independent of the actual distribution of this fish (Hondorp and Brandt 1996; Brandt 1993; Brandt et al., 1992). We assume therefore, that a fish conforming to the behavioural bioenergetic distributional process, will aggregate in areas that maximize its growth rate (in areas of highest growth rate potential).

Goyke and Brandt (1993) attempted to relate fish distributions to maximum growth rate potentials, and concluded that (1), the proportion of the environment able to support species specific positive growth rate varies substantially over time (Mason et al., 1995; Brandt and Kirsch 1993; Goyke and Brandt 1993) and (2), the degree of overlap between the areas of maximum growth rate potentials and the actual fish distribution also varied with time (Goyke and Brandt 1993). This suggests that behavioural bioenergetics as a distributional process may also be subject to temporal dynamics, and that its ability to predict fish distributions is time dependent.

Sampling Limitations

To evaluate the relative importance of each of the distributional processes described above we chose to perform an *in situ* examination of predator distribution at one particular area of a lake system over time. *In situ* estimates of ecological parameters are generally more useful than laboratory derived estimates because the latter tend to misrepresent the actual environmental processes with which they are involved (Hansen et al., 1993; Ney 1993; Gorbas et al., 1989; Bartell et al., 1986). Choosing an *in situ* study however, makes the acquisition of fish distribution measurements over time problematic as the aquatic environment is generally not conducive to high temporal resolution sampling schemes.

Gillnets

Olson et al., (1988) used six vertical gillnets to determine the distribution of salmonids in south-central Lake Ontario. Gillnets however, are size and species selective (Hubert

1996). The distribution of fish caught in the gillnets is proportional to the size of the net perforations. Very large fish are unable to fit through the mesh and will not get tangled, while smaller ones will swim through (Hubert 1996). Certain species are capable of detecting the nets by olfaction or sight, and actively avoid them altogether (Hubert 1996). Most fish caught in gillnets die or are mortally wounded by the experience, ultimately removing them form the population under study (Hubert 1996; Leadley pers. communication, Great Lakes Inst.for Env. Res.). The efficiency of gillnets is also time dependent — catch size typically increases with the length of net deployment (Hubert 1996). The sampling resolution with which gillnets can be used is limited by the deployment and collection times, as well as the time required to fish the nets efficiently (Hubert 1996).

Trawling

Directed trawling has been used successfully to measure fish distributions in a variety of systems (Brandt et al., 1980; Foltz and Norden 1977; Wells 1968). Again, however, trawl sampling resolution is largely determined by the deployment and retrieval rates, as well as the time needed to perform the trawls efficiently (Hayes et al., 1996). Because trawls require nets to be pulled through the habitat by a vessel, the actual area sampled may vary depending on the manoeuverability of the boat and the driving skills of the captain (Hayes et al., 1996). It has also been argued that trawls are species and size selective as large, fast-swimming fish may perceive and avoid the passing nets (Brandt 1996; Hayes et al., 1996; Brandt et al., 1991; Levy 1991; Thorne 1983; Brandt et al., 1980). Other bottom dwelling species may avoid trawls by finding refuge in bottom depressions where the nets are unable to reach (Brandt 1996; Argyle 1992). Trawls have also been shown to wound or kill collected fish by subjecting them to large pressure changes when they are quickly brought to the surface (Hayes et al., 1996). Thus, trawling also removes the fish used to make inferences about distribution from the population and potentially skews resulting estimates.

Biotelemetry

In an alternative approach, Takai et al., (1997), used ultrasonic biotelemetry to monitor the distribution and spawning behaviours of Lake Biwa catfish (*Silurus biwaensis*). Temporal resolution of samples taken with telemetry are not as sensitive to sampling protocol as are trawl tows or gillnets. Still, studies show that telemetry devices substantially influence the swimming performance, metabolic costs, and natural behaviour of fish in which they have been implanted (Adams et al., 1998; Mellas and Haynes 1985; McCleave and Stred 1975). This, to a certain extent, defeats the study's purpose, especially when used to describe physiology and natural behaviour (Adams et al., 1998). Telemetry devices can also be costly, and the number of devices used may be restricted to only a few individuals within the studied population (e.g. Takai et al., 1997). Conclusions derived from the observations of selected individuals may not necessarily apply to the entire population.

Hydroacoustics

Hydroacoustics uses a directed beam of sound characterized by a particular frequency, wavelength, and pulse duration generated by a transducer or echo-sounder (Peterson et al., 1976). The generated sound waves move through the water in a unique (transducer dependent) directivity pattern along a central 'acoustic axis' (Brandt 1996; MacLennan and Simmonds 1992; Clay and Medwin 1977). The sound propagation is strongest along this axis and diminishes with increased angular displacement (Brandt 1996; MacLennan and Simmonds 1992; Rose and Leggett 1988; Clay and Medwin 1977; Peterson et al., 1976). Generated sound waves travel through the water at approximately 1500 m s^{-1} and when encountering an object having a different density than that of the surrounding water they scatter in a spherical wave-like pattern (Brandt 1996; MacLennan and Simmonds 1992). Portions of the scattered sound are directed back toward their source of origin. Devices register the reflected sound as an electrical voltage of characteristic length and amplitude which is later converted to a target size. The length of time it takes the incident sound pulse to reach, scatter, and return to the transducer is a robust estimate of the object's distance from the transducer face (Hondorp and Brandt 1996; Brandt 1996; MacLennan and Simmonds 1992; Rose and Leggett 1988; Thorne 1983; Clay and Medwin 1977).

Hydroacoustics is particularly amenable to fish distributional studies because of its ability to continuously sample the pelagic environment of aquatic systems. The increase in potential sampling resolution allows for more accurate estimations of distribution over time (Stables and Thomas 1992). Also, the non-obtrusive nature of the sound signal has been shown to have negligible influence on fish performance and behaviour (Brandt 1996).

Traditionally, hydroacoustics has been used to replace or enhance more conventional stock assessments methods (Algen 1996; Porteiro et al., 1996; Thompson and Love 1996; Argyle 1992; Stables and Thomas 1992; Bjerkeng et al., 1991; Brandt et al., 1991; MacLennan and MacKenzie 1988; Burczynski and Johnson 1986). For example, Wespestad and Megrey (1990) showed that commercial fisheries and research vessel bottom trawl data greatly underestimated walleye pollock (*Theragra chalcogramma*) abundances in the North Pacific Ocean. The integration of hydroacoustics in the annual stock assessment protocol lead to the discovery of a large, previously undetected walleye pollock biomass in the pelagic environment of this system (Wespestad and Megrey 1990).

The advent of more sophisticated systems expanded the use of hydroacoustics to include studies into fish behaviour, distributions of zooplankton and phytoplankton, and studies of egg production (Fréon et al., 1996; Hampton 1996; Hewitt and Demer 1996; Marchal and Lebourges 1996; Martin et al., 1996; Pitcher et al., 1996; Selivanovsky et al., 1996; Stanton et al., 1996; Tameishi 1996). More ecologically derived investigations have coupled the high resolution capabilities of hydroacoustics with bioenergetic and foraging calculations to develop spatially explicit models of fish growth and consumption (Hondorp 1998; Hondorp and Brandt 1996 Mason and Brandt 1996; Mason et al., 1995; Brandt and Kirsch 1993; Goyke and Brandt 1993; Luo and Brandt 1993; Brandt et al., 1992). These models characterize the spatial heterogeneity (patchiness) of the environment in terms of a particular species, and partition the habitat into different areas capable of supporting different levels of growth and consumption. In particular reference to growth, these models help define the species specific suitability or quality of the sampled habitat. Mason et al., (1995) used such spatially explicit definitions of habitat quality to compare and contrast the relative abilities of Lakes Ontario and Michigan to support salmonid growth. Perhaps the major caveat of spatially explicit habitat quality indices is their failure to consider temporal changes in the quality of these habitats.

Study Outline

The overall purpose of this study is to determine the relative importance of different distributional processes such as temperature, prey distributions, and the combination thereof in describing predator distribution in the pelagia of dynamic aquatic systems over time. In the second chapter, I will develop a temporally explicit model of fish growth at two time scales. The first time scale models fish growth rate potential at 1 minute intervals over a 24-hour period and demonstrates how models of growth rate distributions within a sampled environment change on a fine scale. Coarse scale dynamics of growth rate distributions are modelled at monthly intervals form May 1997 to mid-October of the same year. This novel approach in assessing growth rate potentials of fish follows a development similar to that of Brandt et al., (1992) but models time as an explicit feature of the environment rather than space. To this end, we use hydroacoustics to collect high temporal resolution images of fish distributions in one area of Lake Ontario over time. These remotely sensed images of fish distribution allow distinction between predator and prey based on the size of the acoustic targets. Because chinook salmon account for more than 40% of the top-predators stocked in this system, it will be assumed that all predators distributions are of chinook salmon. Likewise, past records indicate that the most abundant forage species in this system is the alewife (almost 67%) (Schaner and Lantry 1998; Stewart and Schaner 1998; O'Gorman et al., 1997 a; O'Gorman et al., 1997 b;

Goyke and Brandt 1993; GLFC Lake Ontario committee task force 1992; Brandt 1986). Thus, prey distributions will be assumed to be those of this species only.

Measurements of Fish distributions are complemented by water temperature profiles collected in the same area over time. Prey fish distribution and temperature were combined in bioenergetic and foraging calculations to determine growth rate potential, and thus habitat quality of chinook salmon in the sampled environment over time. Monitoring the habitat quality through time in this fashion can provide valuable insight for both managers and researchers into the dynamics of the habitat and its influence on the economically important or endangered species.

The primary goal of the third chapter, is to assess the relative importance of different distributional processes to chinook salmon distribution in (one area of) western Lake Ontario over time. To achieve this goal, I compare actual chinook distributions measured acoustically to predicted distributions based on the 3 distributional processes outlined above, namely; behavioural thermoregulation, optimal foraging, and behavioural bioenergetics. Chapter III uses the habitat quality estimates obtained in Chapter II to delimit the sampled environment in terms of behavioural bioenergetics. The relative importance of each distributional process is assessed at both fine (1 minute intervals over 24 hours) and coarse (monthly intervals) scales of observation. The degree of congruence or overlap between the actual chinook distribution and the predicted distributions using each individual distributional process is statistically quantified using correlation analysis. The distributional process with the highest significant degree of congruence is ranked as the best descriptor of chinook distribution over a specified time interval. This approach has the implicit assumption that chinook distribution is indicative of its environmental preference.

Significance

The significance of this study is to demonstrate that the environment in which the fish find themselves is dynamic on many scales, and that the fish will respond to these changes based on what is available and what they require. Measurements of fish distributions and environmental conditions made at arbitrary scales of time may show a strong relationship, but this relationship may be distinct only to that particular time interval. Moreover, changes in the environmental conditions can change this relationship based on fish needs and the ability of the ambient environment to fill that need. Understanding how changes in environmental conditions can influence fish distribution over time can help describe what fish needs are, when. Insight into the needs of the fish, and its response to those needs gives insight into behaviour of the fish and the relation of these behaviours to the dynamics of this environment. The scale at which these behaviours are observed is critical, as certain behaviours may be elicited by spontaneous punctuated events, while others by more predictable prolonged ones. Although the question of where fish can be found, is of great importance to both managers and researchers when attempting to describe fish distribution and abundances, the question of when the fish can be found is equally important.

References

Adams, N., D. Rondorf, S. Evans, J. Kelly, and W. Perry. 1998. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 55:781-787.

Alcock, J., 1988. Animal Behavior. 4th ed. Sinauer Associated Pres, Sauderland. Massachusetts

Algen, A. 1996. Impact of fish distribution and species composition on the relationship between acoustic and swept-area estimates of fish density. *ICES Journal of Marine Science*, 53:501-05.

Argyle, R. 1992. Acoustic as a tool for the assessment of Great Lakes forage fishes. *Fish. Res.*, 14:179-96.

Bartell, S., J. Breck, R. Gardner, and A. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Can. J. Fish. Aquat. Sci.* 43:160-68.

Bevelhimer, M., and S. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* 50:2336:49.

Bjerkeng, B., R. Borgstrom, A. Brabrand, and B. Faafeng. 1991. Fish size distribution and total fish biomass estimated by hydroacoustical methods: a statistical approach. *Fish. Res.* 11:41-73.

Brandt, S. 1996. Acoustic assessment of fish abundance and distribution. Chapter 13 in Fisheries Technologies. 2nd ed. B. Murphy, and D. Willis eds. American Fisheries Society publication. Bethesda. Maryland.

Brandt, S. 1993. The effects of thermal fronts on fish growth: A bioenergetics evaluation of food and temperature. *Estuaries* (1):142-59.

Brandt, S., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Trans. Am. Fish. Soc.* 122:845-69.

Brandt, S., D. Mason, and V. Patrick. 1992. Spatially-explicit models of fish growth rate. *Fisheries.* 17(2):23-33.

Brandt, S., and six co-authors. 1991 .Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 48:894-908.

Brandt, S. 1986. Food of trout and salmon in Lake Ontario. *J. Great. Lakes. Res.* 12(3):200-05.

Brandt, S., and V. Wadley. 1981. Thermal fronts as ecotones in zoogeographic barriers in marine and freshwater systems. *Proceedings of the Ecological Society of Australia.* 11:13-26.

Brandt, S., J. Magnuson, and L. Crowder. 1980. Thermal partitioning by fishes in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 37:1557-64.

Brett, J. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zoologist.* 11:99-113.

Brett, J. 1952. Temperature tolerance in young pacific salmon genus *Oncorhynchus. J. Fish. Res. Bd. Can.* 9(6):265-309.

Burczynski, J., and R. Johnson. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 43:1776-88.

Carpenter, S., and J. Kitchell. 1987. The temporal scale of variance in limnetic primary production. *Am. Nat.* 129:417-33.

Carpenter, S., J. Kitchell, and J. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience.* 35(10):634-39.

Christie, G., and H. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. *Can. J. Fish. Aquat. Sci.* 45:301-14.

Clark, W., and D. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon in the antipredation window. *Am. Nat.* 131:271-90.

Clay, C., and H. Medwin. 1977. Acoustical Oceanography: principles and applications. Wiley, New York.

Crowder, L., and J. Magnuson. 1983. Cost-benefit analysis of temperature and food resource use: A synthesis with examples from the fishes. In Behavioral Energetics: The cost of survival in vertebrates. W. Aspey, and S. Lustick eds. Ohio State University Press. Columbus.

Dodson, S. 1998. What is Ecology? In Ecology. S. Dodson, T. Allen, S. Carpenter, A. Ives, R. Jeanne, J. Kitchell, N. Langston, and M. Turner. Oxford University Press. Oxford, England.

Dolloff, C., P. Flebbe, and M. Owen. 1994. Fish habitat and fish populations in a southern Appalachian watershed before and after hurricane Hugo. *Trans. Amer. Fish. Soc.* 123:668-78.

Eckert, R. 1988. Animal Physiology: Mechanisms and Adaptations. 3rd ed. W. H. Freeman and Company. New York.

Filbert, R., and C. Hawkins.1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in Green River, Utah. *Trans. Am. Fish. Soc.* 124:824-835.

Foltz, J., and C. Norden. 1977. Food habits and feeding chronology of rainbow smelt, *Osmerus mordax*, in Lake Michigan. *Fish. Bull.* 75:637-40.

Frank, K., and W. Leggett. 1982. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*), and its application to the match/mismatch hypothesis. *Can. J. Fish. Aquat. Sci.* 39:691-99.

Fréon, P., F Gerlotto, and M. Soria. 1996. Diel variability of school structure with special reference to transition periods. *ICES Journal of Marine Science*. 53:459-64.

Gaston, K., and J. Lawton. 1990. Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos* 58:329-335.

Gerritsen, J., and J. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Bd. Can.* 34:73-82.

Gorbas, F., D. Bedard, J. Ciborowski, and D. Haffner. 1989. Bioaccumulation of chlorinated hydrocarbons by the mayfly (*Hexagenia limbata*) in Lake St. Clair. *J. Great. Lakes. Res.* 15(4):581-88.

Goyke, A., and S. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. *Trans. Am. Fish. Soc.* 122:870-83.

Hampton, I. 1996. Acoustic and egg-production estimates of South African anchovy biomass over a decade: Comparison, accuracy, and utility. *ICES Journal of Marine Science*. 53:493-500.

Hansen, M., and six co-authors. 1993. Applications of bioenergetics models to fish ecology and management: Where do we go from here? *Trans. Am. Fish. Soc.* 122:1019-30.

Harris, G. 1980. Temporal and spatial scales in phytoplankton ecology, mechanisms, methods, and management. *Can. J. Fish. Aquat. Sci.* 37:877-900.

Hayes, D., P. Ferreri, and W. Taylor. 1996. Active fish capture methods. Chapter 7. In Fisheries Technologies. 2nd ed. B. Murphy, and D. Willis eds. American Fisheries Society publication. Bethesda. Maryland.

Hewett, S., and B. Johnson. 1992. A generalized bioenergetics model of fish growth for microcomputers, version 2.0. University of Wisconsin Sea Grant Institute. Madison. WI.

Hewitt, R., and D. Demer. 1996. Lateral target strength of antarctic krill. *ICES Journal of Marine Science.* 53:297-302.

Holling, C. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* 62(4):447-502.

Holt, R. 1997. From Metapopulation dynamics to community structure: Some consequences of spatial heterogeneity. In Metapopulation Biology, Ecology, Genetics, and Evolution. I. Hanski, and M. Gilpin eds. Academic Press. San Diego.

Hondorp, D. 1998. Spatial distributions of planktivorous fish and zooplankton in western Lake Ontario: Implications for fish thermal ecology, fish bioenergetics modeling and trophic interactions. M. Sc. thesis State Univ. New York Coll. Buff. New York. 126 p.

Hondorp, D., and S. Brandt. 1996. Spatially-explicit models of fish growth rate: Tools for assessing habitat quality. *Great. Lakes. Res. Rev.* 2(2):11-19.

Hubert, W. 1996. Passive capture techniques. Chapter 6. In Fisheries Technologies. 2nd ed. B. Murphy, and D. Willis eds. American Fisheries Society publication. Bethesda. Maryland.

Janssen, J., and S. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 37:177-84.

Javaid, M., J. Anderson, 1967. Influence of starvation on selected temperature of some salmonids. *J. Fish. Res. Bd. Can.* 24(7):1515-19.

Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area restricted search. *Am. Nat.* 130:233-70.

Kelsch, S. 1996. Temperature selection and performance by bluegills: Evidence for selection in response to available power. *Trans. Am. Fish. Soc.* 125:948-55.

Kitchell, J., D. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Bd. Can.* 34:1922-35.

Krebs, J., and A. Kacelnik. 1993. Decision-making. *In* J. Krebs, and N. Davies. Eds. Behavioural Ecology: An evolutionary approach. 3rd edition. Blackwell Scientific Publications. Oxford.

Lawton, J. 1987. Problems of scale in ecology. *Nature*. 325:206.

Legendre, P., and S. Demers. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.* 41:2-19.

Legendre, P., and M. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107-38.

Levandowsky, M., and B. White. 1977. Randomness, time scales, and evolution of biological communities. *Evol. Biol.* 10:69-161.

Levin, P. 1994. Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Environmental Biology of Fishes*. 40:271-81.

Levin, S. 1992. The problem of pattern and scale in ecology. *Ecology*. 73(6):1943-67.

Levy, D. 1991. Acoustic analysis of diel vertical migration behavior of *mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. *Can. J. Fish. Aquat. Sci.* 48:67-72.

Levy, D. 1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia Lakes. *Can. J. Fish. Aquat. Sci.* 47 1755-64.

Luo, J., and S. Brandt. 1993. Bay anchovy *Anchoa mitchilli* production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. *Mar. Ecol. Prog. Ser.* 98:223-36.

Mac, M. 1985. Effects of ration size on preferred temperature of lake char *Salvelinus namaycush*. *Env. Biol. Fish.* 14(2-3):227-31.

MacLennan, D., and G. MacKenzie. 1988. Precision of acoustic fish stock estimates. *Can. J. Fish. Aquat. Sci.* 45:605-16.

MacLennan, D., and J. Simmonds. 1992. Fisheries Acoustics. Chapman Hall. London.

Magnuson, J., L. Crowder, and P. Medvick. 1979. Temperature as an ecological resource. *Amer. Zool.* 19:331-43.

Marchal, E., and A. Lebourges. 1996. Acoustic evidence for unusual diel behaviour of a mesopelagic fish (*Vinciguerria nimbaria*) exploited by tuna. *ICES Journal of Marine Science* 53:443-47.

Martin, L., T. Stanton, P. Wiebe, and J. Lynch. 1996. Acoustic classification of zooplankton. *ICES Journal of Marine Science* 53:217-24.

Mason, D., and S. Brandt. 1996. Effects of spatial scale and foraging efficiency on the predictions made by spatially explicit models of fish growth rate potential. *Env. Biol. Fish.* 45:283-98.

Mason, D., A. Goyke, and S. Brandt 1995. A spatially explicit bioenergetics measure of habitat quality for adult salmonines: Comparison between Lakes Michigan and Ontario. *Can. J. Fish. Aquat. Sci.* 52:1572-83.

McCleave, J., and K. Stred. 1975. Effect of dummy telemetry transmitters on stamina of Atlantic salmon (*Salmo salar*) smolts. *J. Fish. Res. Bd. Can.* 32:559-63.

Mc Eadie, J., and A. Keast. 1983. Resource heterogeneity and fish species diversity in Lakes. *Can. J. Zool.* 62:1689-95.

Mellas, E., and J. Haynes. 1985. Swimming performance and behavior of rainbow trout (*Salmo gairdneri*) and white perch (*Morone americana*): effects of attaching transmitters. *Can. J. Fish. Aquat. Sci.* 42:488-93.

Moyle, P., and J. Cech. 1996. Fishes: An Introduction to Ichthyology. 3rd ed. Prentice Hall. Upper Saddle River, New Jersey.

Ney, J., 1993. Bioenergetics modeling today: Growing pains on the cutting edge. *Trans. Am. Fish. Soc.* 122:736-48.

Ney, J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences.* 2:55-81.

O'Gorman, R., O. Johannsson, C. Schneider.1997 a. Age and growth of alewives in the changing pelagia of lake Ontario, 1978-1992. *Trans. Am. Fish. Soc.* 126:112-26.

O'Gorman, R., R Owens, C. Schneider, and T. Eckert. 1997 b. The status of the major prey fish stocks in the U.S. waters of Lake Ontario, 1996. In 1996 annual Report, Bureau of Fisheries and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.

Olson, R., J. Winter, D. Nettles, and J. Haynes. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. *Trans. Am. Fish. Soc.* 117:552-59

Perry, I., and S. Smith. 1994. Identifying habitat association of marine fishes using survey data: An application to the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 51:589-602.

Peterson, M., C. Clay, and S. Brandt. 1976. Acoustic estimates of fish density and scattering function. *J. Acoust. Soc. Am.* 60(3):618-22.

Pitcher, T., O. Misund, A. Fernö, B. Totland, and V. Melle. 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. *ICES Journal of Marine Science* 53:449-52.

Porteiro, C., P. Carrera, and J. Miquel. 1996. Analysis of Spanish acoustic surveys for sardine, 1991-1993: Abundance estimates and inter-annual variability. *ICES Journal of Marine Science* 53:429-33.

Rand, P., and D. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: A test of a bioenergetics model prediction. *Can. J. Fish. Aquat. Sci.* 55:307-17.

Rand, P., B. Lantry, R. O'Gorman, R. Owens, and D. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978-1990: Implications of salmonine energetics. *Trans. Am. Fish. Soc.* 123:519-34.

Rose, G., and W. Leggett. 1988. Hydroacoustic signal classification of fish schools by species. *Can. J. Fish. Aquat. Sci.* 45:597-604.

Ryer, C., and B. Olla. 1995. Influences of food distribution on fish foraging behaviour. *Anim. Behav.* 49:411-18

Schaner, T., and B. Lantry. 1998. Pelagic planktivores. In 1998 Annual Report, Lake Ontario Management Unit. To the Great Lakes Fishery Commission, lake Ontario Committee.

Schmidt-Nielsen, K. 1990. Animal Physiology: Adaptation and Environment. 4th ed. Cambridge University Press. Cambridge.

Selivanovsky, D., P. Stunzhas, and I Didenkulov. 1996. Acoustical investigation of phytoplankton. *ICES Journal of Marine Science* 53:313-16.

Sih, A. 1980. Optimal foraging: Partial consumption of prey. *Am. Nat.* 116:281-90.

Stables, T., and G. Thomas. 1992. Acoustic measurement of trout distribution in Spada Lake, Washington, using stationary transducers. *J. fish. Biol.* 40:191:203.

Stanton, T., D. Chu, and P. Wiebe. 1996. Acoustic scattering characteristics of several zooplankton groups. *ICES Journal of Marine Science* 53:289-95.

Stewart, D., and M. Iberra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-1988. *Can. J. Fish. Aquat. Sci.* 48:909-22.

Stewart, D., D. Weininger, D. Rottiers, and T. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: Application to the Lake Michigan population. *Can. J. Fish. Aquat. Sci.* 40:681-98.

Stewart, T., and T. Schaner. 1998. Alewife and their role in structuring the Lake Ontario fish community. *Great. Lak. Res. Rev.* 3(2):28-31.

Stommel, H. 1963. Varieties of oceanographic experience. *Science* 139:572-76.

Takai, N., W. Sakamoto, M. Maehata, N. Arai, T. Kitagawa, and Y. Mitsunaga. 1997. Settlement characteristics and habitats use of Lake Biwa catfish *Silurus biwanensis* measured by ultrasonic telemetry. *Fish. Sci.* 63(2):181-87.

Tameishi, H., H. Shinomiya, I. Aoki, and T. Sugimoto. 1996. Understanding Japanese sardine migrations using acoustic and other aids. *ICES Journal of Marine Science* 53:167-71.

Thomas, C. 1991. Spatial and temporal variability in a butterfly population. *Oecologia* 87:577-80.

Thompson, C., and R. Love. 1996. Determination of size distribution and areal densities using broadband low-frequency measurements. *ICES Journal of Marine Science* 53:197-201.

Thorne, R. 1983. Assessments of population abundance by hydroacoustics. *Biol. Oceano.* 2:(2-3-4):253-62.

Turner, M. 1998. Landscape ecology: Living in a mosaic. In Ecology. S. Dodson, T. Allen, S. Carpenter, A. Ives, R. Jeanne, J. Kitchell, N. Langston, and M. Turner. Oxford University Press. Oxford, England.

Tyler, J., and J. Gilliam. 1995. Ideal free distributions of stream fish: a model an test with minnows, *Rhinicthys aratulus*. *Ecology*. 76(2):580-92.

Tyler, J., and K. Rose. 1996. Effects of individual habitat selection n a heterogenous environment on fish cohort survivorship: A modelling analysis. *J. Anim. Ecol.* 65:1-15.

Warwick, W. 1996. Assessing chemical contamination in the St. Clair River using morphological deformities in choronomid larvae. (Diptera: Choronomidae). Prepared for: Ontario Ministry of the Environment Detroit / St. Clair / St. Mary's River Project. 1094 London Rd. Sarnia Ontario.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. *Fish. Bull.* 67(1):1-15.

Wespestad, V., and B. Megrey. 1990. Assessment of Walleye pollock stocks in the eastern North Pacific Ocean: an integrated analysis using research survey and commercial fisheries data. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.* 189:33-49.

Wildhaber, M., and L. Crowder. 1991. Mechanisms of patch choice by bluegills (*Lepomis macrochirus*) foraging in a variable environment. *Copeia* 2:445-60.

Wildhaber, M., and L. Crowder. 1990. Testing a bioenergetics-based habitat choice model: Bluegill (*Lepomis macrochirus*) responses to food availability and temperature. *Can. J. Fish. Aquat. Sci.* 47:1664-71.

CHAPTER II: Temporally explicit models of chinook (*Oncorhynchus tshawytscha*) growth rate potential in western Lake Ontario.

Introduction

Processes defining environmental conditions are inherently heterogenous in time and space (Horne et al., 1996). This environmental heterogeneity imposes patterns in resources and in organism response to the distribution of these resources. The perception of environmental heterogeneity, however, is mitigated by the scale at which observations are made (Sale 1998; Holling 1992; Levin 1992; Carpenter and Leavitt 1991). For example Rose and Leggett (1990), demonstrated that the correlation between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) distributions varied widely over the scales at which they were measured. This leads to the notion that environmental heterogeneity is expressed in a scale dependent fashion.

Patterns in ecological systems and scaling principles are intimately related where patterns observed at one particular scale may mask others occurring at a variety of other scales (Sale 1998; Holling 1992; Levin 1992; Jassby et al., 1990). Carpenter and Leavitt (1991), demonstrated that the influences of El Niño Southern-Oscillation (ENSO) events were not readily recognized from a lakes' paleolimnological record until the 5 year periodicities associated with the trophic cascades of the system were removed.

Other patterns observed in data are a function of processes that are interdependent on several scales of observation. For example, Stommel (1963) contends that a description of the surface temperature of the sea would require the consideration of factors ranging in scale from unitary measures of vertical heat transfer (fine scale) to

shifts in continental currents and meteorological events (coarse scale).
Ecological studies which consider heterogeneity of the environment, and associated scaling principles, can lead to significant contributions in ecology. Lasker (1978) demonstrated that the success of the northern anchovy in the California Current relied on the principle of differential starvation. Successful larvae were able to co-occur in unevenly distributed, dense patches of food particles occurring sporadically within the current. Larvae unable to reach these patches before first-feeding, starve (Lasker 1978). The consideration of spatial complexity in the above study elucidates the stochastic nature of recruitment success in this fishery.

Pearson et al., (1995) demonstrated that certain phenomena or events can have varying degrees of influence depending on the scale at which they are observed. The winter foraging pattern of bison (*Bison bison*) in Yellowstone National Park appears to be random, with no particular selection method in terms of grazing area (Pearson et al., 1995). However, when the scale of observation was extended to include many such grazing areas, bison foraging became highly associated with recently (2-3 year previous) burned grass fields. Further expansion of the spatial resolution (or grain) to include almost 7 500 ha indicated that bison grazing typically occurred on southern-facing slopes of large hills, where snow accumulation and density tended to be less (Pearson et al., 1995). The bison study demonstrated that, at small spatial resolution (fine grain) patterns are random or even absent, however, as the resolution is expanded (coarse grain) the behavioural pattern of bison winter foraging emerges.

Other phenomena meanwhile, have the power to entrain patterns transcending many different scales. Frank and Leggett (1981; 1982a; 1982b) suggested that the emergence of larval capelin from their beach spawning beds, is predicated by onshore winds mediating decreased predation pressure, increased food availability, and the provision of optimal temperature and salinity. The frequency of such onshore winds ultimately determines the size and success of the capelin year-class which is used both as a natural resource, and as forage for other commercially important fish stocks (Frank and Leggett 1981; 1982a; 1982b; 1983).

Environmental and resource heterogeneity are characterised by both spatial and temporal dimensions (Turner 1998; McEadie and Keast 1984). Yet in aquatic ecology, and especially in fisheries, studies tend to deal more with spatial rather than temporal complexities (Hondorp 1998). This can be reconciled by the fact that many fisheries studies are geared toward understanding the complex relationships between the abiotic and biotic conditions within the environment, and the ability of these environments to sustain economically important fish stocks (Rand and Stewart 1998; Rand et al., 1994; Bevelhimer and Adams 1993; Stewart and Iberra 1991; Stewart et al., 1983). Traditionally however, many of these studies calculated species sustainibility based on system-wide averages of environmental parameters such water temperature, prey density, and others. Although useful for generating robust estimates of habitat suitability, these studies generalize the importance of spatial relationships leading to extremely inaccurate estimation of environmental sustainability (Hondorp 1998; Brandt and Kirsch 1993; Brandt et al., 1992)

Brandt et al., (1992) formalized a spatially explicit model specifically designed to take into consideration spatial complexities within aquatic systems. Spatially explicit modelling typically separates the sampled environment into a raster or grid-based system (Turner 1998; Brandt et al., 1992). Depending on the resolution of observations, cell size within the grid can be adjusted so that a particular set of environmental conditions may be considered homogenous within each cell. Environmental conditions in neighbouring cells, however, can be very different. Together these unitary cells combine to form a mosaic representation of the environment demonstrating its internal spatial structure (Turner 1998). Brandt et al., (1992), used such an approach to model fish growth rate potential, which they equate with habitat quality, of a variety of economically important fish species in various systems (Hondorp and Brandt 1996; Mason et al., 1995). A specific modelling effort conducted for striped bass (*Morone saxatilis*) in the Chesapeake Bay system demonstrated that system-wide estimates of growth rate potentials exceeded those measured using the spatially-explicit approach by 176-400 % (Brandt and Kirsch 1993).

A major caveat to the spatially explicit modelling approach is the implicit assumption of temporal stability within the environment (Mason and Patrick 1993; Brandt et al., 1992). Such studies demonstrate essential spatial relationships, but conjure the notion of a static environment, or at the very least, one that changes in a predictable linear fashion with time. Many fisheries studies are sensitive to temporal change, but more often than not, ecological studies omitting rates of change in measured variables, assume the system has reached an ecological equilibrium state. Holling (1992), Steele (1985), and May (1977), all argue separately that even if such a theoretical equilibrium state of the ecosystem existed, the probability that the ecosystem under study is actually at this equilibrium state is infinitesimally small. Rather, most ecosystems are in perpetual states of flux always tracking the equilibrium state which is itself dynamic with time. As such, studies assuming static environmental conditions offer little more than a 'snapshot' of actual ecosystem function. Thus, although aquatic systems may be spatially complex, they also have an inherent temporal dynamic which is often overlooked.

In this chapter, a modification of the spatially explicit approach is developed to quantify fish growth at two time scales. The first time scale models fish growth rate potential at 1 minute intervals over a 24-hour period to quantify changes in growth rate potential on a 24-hour basis. Coarser scale dynamics of growth rate potential were also modelled at monthly intervals from May 1997 to mid-October of the same year. This novel approach in assessing growth rate potential of fish, as it relates to habitat suitability, follows a development similar to the spatial studies of Brandt et al., (1992) but models time as an explicit feature of the environment rather than space.

The western end of Lake Ontario is a temporally dynamic system (Boyce et al., 1991) with well established fish species assemblages. The Lake Ontario system is annually stocked by large piscivorus salmonids which use alewife (*Alosa pseudoharengus*) as their principal forage (Stewart et al., 1998; O'Gorman et al., 1997; O'Gorman et al., 1987). The original goals of the stocking process were primarily to re-establish predatory control over the abundant alewife population, and to create a substantial recreational fishery for these large pleasing predatory fish (Stewart and Schaner 1998; O'Gorman et al., 1986). Pacific salmonids such as chinook

(*Oncorhynchus tshawytscha*), and Coho (*O. Kisutch*) were chosen primarily on the basis of their natural affinity to select alewife as prey items. Because these fish have little to no natural reproduction in this system, their populations are maintained by annual stocking (Stewart and Schaner 1998; Stewart et al., 1998; Rudstam et al., 1996; Goyke and Brandt 1993; Jones et al., 1993).

The economical benefits associated with the creation of this recreational fishery have become very important to the economic stability of the region. Over the years, accrued benefits motivated increases in stocking rates which peaked in 1986 (Elrod and O'Gorman 1991). Stocking levels were maintained near 1986 levels through the early 1990's, after which studies showed considerable alewife stock decline.

Presently, there is concern that the stocked salmonids are imposing too high a predatory demand on the Lake Ontario alewife population (Stewart et al., 1998; O'Gorman et al., 1997). Stocking rates have since been curbed, but anxiety remains about the decreasing availability of the alewife to salmonids. Does the Lake Ontario system continue to provide suitable habitat for growth of the stocked salmonid predators? If so, are the habitat conditions optimizing growth stable or dynamic through time? I predict that temporal variability in resources availability (alewife prey), and habitat quality (temperature) regulates the growth rate potential of salmonids in western Lake Ontario, and that the amount of growth supported is dynamic with time. This hypothesis is tested using a novel, high resolution, stationary acoustic sampling technique.

Methods

Acoustic sampling

I collected acoustic data continuously over 5 different sampling events during May 27-28, June 19-20, July 30-31, September 5-6, and October 18-19, 1997. All data were collected at one station established in the south western portion of Lake Ontario (Figure 2.1). Station location was primarily chosen to avoid areas of high navigational traffic, yet remain in the meso-pelagic environment. The occurrence of sampling events and their duration was predicated by weather conditions and research vessel time availability. Each sampling event was anticipated to last 24 hours, however, September and October sampling events were interrupted because of deterioration of sea conditions, and data contamination form artificial light levels.

Acoustic data were collected using a downward facing, 120 kHz, EY500 Simrad® echo-sounder equipped with a split-beam transducer. The transducer was mounted to a stable platform, which kept it in a near-perfect vertical position within the water column and was specifically designed to de-couple the device from the surface activity of the water. The acoustic signal was characterized with a pulse length of 0.3 ms, and had a pulse repetition rate of 2 pulses s^{-1}. The acoustic signal was corrected for spreading and absorption in the water by applying a $40 \log_{10} R$ (where R is distance) time-varied gain (TVG), and recorded to magneto-optical disk. Before the start of each sampling event, acoustic system parameters and performance were evaluated using an internal oscillator test with software provided by the manufacturer. In June, the transducer used during the May sampling event, specified by a ½ beam width of 7.1°, was temporarily replaced by one having a ½ beam width of 6.7°. From July onward, the temporary transducer used during June was permanently replaced by one characterized with a ½ beam width of 7.2°. Acoustic systems were calibrated by suspending a standard tungsten carbide reference sphere of known target strength (-40.4 dB) under the transducer at varied depths. The difference between the mean target strengths emanating from the sphere within the beam, and its standard, was used as a calibration correction factor for the acoustic data collected during a particular sampling event. Calibration of the acoustic system was performed during the May, June, and July sampling events. Inclement weather during the September and October sampling events prevented calibration. Because the acoustic system used during these latter two sampling events was the same as that used for the July sampling event, the July calibration correction factor was applied to the acoustic data collected in September and October.

Once collected, the acoustic data was transferred to permanent CD-ROM medium. and processed on a Hewlett-Packard® UNIX work station using digital echo visualization and integration system (DEVIS; Jech and Luo 1998). Echo-integration converts echoes received from targets within the acoustic beam to measures of relative fish density. The speed of sound in water (approximately 1500 m s^{-1}) allows for each target to be insonofied many times. Absolute fish numerical density (# m^{-3}) can be derived by dividing relative densities by the mean target strength (estimate of target size) received from each individual target. Absolute numerical fish density data was log $_{10}$ transformed and resolved into a 2 dimensional representation of the water column using time and depth as indices. This procedure separated the water column into cells of 1min by 1m (see results).

Individual acoustic target strengths (TS) were converted to fish lengths (L) using a target strength—fish length relationship derived for Lake Ontario species corroborated by several years of trawl catch data (Figure 2.2; Schneider and Schaner 1994). Fish density for each sampling event was separated by size to segregate prey fish from predators. Because echoes scattered by targets of different fish species are not readily distinguishable (Brandt 1996; MacLennan and Simmonds 1992; Rose and Leggett 1988), all prey targets were considered to be alewife (*Alosa pseudoharengus*). This assumption is validated by the fact that alewife, although decreasing in abundance over the past several years, remains the dominant planktivore in the Lake Ontario system, comprising almost 67% of the system's forage base (O'Gorman et al., 1997; 1987). Maximum alewife size in trawls conducted routinely over the last 8 years along the south shore of Lake Ontario by the New York Department of Environment Conservation (NYDEC) revealed a maximum alewife size of above 180 mm only in 1990. After the 1990 sampling year, maximum alewife length was consistently below the 180 mm mark (Figure 2.3). Therefore, I conservatively used 180 mm as a threshold below which all targets were considered to be alewife. Targets above the set threshold were excluded from further analysis (Figure 2.4).

Time period formation

Because fish, and certainly alewife distributions have been shown to respond to light intensity shifts, the collected acoustic data was separated into 4 time periods associated with the diel light intensity cycle during a typical 24 hour period, namely;

dawn, day, dusk, and night (Appenzeller and Leggett 1995; Janssen and Brandt 1980).

The formation of the time periods was based on exact sunrise and sunset times collected by the United States Astrological & Naval Time Department, working in cooperation with the National Weather Service (NWS). The sunrise-sunset times were taken for the topographical latitude and longitude corresponding to Buffalo New York, USA, set on eastern standard time. One hour was added to the posted times to account for daylight savings. Because sunrise and sunset are not instantaneous, 1.5 hours was added to sunset times to form the dusk period, while the same was subtracted from sunrise to create the dawn period. This was based on the assumption that sunrise and sunset times provided by the NWS corresponded to the exact times the sun broke the horizon (Bodwitch 1982; Mixter 1966). All daylight hours not included within dawn or dusk formed the day period, while all dark hours after sunset and leading to dawn were considered night.

Temperature sampling

Temperature profiles of the water column were collected synoptically with the acoustic data using a Seabird SBE 19-03 conductivity, temperature and depth profiler (CTD). Temperature profiles were collected by dropping the CTD to near bottom depths and setting the device to sample water temperature every half second as it was retrieved. The water column was divided into 1 m depth cells characterized by the median of the temperature values collected within each cell.

For each sampling event, a temperature cast was taken immediately upon arrival on station, and repeated every hour thereafter. The use of one hour intervals is justified because it has been demonstrated that fluctuations in the thermal regime of the water column at smaller temporal scales is assumed to be negligible (Boyce et al 1991). Water column temperature within each depth cell was resolved per minute between casts using linear interpolation. These data manipulation techniques allowed the temperature data to be resolved into a 2 dimensional structure indexed by time in minutes, and depth by metre, similar to that of the acoustic data format. Once in the 2-dimensional format, the temperature data was split into their respective time-delimited periods as per the acoustic data (see above). A synopsis of the data collected is available in Table 2.1.

Model Development

Foraging sub-model

The format of both the acoustic and the temperature data allowed the development of a species-specific, temporally explicit model of fish growth rate potential. Temporally explicit modelling fractionates the time period over which data are collected, into unitary cells indexed by time and depth. Environmental conditions within each cell are considered homogenous in terms of prey (alewife) density and temperature. Within each cell, a species-specific foraging model determines the potential prey available to a particular predator occurring in that cell based on the following equation adapted from Tyler (1998).

$$PA = VS\ PD\ C_{eff}\ \frac{(ED_{prey})}{(ED_{pred})} \qquad (1)$$

Where **PA** = Prey available to the predator,
VS = Volume searched by a particular predator (m^3),
PD = Prey biomass density ($g\ m^{-3}$),
C_{eff} = Predator capture efficiency (prey encountered / prey consumed),

ED_x = Energy density of x, being either prey or predator (cal g^{-1})

Volume searched by a particular predator (VS), can be expressed generally as;

$$VS = \frac{2\Pi\ RD^2\ SS\ L\ TF}{10^6} \tag{2}$$

Where RD= The reactive distance of the predator (i.e. detection distance),
SS = Swimming speed of the predator (body lengths L (mm) s^{-1}), and
TF = Time spent foraging (sec).

Prey availability (PA), as defined by this particular foraging model, uses environmental conditions and empirically derived predator foraging abilities to delimit the amount of prey actually available to the predator within each cell. PA become an integral part of the bioenergetics model (described below) as it used as a boundary to the consumption rate (C) achieve within a cell, provided conditions within that cell are insufficient for the predator to reach maximum consumption (see below). Foraging model parameters used in this study, and their sources are available in Table 2.2.

Bioenergetics sub-model

Bioenergetic models relate environmental conditions to species-specific, size-dependent growth rates taking into account the inherent non-linear aspects of this relationship (Brandt and Kirsch 1993; Brandt et al., 1992). Growth rate potential describes the amount of growth that could potentially be achieved by a size-specific chinook if placed within a pre-determined volume of water characterized by a particular suite of environmental conditions. I used the Wisconsin bioenergetic model initially developed by Kitchell et al., (1977) later modified by Hewett and Johnson (1992), to determine the growth rate potential for a 512g, 300 mm chinook salmon (*Oncorhynchus tshawytscha*) in western Lake Ontario.

Chinook salmon was selected as it accounts for upwards of 40 % of the salmonid predators stocked into the Lake Ontario system. Chinook are considered the most voracious, and impose the strongest predation pressure on alewife of all the top-predator species present in the system (Stewart et al., 1998; Mason and Brandt 1996; Goyke and Brandt 1993; Brandt et al., 1991). Anecdotal accounts suggest that, this particular sized chinook correspond to fish in their initial stages of lake residency, where growth is critical to continued survivorship.

The modified Wisconsin bioenergetic model describes the change in growth rate (G g g^{-1} d^{-1}) by the following equation:

$$G = C - (R + F + U) \tag{3}$$

Where C = consumption,
R = metabolism and respiration,
F = egestion, and,
U= excretion.

Where consumption (C) is defined in terms of growth by the formula;

$$C = a_c W^{b_c} \cdot f(T) \cdot P \tag{4}$$

Here, a_c = maximum <u>rate</u> of consumption achieved at optimal temperature,
W= wet weight of the predator fish,
b_c = exponent describing the predator's weight-dependent consumption (a fish of a certain size can consume only a finite amount of prey),
T = the ambient temperature, and,

P = the proportion (ranging form 0 - 1) of maximum consumption (C_{max}) possible for a given species at a given temperature and prey availability (PA) where;

$$P = \frac{PA}{C_{max}} \qquad (5)$$

C_{max} = the ceiling value of consumption for a particular sized predator at its optimal temperature, where C_{max} is defined as:

$$C_{max} = a_c W^{b_c} \qquad (6)$$

Prey availability (PA defined in equation 1) will contribute to consumption only until P in the consumption equation (equation 4) reaches 1. When PA > C_{max}, P is set to 1, as further increases in prey availability cannot be utilized by the predator due to physiological constraints such as gut fullness, and digestion rate (see Brandt 1993; and Brandt et al., 1992).

In a similar way, respiration is also modelled as a function of predator weight, ambient temperature and prey availability according to the following;

$$R = a_r W^{b_r} \cdot f(T) \cdot A \;\; + S(C-F) \qquad (7)$$

Prey availability in this case, however, is related to respiration only through its influence on consumption, C.

Where a_r = the standard respiration rate of a predator achieved at optimal temperature for respiration,
b_r = the exponent relating weight dependent respiration,
W= the wet weight of the predator,
T = the ambient temperature,

A = the activity index of respiration rates above standard level,
S = a coefficient related to the cost of digestion, absorption and assimilation of energy, and,
F = the egestion term of the growth equation (equation 3).

Egestion (F, above) is defined by the following formula:

$$F = C \cdot a_f \, T^{b_f} \cdot e^{(g_f \cdot P)} \tag{8}$$

Where C = consumption as detailed in equation (4),
T = the ambient water temperature,
a_f is the proportion of consumption egested when the fish is at 1°C (Brandt 1993),
b_f is the exponent relating temperature to egestion,
g_f is a coefficient relating the feeding level P to the egestion rate.

And excretion (U, equation 3), can be derived as per egestion (equation 7), by substituting (C-F) for C, and replacing the subscripts f with u (see Brandt 1993).

Thus, this bioenergetic model takes environmental conditions, and predator abilities, both in terms of foraging and growth, into account to describe potential growth within each cell. Summation of the growth potential in all cells from a pre-determined time interval describes the amount of growth that can be achieved under the prevailing environmental conditions within the specified time frame (Figure 2.5). This modelling framework outlines potential growth rather than actual growth, and can be used to assess the quality of the environment in terms of its ability to support species-specific growth (Hondorp and Brandt 1996; Goyke and Brandt 1993; Brandt and Kirsch 1993). Because environmental conditions have inherent temporal dynamics, growth models reflecting these temporal fluxes will be more accurate in describing species-specific habitat quality than will those relying on environmental consistencies.

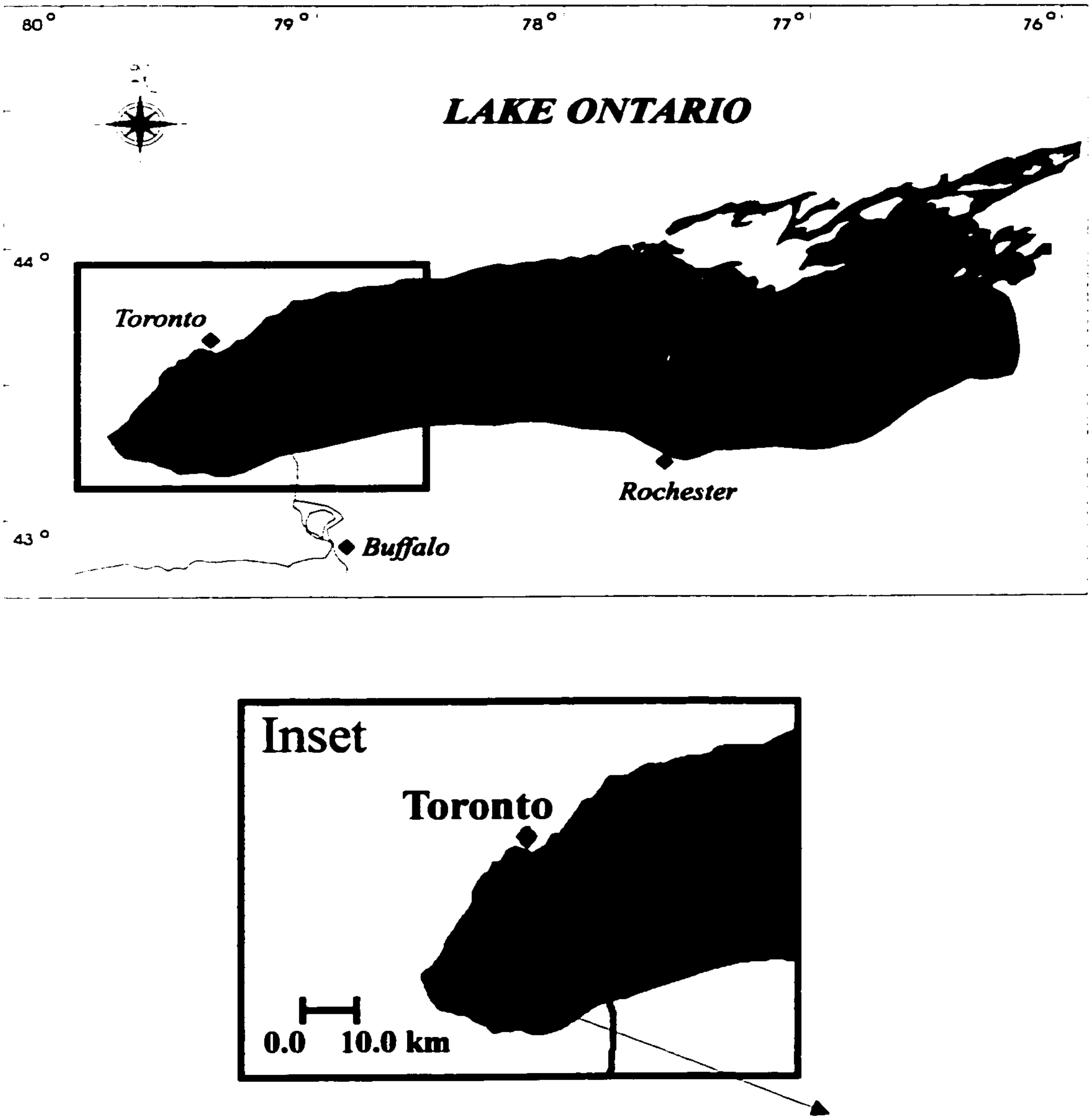
I used the above modelling framework to measure changes in chinook growth rate potential over different time periods (dawn, day, dusk, and night) within a 24 hour sampling event, and during different sampling events (May, June, July, September, and October) within the growing season. Values used for specific bioenergetic parameters described above are available in appendix 3 of Hewett and Johnson (1992).

Data Analysis

Kruskall-Wallis analysis was used to assess significant differences among the mean chinook salmon growth rate potential per minute calculated, for the 4 time periods (3 in September) within one sampling event, and among the 5 sampling events within the 1997 growing season. For this particular analysis, the chinook growth rate potential was pooled through depth, per minute, to emphasize the temporal rather than the spatial variations. Kruskall-Wallis analysis was used because the data did not conform to the 'independence' assumption for comparable parametric analysis (Sokal and Rohlf 1995; Zar 1984).

Results of the Kruskall-Wallis analysis suggested the use of post-hoc comparisons (Kolmogorov-Smirnov tests) to further determine significant differences in chinook growth rate potential between specific time periods within a sampling event, and specific sampling events within the growing season. In this case, the chinook salmon growth rate potential data were not pooled by depth, but used in their original 2-dimensional form for analysis. Kolmogorov-Smirnov (K-S) test statistics were evaluated against critical D-values adjusted for multiple comparisons (see Sokal and Rohlf 1995). I selected unplanned comparisons to evaluate K-S statistics because critical D-values adjusted for multiple comparison are generally more conservative, reducing the risk of type II errors (Sokal and Rohlf 1995; Zar 1984). All statistical tests were accomplished using software specifically designed to manipulate large data arrays written in Interactive Data Language (IDL®; Research Systems Inc.) and evaluated at the $\alpha=0.05$ level of confidence.

Figure 2.1 — Stationary sampling location in western Lake Ontario.



Stationary sampling position
43°13.28'N 079°18.00'W

Figure 2.2 — Acoustic target strength-fish length relationship derived for Lake Ontario fish species allowing echo-integrated target backscatter to be converted to fish lengths (adapted from Schneider and Schaner 1997).

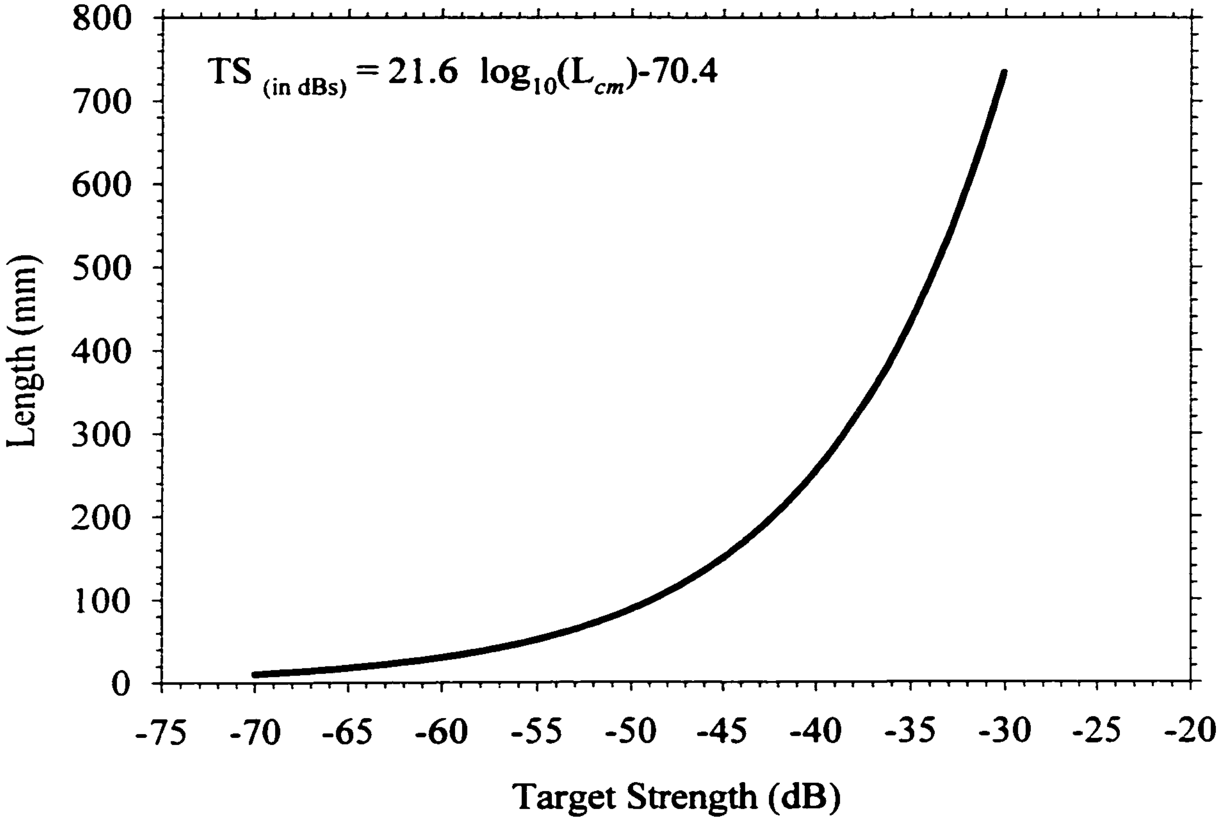

TS (in dBs) = 21.6 log10(Lcm)-70.4
Length (mm)
800
700
600
500
400
300
200
100
0
-75
-70
-65
-60
-55
-50
-45
-40
-35
-30
-25
-20
Target Strength (dB)

Figure 2.3 — Maximum alewife (*Alosa pseudoharengus*) length (mm) in Lake Ontario from 1990-1997 sampling years. Dashed line indicates the maximum length set for this study. Data adapted from New York State Department of Environmental Conservation, and Ontario Ministry of Natural Resources, Lake Ontario management Unit historical data.

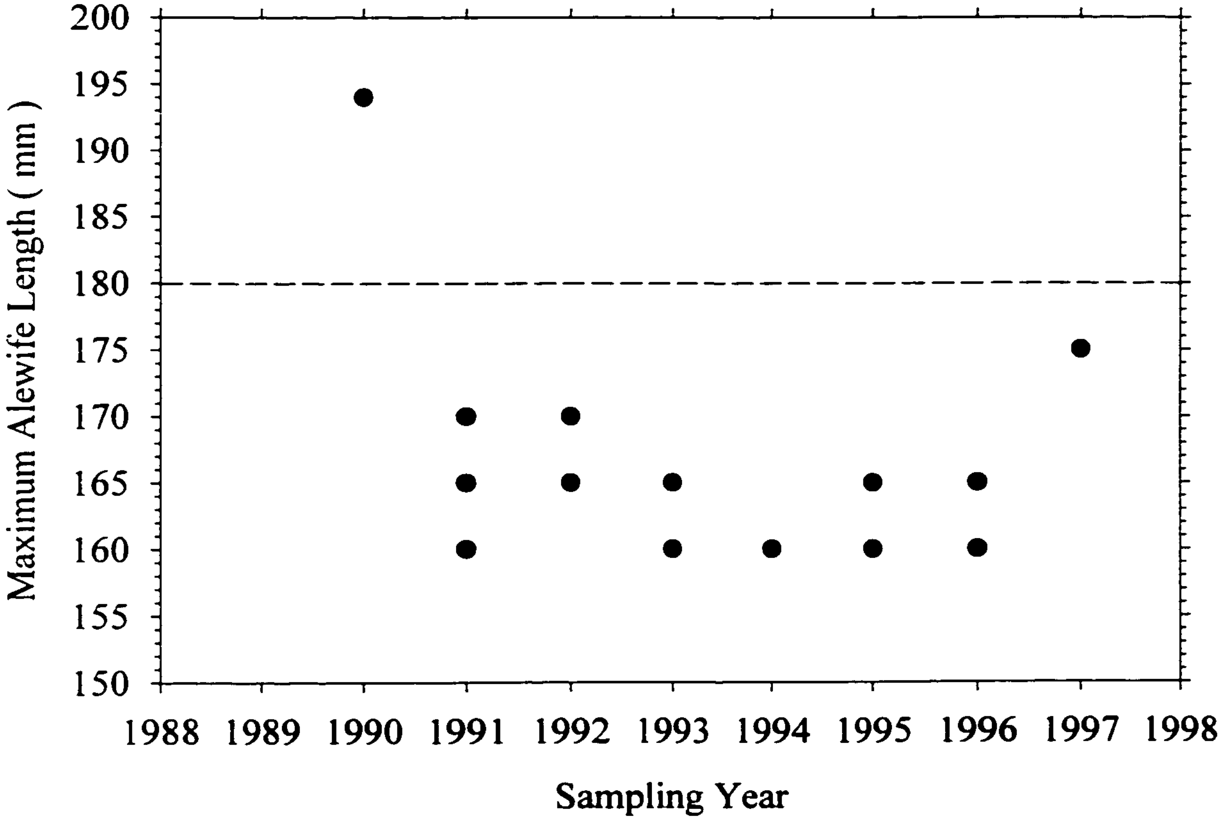

Maximum Alewife Length (mm)
200
195
190
185
180
175
170
165
160
155
150
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
Sampling Year

Figure 2.4 — Frequency distribution of fish length (mm) converted from acoustic targets collected during all 5 stationary sampling events conducted throughout the 1997 growing season in western Lake Ontario. Fish length to the left of the hatched line (≤ 180 mm) are considered alewife (*Alosa pseudoharengus*), while those to the right (>180 mm) have been excluded from further analysis.

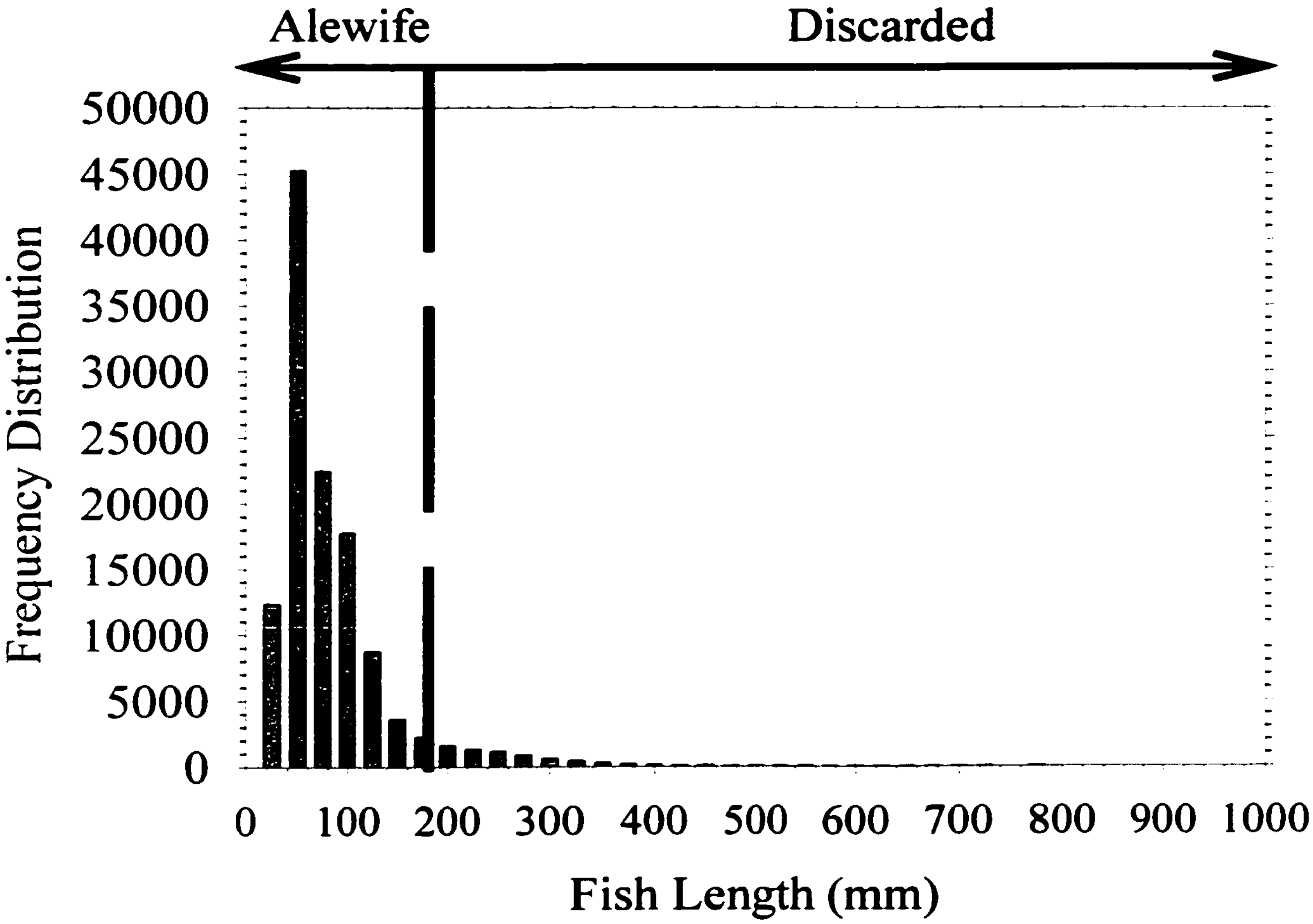

Alewife
Discarded
Frequency Distribution
50000
45000
40000
35000
30000
25000
20000
15000
10000
5000
0
0
100
200
300
400
500
600
700
800
900
1000
Fish Length (mm)

Figure 2.5 — Conceptualization of the temporally explicit modelling framework, dividing the sampled environment into unitary cells indexed by time and depth. Each cell (Cell_i) is characterised by a particular suite of environmental conditions which are entered into a foraging (f) and growth (g) sub-models which determine species-specific, predator production within that cell. Conditions within each cell are updated every time interval (1 min) and provide temporal evaluation of predator potential production within each cell. The production measured in all cells (Σ all Cell_i s) demonstrates the evolution of potential predator production of the sampled environment over time (adapted from Brandt and Kirsch 1993).

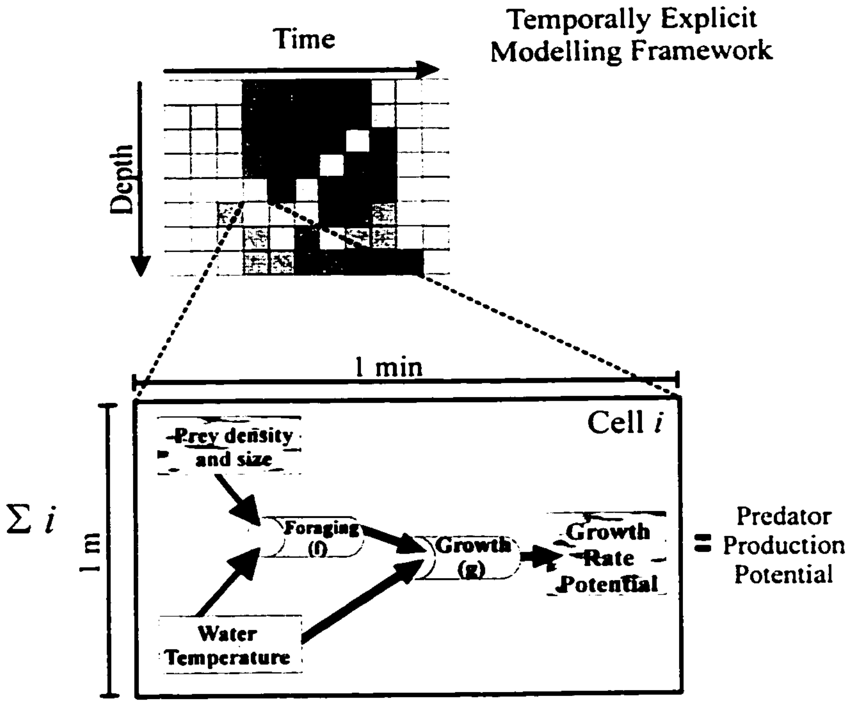

Time
Temporally Explicit Modelling Framework
Depth
1 min
Cell i
Prey density and size
Foraging (f)
Growth (g)
Growth Rate Potential
Water Temperature
$\Sigma\, i$
1 m
= Predator Production Potential

Table2.1-Summary of Lake Ontario stationary sampling protocol indicating dates and types of data collected in 1997.

	May 27th	June 19th	July 30th	Sept 5th	Oct 18th
Time at Station (in hrs)	24.0	24.0	24.0	12.0	24.0
Acoustic data collected (in hrs)	24.0	23.8	24.0	11.9	19.1
Temperature data collected (# of casts)	24	24	24	12	22

Table 2.2—. List of parameters and values used in the foraging model adapted from Tyler 1998 modelling chinook salmon feeding on alewife in western Lake Ontario.

Parameter	Value	Assumptions/Sources
Predator Length:	300 mm	
Weight:	512 g	Smallest size of Chinook entering Lake Ontario.
Target L-W constant : a_i	4.49×10^{-4}	From formula as follows; $W=a\ L^{b}$ used to convert target length (determined acoustically) to prey biomass available to the predator. Derived for Lake Ontario alewives by Rand et al., 1994.
Target L-W exponent: b_i	2.144	
Reactive distance (RD):	0.5 m	Prey detection distance (Mason and Brandt 1996).
Time spent foraging (TF):	9.0 hrs	Estimated time foraging corresponding to mean number of dark hours in sampling event. Chinook are presumed to feed more heavily at night.
Foraging efficiency (C_{eff}):	0.05	Ratio indicating the number of prey captured per prey encountered. Conservative estimate from Mason and Brandt 1996.
Swimming Speed (SS):	0.32 body lengths s^{-1}	Stewart and Iberra 1991.
Prey energy density (ED_{prey})	1323 cal g^{-1}	For Lake Ontario alewives, Rand et al., 1994.
Predator energy density (ED_{pred}):	1498 cal g^{-1}	Stewart and Iberra 1991.

Results

Overall, variations in water temperature were more prominent over the growing season, whereas that of alewife density were obvious at both the seasonal and diel time scales (Figure 2.31 & 2.32).

May 27-28

In May, the temperature structure of the water column was relatively constant with a noticeable thermocline at approximately 5m (Figure 2.6a, 2.7a, 2.8a, 2.9a). A slight oscillation of this thermocline was observed late during the day period (Figure 2.7a). The water temperature was characterized by a maximum and minimum of 10.23 °C, and 4.89 °C respectively, and a mean temperature of 6.17 °C with a variance of 2.03 °C.

May Dawn 04:13-05:42

Alewife distribution was more dense during the first half of the dawn period with highest densities at, or near the thermocline region (Figure 2.6b). Alewife distributions were more abundant within, but not exclusively restricted to, the upper thermal layer.

Chinook growth rate potential (0-0.006 g g^{-1} day^{-1}) was highly reflective of alewife distribution with the most intense growth occurring in warmer waters at, and above the thermocline (Figure 2.6c). Chinook growth rate potential calculated for the dawn period was mostly negative with very little portions of the time period supporting positive growth (Figure 2.10).

May Day 18:51-2041 & 05:45-18:01

Alewife distributions during the day were irregular with several more persistent aggregations appearing later in the day. Highest alewife densities were associated with the warmer water regions (Figure 2.7b).

Chinook salmon growth rate potential during the day corresponded closely to alewife distributions (Figure 2.7c). The most intense growth rate potential occurred when alewives were present in high densities within the cooler epilimnetic water. Day conditions provided slightly more positive chinook growth rate potential than did the dawn period. Overall habitat quality, however, remained low (Figure 2.10).

May Dusk 20:24-22:13

Alewife distributions during dusk period were mostly confined to the hypolimnion with very few, yet high density distributions located near the surface (Figure 2.8b).

Positive chinook salmon growth rate potential was most intense near the surface in the warmer water corresponding to depths containing high alewife densities. Very little positive growth occurred below the first 3 m of the water column (Figure 2.8c). Chinook salmon positive growth rate potential for the entire May sampling event was minimal during this time period, indicating that the dusk conditions represented the time interval when habitat quality was at a minimum for supporting chinook salmon growth (Figure 2.10).

May Night 22:15-04:10

During the night, alewife were distributed more evenly throughout the time interval displaying a more consistent pelagic distribution. Alewife distributions occurred more frequently and were more dense in the shallow warm waters near the surface and above the thermocline. More sporadic high density distributions, however, were also found well into the hypolimnetic region (Figure 2.9b).

Again, chinook growth rate potential was highly reflective of alewife distributions but clearly, the most intense growth was segregated to the warmer epilimnion. Very limited positive chinook growth rate was supported in the cooler hypolimnetic region of the water column (Figure 2.9c). The conditions during the night supported the most positive chinook salmon growth rate potential, and thus had the highest incidence of, chinook salmon habitat quality for the entire May sampling event (Figure 2.10).

May synopsis

No significant differences (*P* >.05) were found among the mean chinook salmon growth rate potential (mean growth rate through all depths per minute), calculated for each time period of the May sampling event (Table 2.3; May 27-28). Pair-wise comparisons of actual chinook growth rate potential (actual growth in each cell indexed by time and depth), however, revealed that, although certain time periods were not statistically different in terms of supporting chinook salmon growth, others were (Table 2.4). Night, found to support the most chinook growth, was not significantly different from dusk which supported the least. Meanwhile, day and dawn conditions for supporting chinook growth were comparable, and not statistically different. Finally, night conditions, although not different from those of dusk in terms of chinook growth rate potential, were found to be significantly different from both those of day and dawn. Qualitatively, however, the growth rate potential of all time periods within the May sampling event were quite similar (Figure 2.10).

June 19-20

The temperature structure of the water column during June consisted of up to three distinct thermal layers (Figure 2.11a, 2.12a, 2.13a, 2.14a). The overall water temperature for the complete June sampling event, was characterized by a minimum of 4.23 °C, and a maximum of 16.47 °C. The water temperature had a mean of 7.81 °C, with a variance of 12.00 °C.

June Dawn 04:10-05:36

During dawn, the thermal structure of the water column was constant with the warmer epilimnetic region reaching a depth of almost 8 m. The thermocline region extended another 5 m below the epilimnion, with the remainder of the water column consisting of the cool hypolimnion (Figure 2.11a).

Alewife distributions were abundant throughout depths and times during the first half of the dawn period, decreasing substantially during the second half. Highest alewife densities were recorded within the warm epilimnetic region (Figure 2.11b).

Chinook salmon growth rate potential was highly overlapping with alewife distributions with intense growth occurring in, and above the thermocline region (Figure 2.11c). Chinook growth rate potential was most intense near the surface in the warmer water and decreased in intensity with decreasing water temperature. Dawn conditions during June supported the most chinook growth rate potential evaluated for the entire June sampling event (Figure 2.15). This suggests that, in June, the dawn period had the best habitat quality for supporting chinook salmon growth.

June Day 08:09-20:58 & 05:38-05:49

The temperature structure of the water column during the day varied much more than that of dawn. The early day was characterized by a warming trend thickening the epilimnion from 3 m to approximately 10 m. The relatively stable thermocline also sank reaching a maximum depth of almost 13 m. This warming trend was quickly followed by a cooling trend which shrank the epilimnion, and gradually mixed the thermocline into the hypolimnetic region. As the day period ended, the epilimnion was very small with an almost isothermal layer underneath (Figure 2.12a). The shifting nature of the water columns' thermal structure may have been caused by an up-welling event or and internal seiche occurring within the Lake Ontario system during this time period.

Alewife distributions occurred sporadically throughout the day lasting various lengths of time and located both in warm and cool waters. Most persistent aggregations occurred during the warming trend and dispersed as the overall thermal structure of the water column cooled. Alewife distributions were densest during the early warming trend at the thermocline and within the epilmnetic region. For most of the day, fish were largely confined to the periphery of the water column leaving most of the mid water regions empty (Figure 2.12b).

Periods supporting positive chinook salmon growth occurred more frequently during the warming trend, and were highly reflective of alewife distributions. Throughout the day, growth rate potential for chinook salmon was most intense at the thermocline and within the warmer epilimnetic regions of the water column. Although the hypolimnion did support some positive chinook growth, it was not as intense as it was within the warmer water regions (Figure 2.12c). The day conditions supported much less habitat suitable for positive chinook growth than did the dawn period (Figure 2.15).

June Dusk 21:01-22:30

The temperature structure during dusk was constant with a shallow epilimnion extending to approximately 4 m. Underneath, the thermocline and hypolimnion were well mixed essentially forming one thermal layer (Figure 2.13a).

Alewife were scattered throughout the depths with more persistent arrangements occurring near the bottom, late during dusk. Alewife densities were highest within the warm epilimnetic waters (Figure 2.13b).

Positive chinook growth rate potential during dusk was highly associated with alewife distributions throughout all depths and time, where the most intense growth occurred within the shallow warm water regions (Figure 2.13c). Chinook habitat quality during dusk was slightly better than that estimated during the day (Figure 2.15).

June Night 22:33-04:07

Thermal structure of the water column during the night was relatively stable with a shallow warm layer extending to almost 3 m, and a large thermocline region spanning approximately 5 m. Although the thermocline and the cool hypolimnion were distinct, this distinction was slight indicating extensive mixing between the two bottom layers. A dip in the epilimnion was observed toward the end of the night. This sudden profusion of warm water into the thermocline was associated with a narrowing of this layer and a segregation of the thermocline-hypolimnetic mix (Figure 2.14a).

For the first half of the night period, alewife formed two distinct types of distributions. The shallow water distributions were dense yet intermittent, while deeper distributions were less dense but much more constant. A large portion of the mid-water depth were vacant in terms of alewife density. As the night progressed, alewife distributions became more uniform, and more consistent throughout depths and time, with high densities accumulating in the warmer epilimnetic and thermocline regions (Figure 2.14b).

Positive chinook salmon growth rate potential during the night mirrored the alewife distributions with the most intense growth occurring in, and above the thermocline region. As the temperature decreased from the top thermal layer, so did the intensity of the growth rate potential (Figure 2.14c). The night conditions were comparable, but less capable of supporting chinook salmon growth than the dawn (Figure 2.15).

June synopsis

Mean chinook growth rate potential calculated for each time interval of the June sampling event were determined to be significantly different from each other ($P <.05$; Table 2.3; June 19-20). Pair-wise comparisons of actual growth rate potential from each time period in June, revealed that the ability of each time period to support chinook salmon growth was statistically different ($P <.05$, Table 2.5). Dawn supported more chinook salmon growth, followed closely by night. Both dusk and day supported much less positive chinook growth than did either dawn or night. Day and dusk, however, were comparable with day supporting slightly less growth than did dusk (Figure 2.15).

July 30-31

The temperature structure of the July water column was more complex than during the previous sampling events, at times consisting of up to 4 thermal layers. Overall, July temperatures were considerably warmer than those encountered during both May, and June. The mean temperature was 17.61 °C with a variance of 12.28 °C, a maximum of 21.87 °C, and a minimum of 9.08 °C. Generally, the top warm water layer was thick reaching depths of more than 16 m, while the other thermal layers were spread within the bottom 4-8 m. The thermocline was very narrow and ranged in depth between 12-16 m (Figures 2.16a, 2.17a, 2.18a, 2.19a).

July dawn 04:26-06:05

The thermal structure of the water column during dawn was constant with a warm broad epilimnetic layer reaching a depth of almost 16 m. The thermocline formed a narrow band extending 2 m below the epilimnion, while the cold hypolimnetic waters formed a thin 2 m layer adjacent to the bottom (Figure 2.16a).

Alewife distributions were both intense and constant in proximity to the thermocline. As time increased, alewife distributions declined and sank into the cooler hypolimnetic layer (Figure 2.16b).

The chinook salmon growth rate potential was limited to a very narrow ribbon along the bottom in the deep cooler hypolimnetic region of the water column. The most intense chinook growth rate potential was observed in early dawn coupled to both the bottom thermal layer and high alewife densities (Figure 2.16c). The ability of the July dawn period to support positive chinook salmon growth was nominal relative to the other July time periods (Figure 2.20).

July Day 10:07-20:36 & 06:08-10:10

During the day, the warm epilimnion expanded and reached a maximum depth of

16.25 m. This was accompanied by the formation of a top warm layer in first 2-3 metres of the epilimnion, and by the mixing of the thermocline-hypolimnetic regions (Figure 2.17a). Once formed, the very warm layer in the shallow 2-3 metres persisted almost until dusk (20:36). In the deeper water however, the warming was ephemeral and followed by a cooling period which enlarged the cool water regions re-forming distinct thermocline and hypolimetic regions. Toward the end of the day another cooling event further broadened the hypolimnetic region. The majority of the water column, however, continued to be dominated by the warmer epilimnetic water (Figure 2.17a).

During the day, most alewives distributions occurred regularly along the bottom in depths associated with the cooler hypolimnetic layer. The highest alewife densities, however, were observed near the surface during the early to mid-morning hours. These particular alewife distributions overlapped with the warm epilimnetic region of the water column. Very few alewife distributions were observed within the mid water regions (Figure 2.17b).

Chinook salmon growth rate potential during the day overlapped with alewife distributions and was persistent only along the bottom of the water column. Alewife distributions above the hypolmnetic and themocline regions did not contribute to positive chinook growth rate potential. Initially, chinook growth rate potential was poor, but increased in intensity toward the end of the day. This trend was repeated in the early morning where the progression of time showed an increase in chinook growth rate potential along the bottom. In both cases, the areas of peak growth coincided with depths characterized by cooler water temperatures, and relatively high alewife densities (Figure

2.17c). The conditions during the day sustaining positive chinook growth was less but comparable to the dawn period (Figure 2.20).

July Dusk 20:39-22:08

The dusk water temperature structure was stable, but thermally stratified into 4 distinct layers. The first 3 metres were warm and rested upon a broader, 8 metre layer of slightly cooler water. The thermocline was nearly 3 metres thick above the colder hypolimnetic region, consisting of approximately 6 metres in thickness (Figure 2.18a).

The alewife distributions during dusk were initially confined to the colder hypolimnetic region, but rose to the proximity of the thermocline after only a short time. Once at the thermocline, alewife distributions became constant, frequently occupying the cooler hypolimnion as well. During dusk, highest alewife densities were observed in the thermocline region (Figure 2.18b).

During dusk, the most intense chinook salmon growth rate potential occurred early, and very close to the bottom. Although other high intensity growth overlapped with alewife distributions, these latter were not of the highest densities observed for the dusk period (Figure 2.18b). Throughout the dusk period, other incidents of high intensity chinook salmon growth rate potential were observed intermittently along the bottom depths. Again, however, this growth was not correspondent to maximum alewife densities for dusk. More consistent chinook growth, of lesser intensity, occurred just below the thermocline at depths which did correspond to highest alewife densities. All positive chinook growth rate potential during dusk coincided in depth with areas of relatively abundant alewife distribution and cooler water temperatures (Figure 2.18b-c).

The amount of positive chinook growth rate potential during dusk was much larger than that observed for both dawn and day periods (Figure 2.20).

July night 22:11-04:23

The thermal structure of the water column for most of the night period was thermally stratified into 4 layers. The warmest top layer extending to 5 metres in depth, and rested upon a slightly cooler layer extending another 6 metres down. The sharp thermocline under the warm top layers was almost 5 metres broad, and extended into the deep water regions. The hypolimnion was narrow and formed a 2-4 metre ribbon of cold water along the bottom. Toward the end of the night, the hypolimnion gradually increased in thickness, the thermocline narrowed and the two warmer top layers mixed together forming one isothermal epilimnion. Once formed, the new epilimnion expanded while both the thermocline and the hypolimnion retracted (Figure 2.19a).

A consistently broad band of alewives formed during the night. This band was centred in the proximity of the thermocline and widened with time reaching a maximum expanse of more than 10 metres near the mid-point in the night. During the second half of the night, this alewife band narrowed and gradually sank into slightly deeper waters. During much of the night period, the large alewife band located at the thermocline extended into, and at times completely filled, the hypolimnetic region of the water column. Highest alewife densities, however, were found at, or just above the thermocline.

No positive chinook salmon growth rate potential was observed above a depth of 14 m, below most high density alewife distributions. A narrow, low intensity band of positive chinook growth was consistently observed at approximately 15 m. This band sank to 17 m toward the end of the night. Below the low intensity band, high intensity chinook salmon growth rate potential appeared irregularly at depths characterized by cool temperature, and medium alewife densities. The most persistent, high intensity period, supporting chinook salmon growth occurred toward the end of the night period and was simultaneous with the widening of the cooler hypolimnetic region, and the sinking of the low intensity growth band (Figure 2.19c). Night conditions were determined to be the best in terms of habitat supporting positive chinook salmon growth during the July sampling event (Figure 2.20).

July synopsis

Significant differences ($P < .05$) were found among the mean chinook growth rate potential calculated for each time period of the July sampling event (Table 2.3; July 30-31). Pair-wise multiple contrasts between actual chinook growth rate potential estimated for each time period demonstrated that the ability of each time period to support chinook salmon growth was significantly different ($P < .05$), with the exception of the dusk and night periods (Table 2.6). During the July sampling event, night supported the best habitat quality in terms of chinook salmon positive growth rate potential, followed by dusk, dawn, and then day (Figure 2.20).

September 5

The thermal structure of the water column during the September sampling event was homogenous and isothermal throughout both depth and time. The temperature reached a maximum of 18.99 °C, and a minimum of 16.19 °C. The overall mean temperature was

18.63 °C with a variance of 0.0383 °C. The September temperature was warmer than the maximum temperatures of both the May and June sampling events, was cooler than that for July.

September day 16:54-19:32

Alewife distributions during the day period were most intense at, and limited to the first 2 metres of the water column. These near-surface distributions appeared repeatedly throughout this time period with very few distributions occurring elsewhere. The majority of the water column during this time period was devoid of fish (Figure 2.21b).

No positive chinook salmon growth rate potential was observed during this time period, suggesting that conditions were inadequate to support positive chinook growth (Figure 2.21c). The potential growth rate calculated for chinook salmon during the day period was negative (Figure 2.24).

September dusk 19:48-21:15

Alewife distributions during the dusk period were more dispersed occupying various depths through time. Most high density distributions were observed near the surface while mid-water distributions were typically less dense (Figure 2.22b).

As during the day, positive chinook growth rate potential was not observed during the dusk period, indicating the condition did not promote chinook growth (Figure 2.22c). Chinook growth rate potential evaluated for the September dusk period was also completely negative (Figure 2.24).

September night 21:17-05:03

Alewife distributions throughout the night were both temporally and spatially variable. Alewife distributions occurring near the surface were less transient and had higher densities, while those in the mid-water and bottom regions tended to be less dense. The number of alewife distributions during the night increased in abundance and concentration with time (Figure 2.23b).

The September night period supported very little positive chinook salmon growth which occurred very close to the bottom (Figure 2.23c). The incidence of positive growth rate potential was seldom, indicating that the general conditions of the habitat during this time period were not suitable in terms of supporting chinook salmon growth (Figure 2.24).

September Synopsis

Despite the absence, or very low occurrence of positive growth, significant differences ($P < .05$) were found among mean chinook growth rate potential evaluated for each time period of the September sampling event (Table 2.3; September 5). Cumulative frequency distributions, and pair-wise comparison of the actual chinook growth rate potential estimated for each time period of the September sampling event, revealed that the night period supported significantly ($P < .05$) more growth than did either the day or dusk periods. These comparisons also demonstrated that the day and dusk periods were not statistically different in terms of their ability to support chinook salmon growth (Table 2.7, Figure 2.24). Overall, the differences between the chinook growth rate potential from each time period during the September sampling event were marginal (Figure 2.24).

October 18-19

The October water temperature structure was essentially thermally unstratified with only slight variations through depth and time. The overall mean temperature was 13.66 °C with a variance of 0.43 °C. The minimum and maximum temperatures encountered were 11.53 °C and 15.90 °C, respectively. In general, the October temperature structure was cooler with respect to that of both July and September.

October dawn 06:03-07:32

The October dawn water column thermal structure was consistently isothermal throughout all depths and time (Figure 2.25a). Alewife distributions were very sparse. Distributions occurring early during dawn were very transient and located near the bottom, whereas later distributions were slightly more persistent and occurred at various depths. Highest density alewife distributions were observed along the bottom at infrequent intervals (Figure 2.25b).

The dawn conditions supported very little positive chinook salmon growth, largely confined to the early dawn period, and corresponding closely to early dawn alewife distributions (Figure 2.25c). Positive chinook salmon growth rate potential calculated for this time period was marginal(Figure 2.29).

October day 16:10-1825 & 07:35-15:53

During the day, the thermal structure of the water column was initially isothermal through depth and time, but very gradually cooled. The degree of temperature change over time was slight, but eventually encompassed the entire water column. Short warming events were observed during the early afternoon (Figure 2.26a).

Alewife distributions during the day were sparse and erratic. Distributions were typically ephemeral and not depth restricted. The majority of the alewife aggregations were associated in time to the gradual cooling trend observed during the day, with few distributions occurring during warmer periods. Highest alewife densities also occurred during the cooling trend and extended through many depths (Figure 2.26b).

Chinook growth rate potential during the day was limited to time intervals with the highest alewife densities. Other alewife distributions did not contribute to chinook growth rate potential. Chinook salmon growth potential observed early in the day demonstrated positive growth occurring evenly throughout depths. Similar events observed during the cooling trend also supported positive chinook growth throughout depths, however, in these cases, the most intense growth occurred in the shallower depths (Figure 2.26c). Chinook growth rate potential during the day was mostly negative, with only a small portion of the time period supporting positive chinook growth rate potential (Figure 2.29).

October dusk 18:27-19:57

The thermal structure of the water column during dusk was essentially homogenous through time. A slight thermal gradient was observed separating the water column into a large, slightly warmer, top layer of approximately 16 metres, and a narrow, cooler, bottom layer of 4 metres (Figure 2.27a).

Alewife distributions occurred periodically throughout dusk, at times lasting several minutes. Early dusk alewife distributions spanned much of the water column, with high densities both at deep and shallow depths. As time progressed, alewives maintained a depth distribution below 9 m, with high densities exhibiting no observable pattern within the distributions either through depth or time (Figure 2.27b).

Chinook salmon growth rate potential for the dusk period was highly reflective of alewife distributions. The intensity of the positive chinook growth rate potential observed was relatively homogenous both through time and depth (Figure 2.27c). The October sampling event chinook salmon growth rate potential was maximal during the dusk period (Figure 2.29).

October night 00:26-06:01

The October night water column was isothermal and well-mixed both through depth and time, with a slight cooling trend toward the end of the period (Figure 2.28a).

Alewives occurred more frequently and were more persistent early during the night period. Early alewife distributions were located either within the first 10 m or at bottom of the water column. As time increased, alewife distribution decreased substantially both in frequency and persistence with very few distributions observed during the middle part of the night. Toward the end of the night, alewife distribution increased in frequency, but remained less persistent than those observed during the early night period. The resurgence of alewife distributions toward the end of the night period was associated with the slight cooling trend observed in the temperature structure of the water column (Figure 2.28b).

The most positive and most intense chinook salmon growth rate potential was observed early during the night period corresponding in time and depth to early night alewife distributions. Other alewife distributions contributed very little to positive growth rate potential calculated for this time period. The positive chinook salmon growth rate potential during the night was much less than that observed during the dusk period, but comparable to that of the dawn and day periods (Figure 2.29).

October synopsis

Significant differences ($P < .05$) were found among the mean chinook growth rate potential evaluated for each time period constituting the October sampling event (Table 2.3; October 18-19). Pair-wise contrasts between actual chinook salmon growth rate potential calculated for each time period indicated that each period was statistically distinct ($P < .05$) in terms of its ability to support chinook salmon growth (Table 2.8). During the October sampling event, positive chinook salmon growth rate potential was much higher during dusk than during the other time periods. Night, day, and dawn supported comparable amounts of chinook growth rate potential with night supporting more than either day or dawn, and day supporting more than dawn (Figure 2.29).

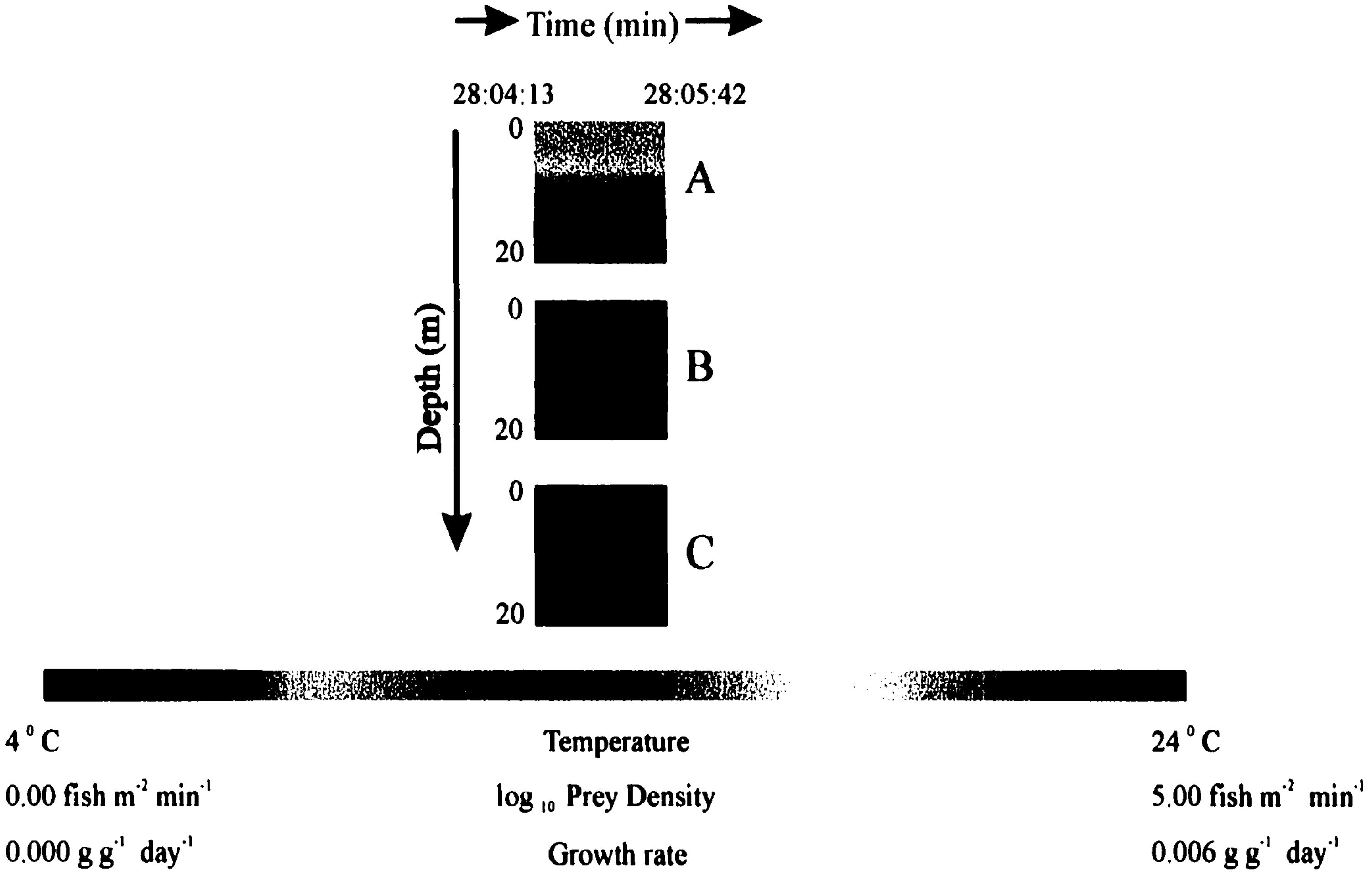
Sampling season synopsis

During May, the chinook growth rate potential was highly reflective of alewife distributions throughout both depth and time. The most intense chinook growth rate potential typically occurred in the warmer water, while growth within cooler water was less intense. This same pattern was observed in June where although positive chinook salmon growth rate potential was highly associated with alewife distribution both in time and depths, the most intense growth was typically found in warmer waters. Alteration to this pattern was observed in July where the warmer surface waters limited the extend of the positive chinook growth rate potential observed.

Chinook growth rate potential during July typically occurred along the bottom, with the most intense growth observed in cooler waters. The warm, well-mixed nature of the September water column inhibited positive chinook growth rate potential, regardless of alewife distributions. During the October sampling event, the water column temperature cooled but remained essentially isothermal. Positive chinook salmon growth rate potential during this sampling event corresponded to only the densest alewife distributions. Other less dense alewife distributions did not contribute to positive chinook growth rate potential.

Significant differences (*P* <.05) were observed among the mean chinook salmon growth rate potential, calculated for each sampling event conducted during the 1997 growing season (Table 2.9). Pair-wise comparisons of actual chinook salmon growth rate potential estimated for each sampling event demonstrated that, within the 1997 growing season, each individual sampling event was significantly different (*P* <.05) in terms of its ability to support chinook growth (Table 2.10). Overall, the June sampling event supported the most positive chinook growth, followed closely by that of July. The May sampling event supported much less positive chinook growth than did either June or July, but supported slightly more than October. October supported very little positive chinook growth, while essentially all of the chinook growth rate potential calculated for September, was negative (Figure 2.30).

Figure 2.6 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dawn (*04:13-05:42*) of May 28, 1997, in western Lake Ontario.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28:05:42
Depth (m)
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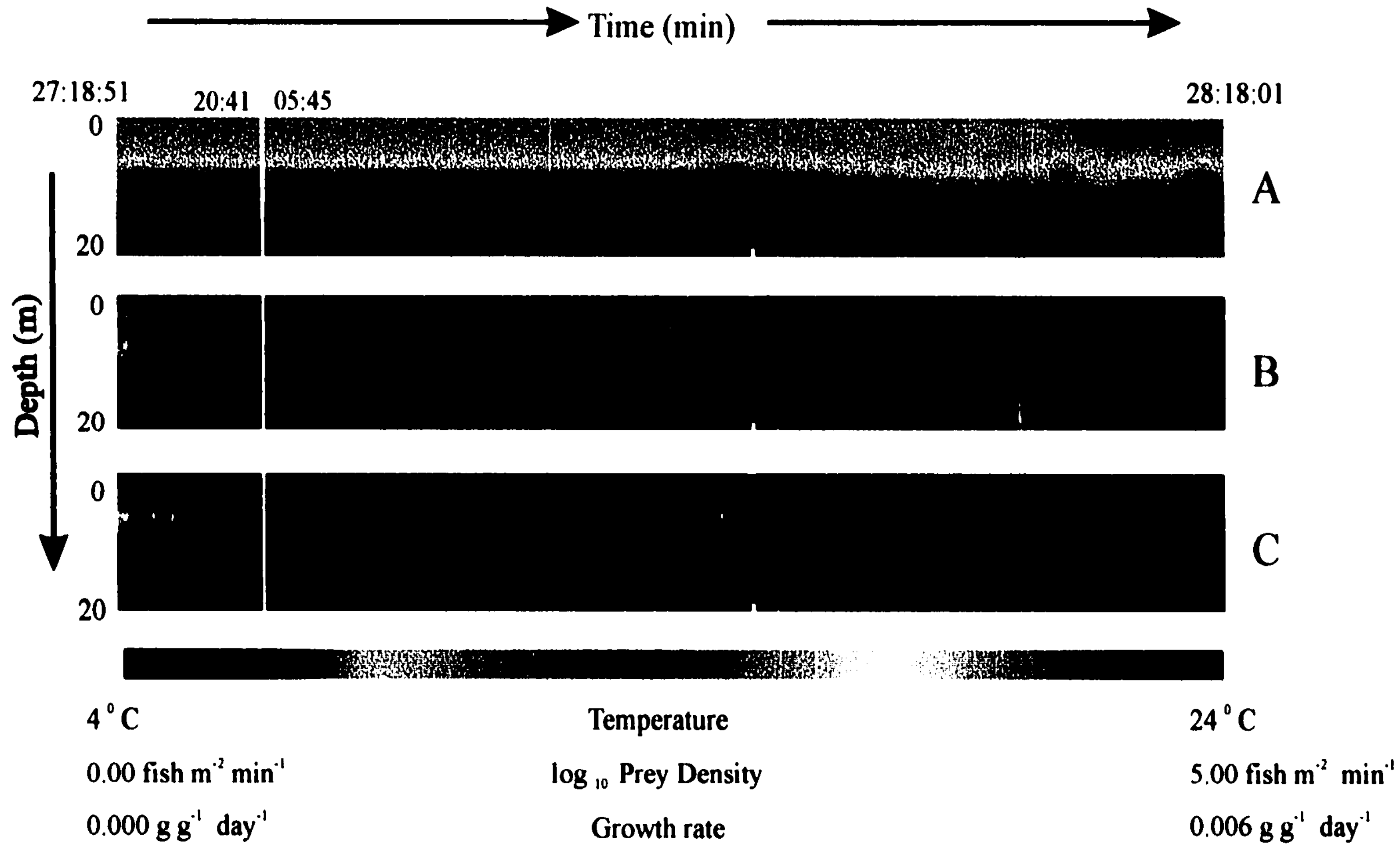
20
A
0
20
B
0
20
C
4 °C
0.00 fish m⁻² min⁻¹
0.000 g g⁻¹ day⁻¹
Temperature
log 10 Prey Density
Growth rate
24 °C
5.00 fish m⁻² min⁻¹
0.006 g g⁻¹ day⁻¹

Figure 2.7 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the day (18*:51-20:41 & 05:45-18:01*) of May 27-28, 1997, in western Lake Ontario.


Time (min)
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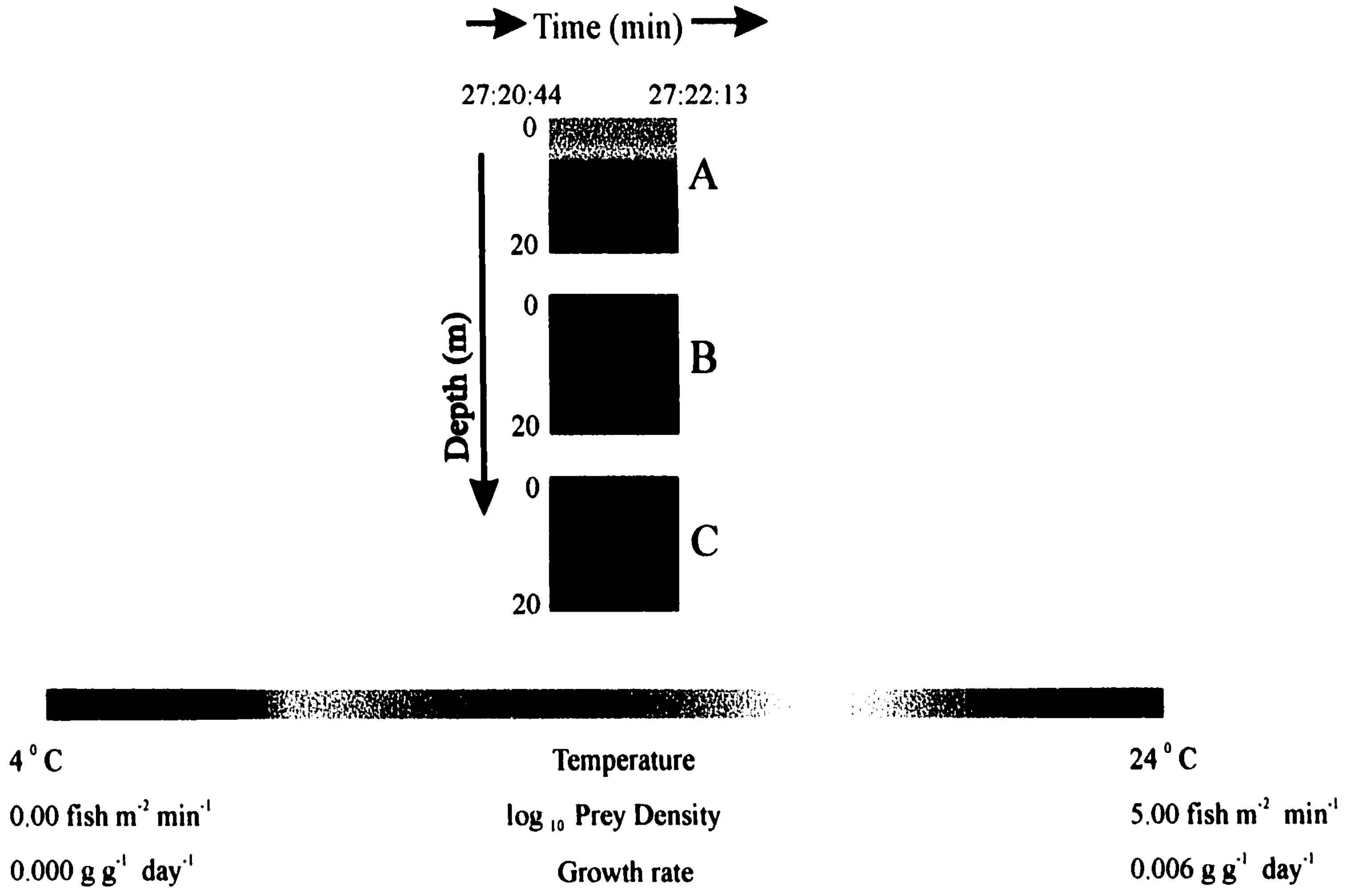
20:41
05:45
28:18:01
Depth (m)
0
20
0
20
0
20
A
B
C
4 °C
Temperature
24 °C
0.00 fish m⁻² min⁻¹
log 10 Prey Density
5.00 fish m⁻² min⁻¹
0.000 g g⁻¹ day⁻¹
Growth rate
0.006 g g⁻¹ day⁻¹

Figure 2.8 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dusk (*20:24-22:13*) of May 27, 1997, in western Lake Ontario.

Time (min)
27:20:44
27:22:13
Depth (m)
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20
A
0
20
B
0
20
C
4 °C
0.00 fish m-2 min-1
0.000 g g-1 day-1
Temperature
log10 Prey Density
Growth rate
24 °C
5.00 fish m-2 min-1
0.006 g g-1 day-1

Figure 2.9 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the night (*22:15-04:10*) of May 27-28, 1997, in western Lake Ontario.

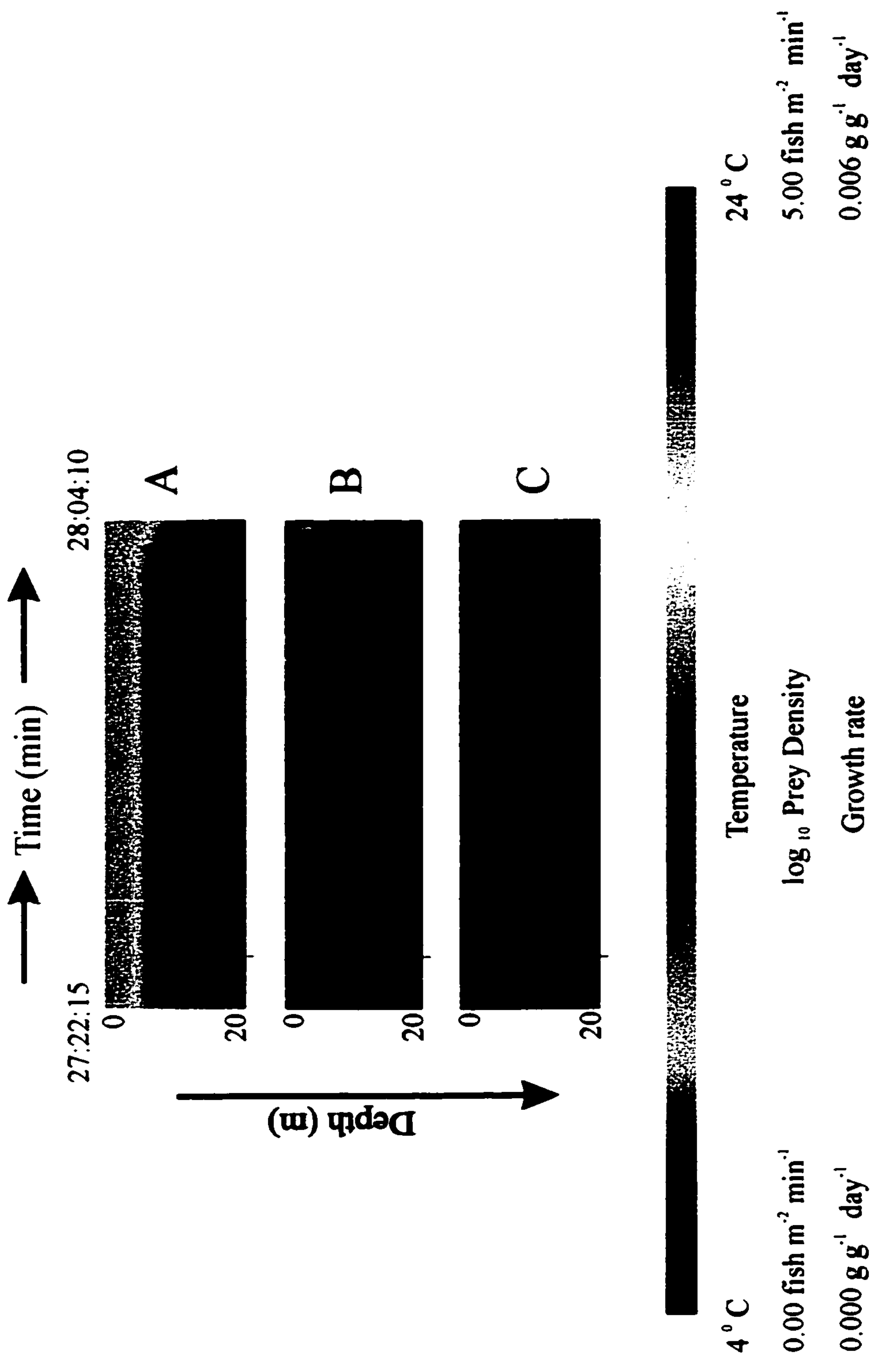

Time (min)
27:22:15
28:04:10
Depth (m)
A
B
C
0
20
0
20
0
20
Temperature
log $_{10}$ Prey Density
Growth rate
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}

Figure 2.10 —Cumulative distribution of the proportion of each time period (dawn, day, dusk, and night) supporting Chinook salmon (*Oncorhynchus tshawytscha*) growth rate potential at one location in western Lake Ontario during the May 27-28 sampling event.

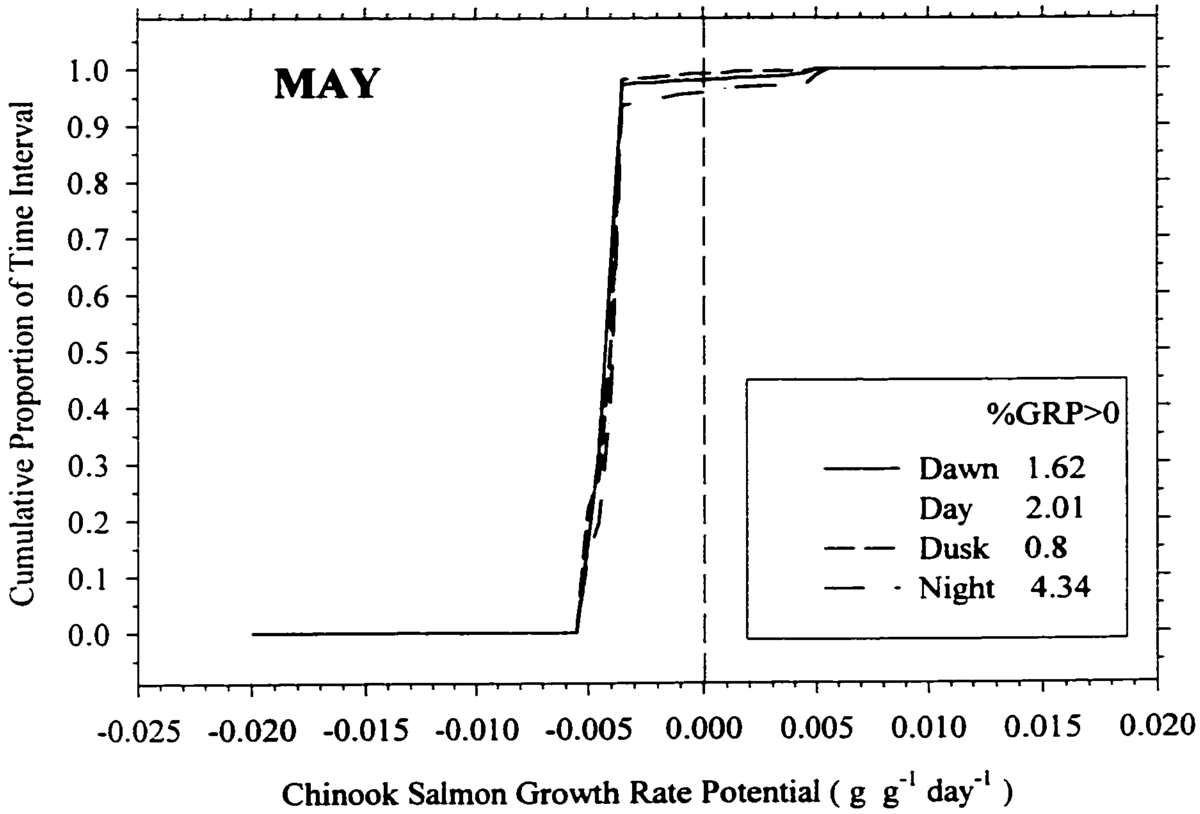
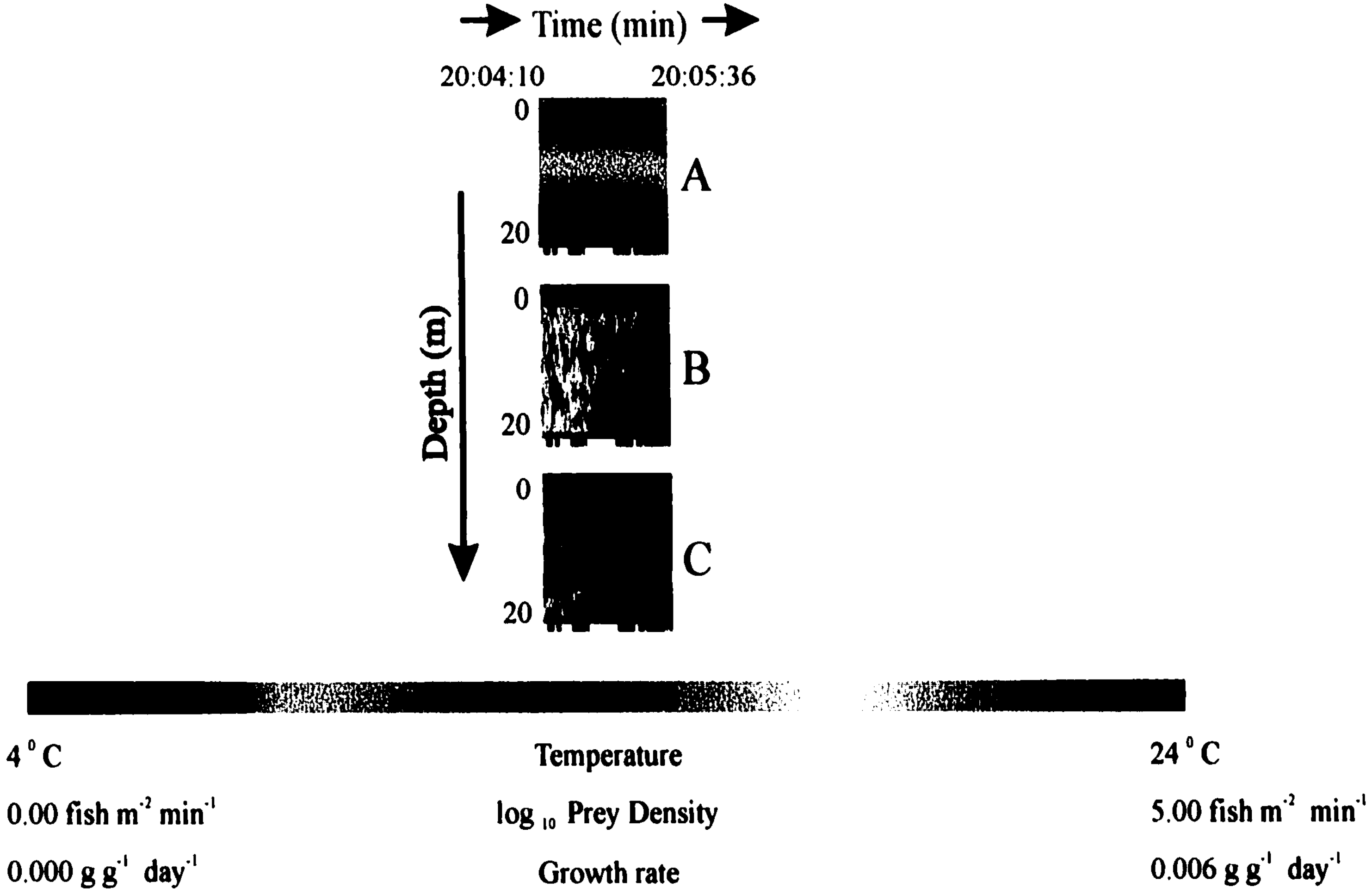

MAY
Cumulative Proportion of Time Interval
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.025
-0.020
-0.015
-0.010
-0.005
0.000
0.005
0.010
0.015
0.020
Chinook Salmon Growth Rate Potential (g g-1 day-1)
%GRP>0
Dawn 1.62
Day 2.01
Dusk 0.8
Night 4.34

Figure 2.11 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dawn (*04:10-05:36*) of June 20, 1997, in western Lake Ontario.


Time (min)
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20:05:36
Depth (m)
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20
A
0
20
B
0
20
C
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Temperature
log$_{10}$ Prey Density
Growth rate
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}

Figure 2.12 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the day (*08:09-20:58 & 05:38-05:49*) of June 19-20, 1997, in western Lake Ontario.

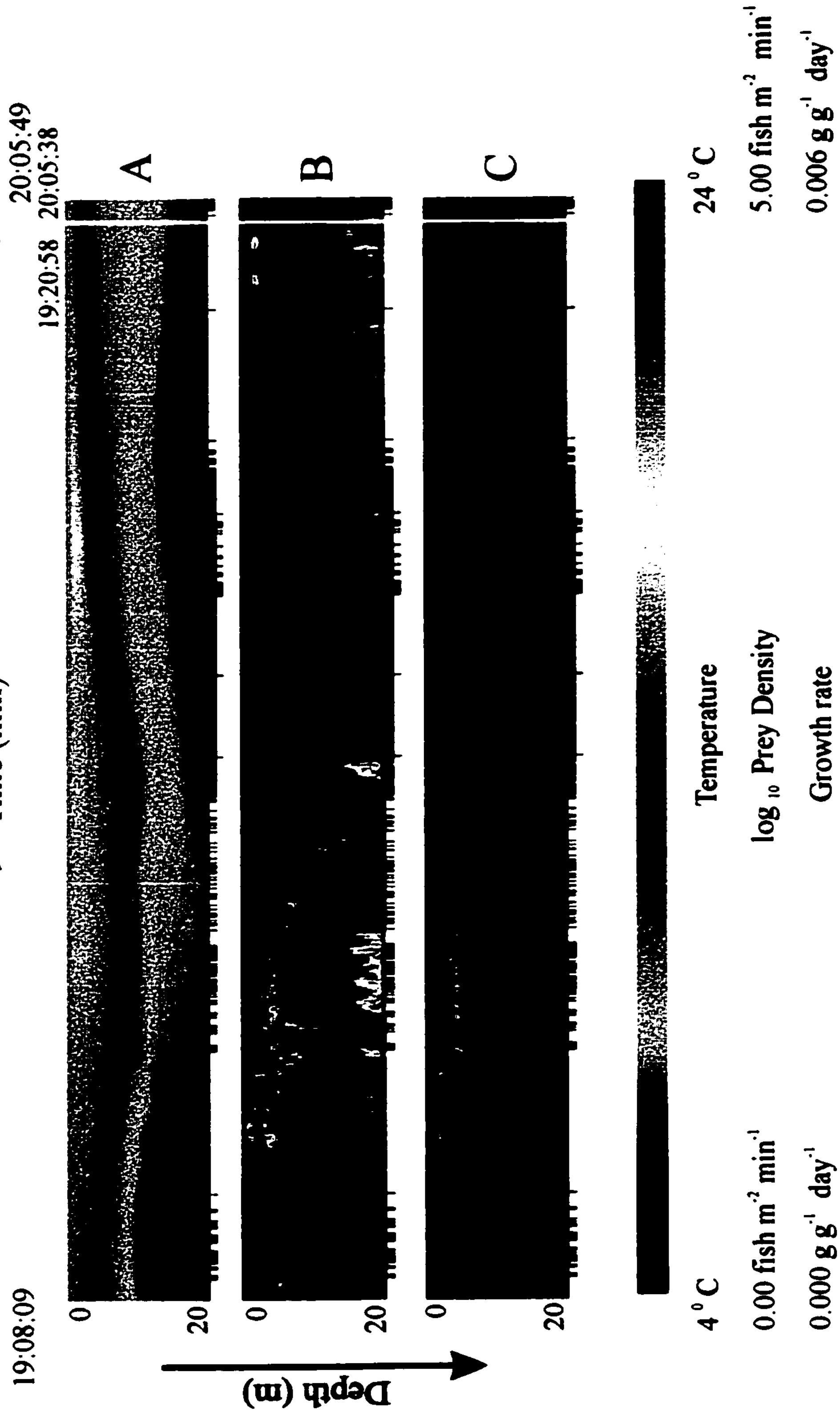

Time (min)
19:08:09
19:20:58
20:05:38
20:05:49
A
B
C
Depth (m)
0
20
0
20
0
20
4 °C
24 °C
Temperature
0.00 fish m-2 min-1
log10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1

Figure 2.13 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dusk (*21:01-22:30*) of June 19, 1997, in western Lake Ontario.

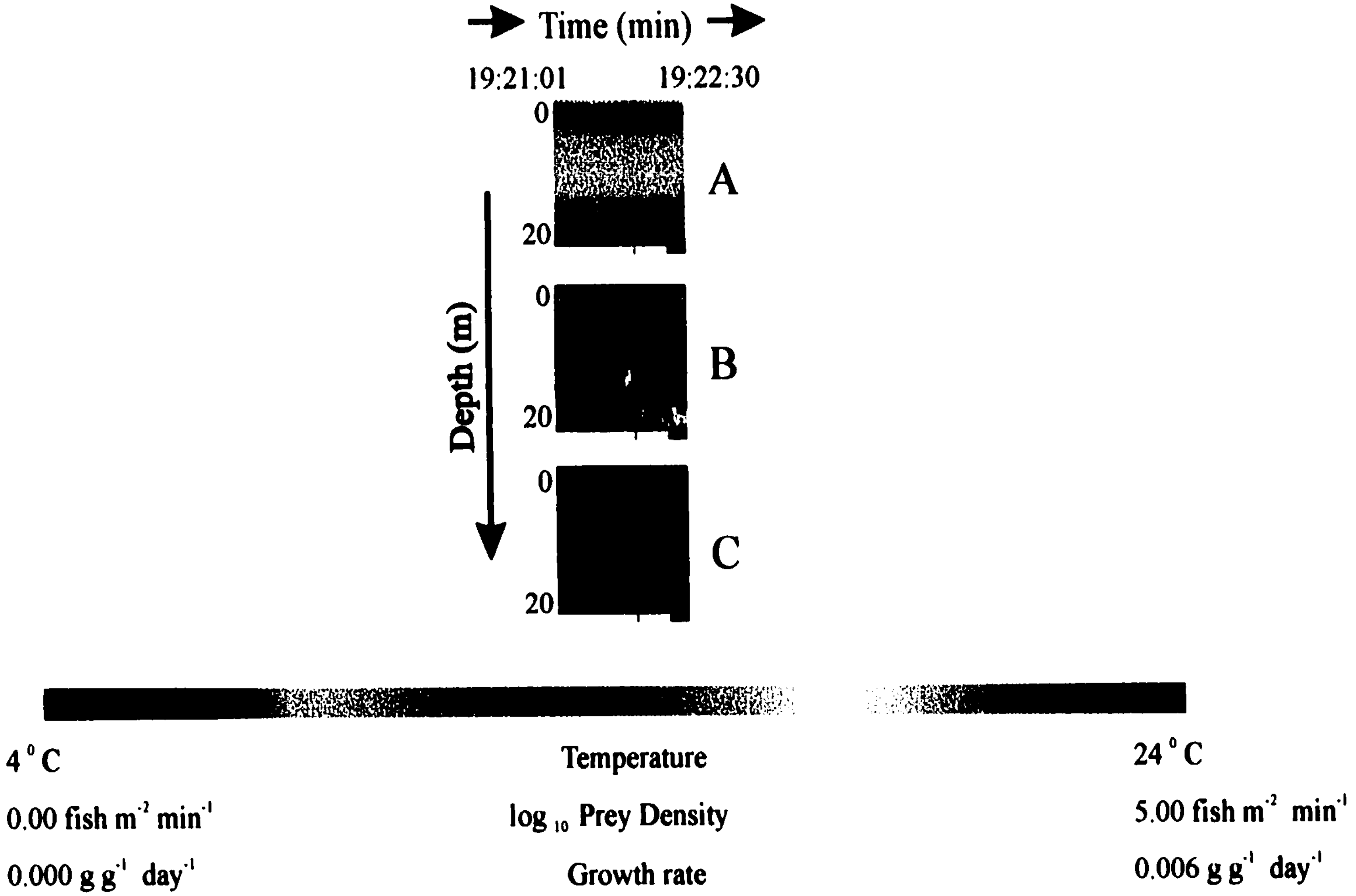

Time (min)
19:21:01
19:22:30
Depth (m)
0
20
A
0
20
B
0
20
C
4 °C
0.00 fish m-2 min-1
0.000 g g-1 day-1
Temperature
log 10 Prey Density
Growth rate
24 °C
5.00 fish m-2 min-1
0.006 g g-1 day-1

Figure 2.14 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the night (*22:33-04:07*) of June 19-20, 1997, in western Lake Ontario.

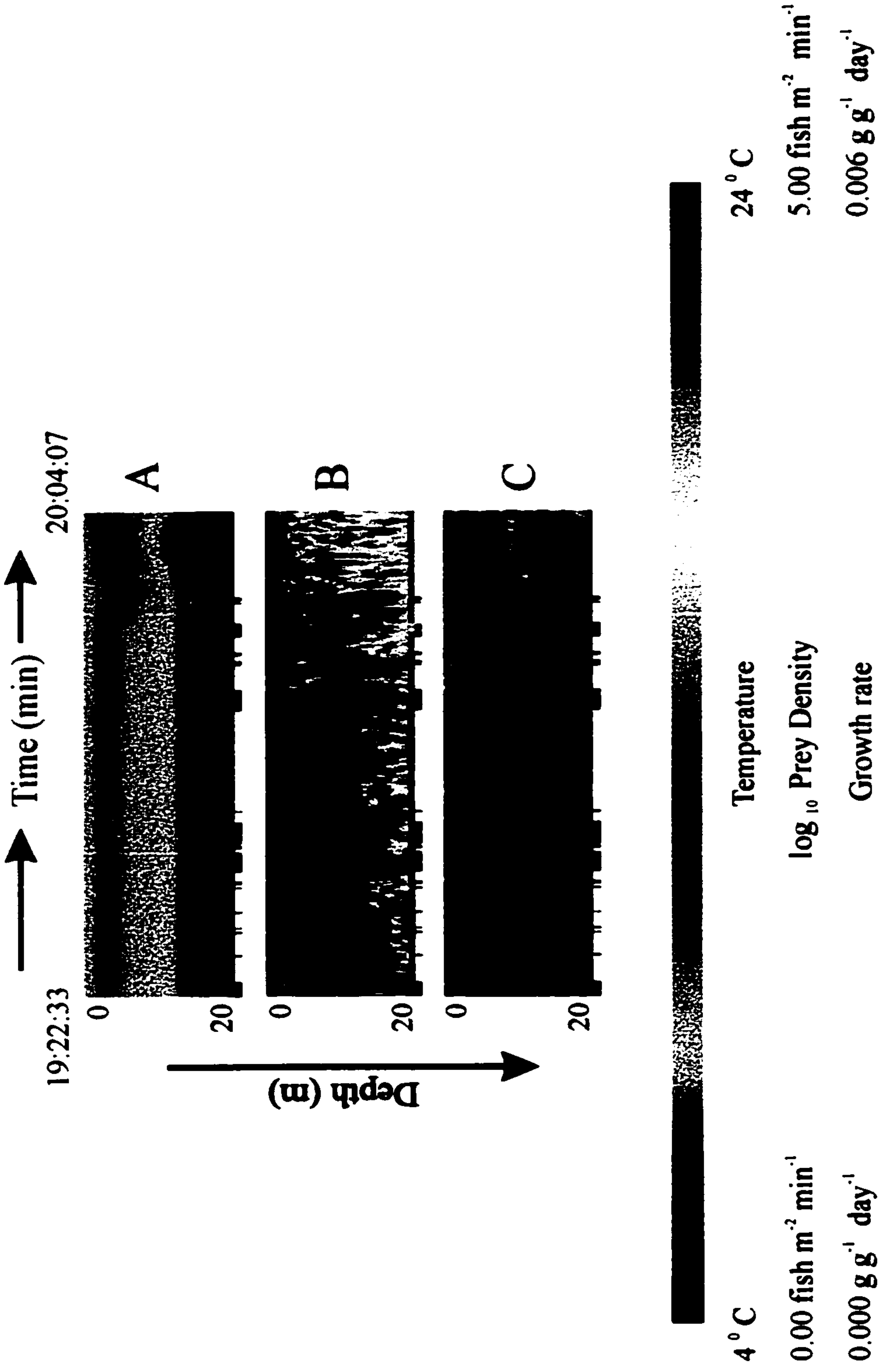

Time (min)
19:22:33
20:04:07
Depth (m)
0
20
A
B
C
4 °C
24 °C
Temperature
0.00 fish m^{-2} min^{-1}
5.00 fish m^{-2} min^{-1}
log$_{10}$ Prey Density
0.000 g g^{-1} day^{-1}
0.006 g g^{-1} day^{-1}
Growth rate

Figure 2.15 —Cumulative distribution of the proportion of each time period (dawn, day, dusk, and night) supporting Chinook salmon (*Oncorhynchus tshawytscha*) growth rate potential at one location in western Lake Ontario during the June 19-20 sampling event.

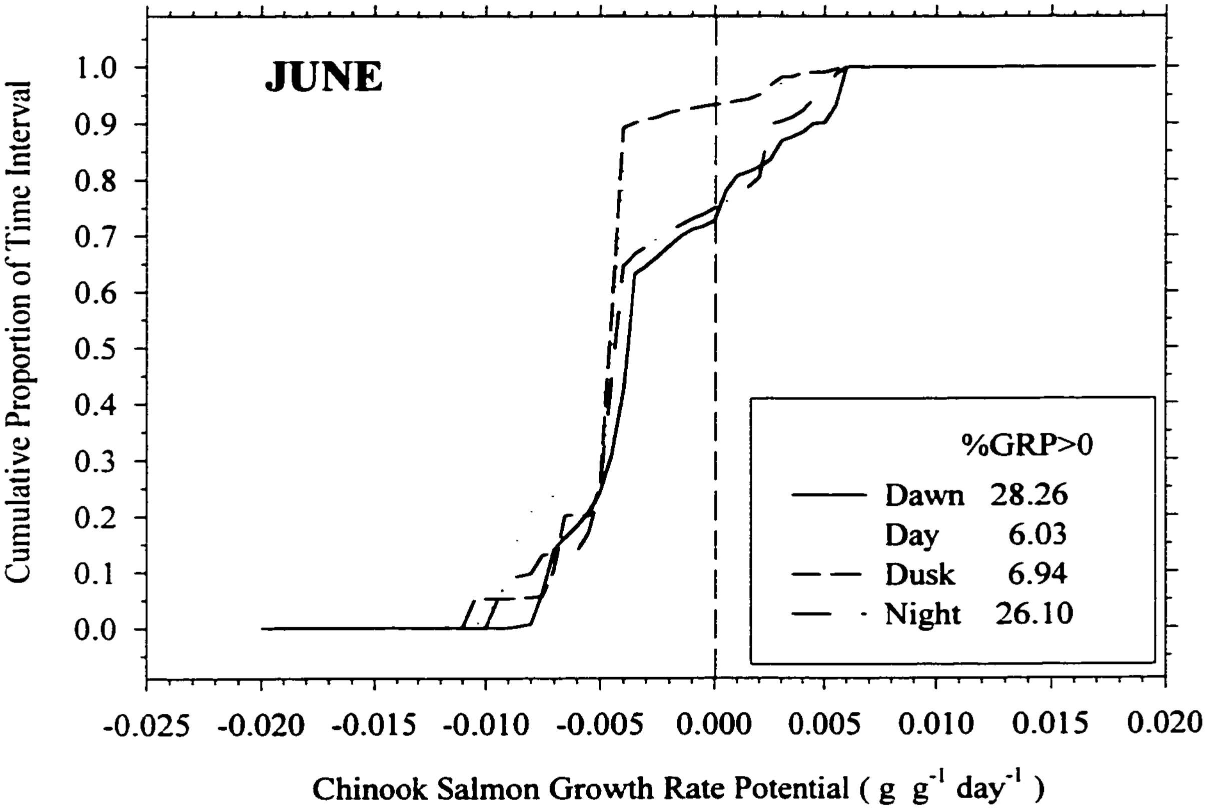

JUNE
Cumulative Proportion of Time Interval
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.025
-0.020
-0.015
-0.010
-0.005
0.000
0.005
0.010
0.015
0.020
Chinook Salmon Growth Rate Potential (g g^{-1} day^{-1})
%GRP>0
Dawn 28.26
Day 6.03
Dusk 6.94
Night 26.10

Figure 2.16 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dawn (*04:26-06:05*) of July 31, 1997, in western Lake Ontario.

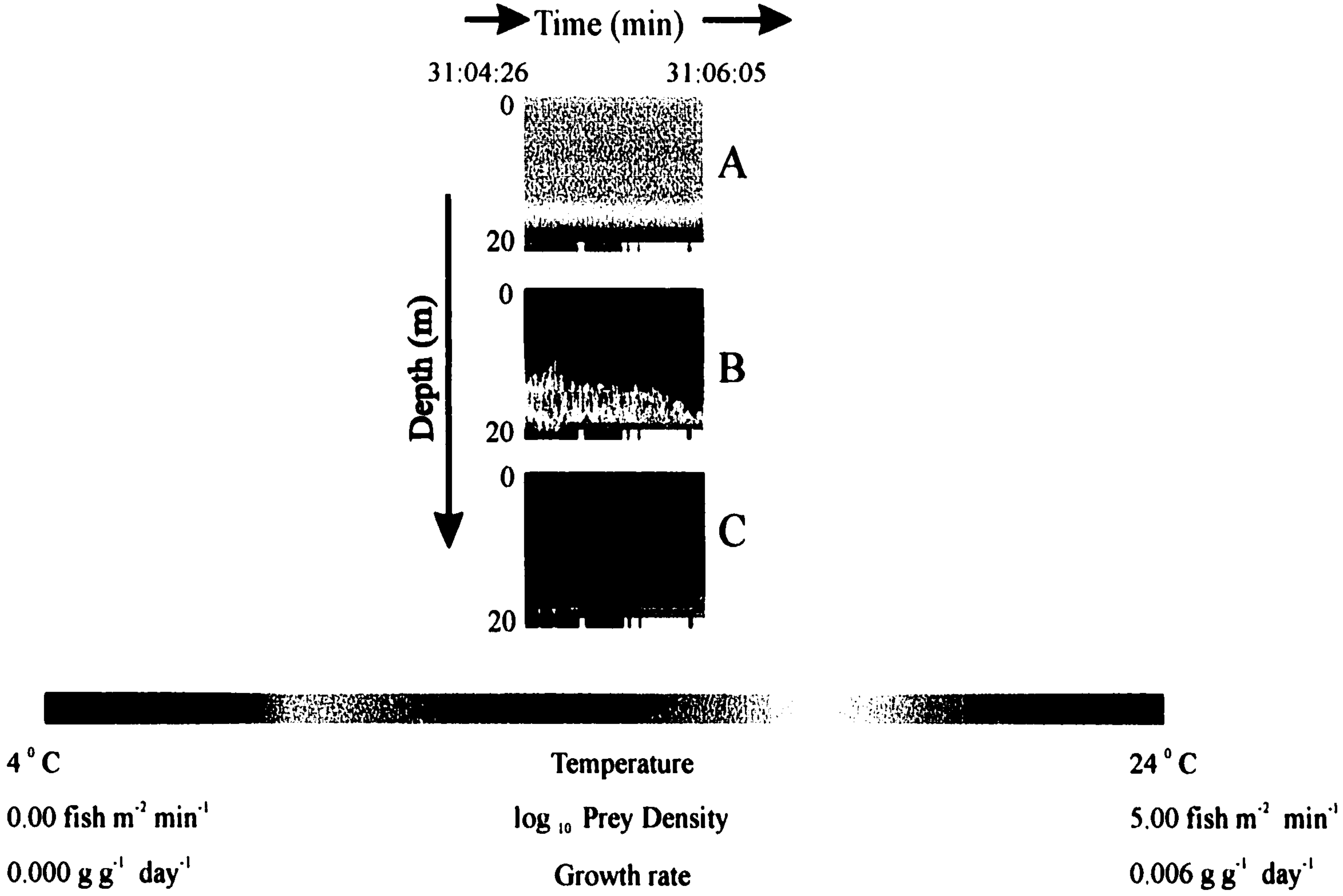

Time (min)
31:04:26
31:06:05
Depth (m)
0
20
A
0
20
B
0
20
C
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Temperature
log$_{10}$ Prey Density
Growth rate
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}

Figure 2.17 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the day (*10:07-20:36 & 06:08-10:10*) of July 30-31, 1997, in western Lake Ontario.

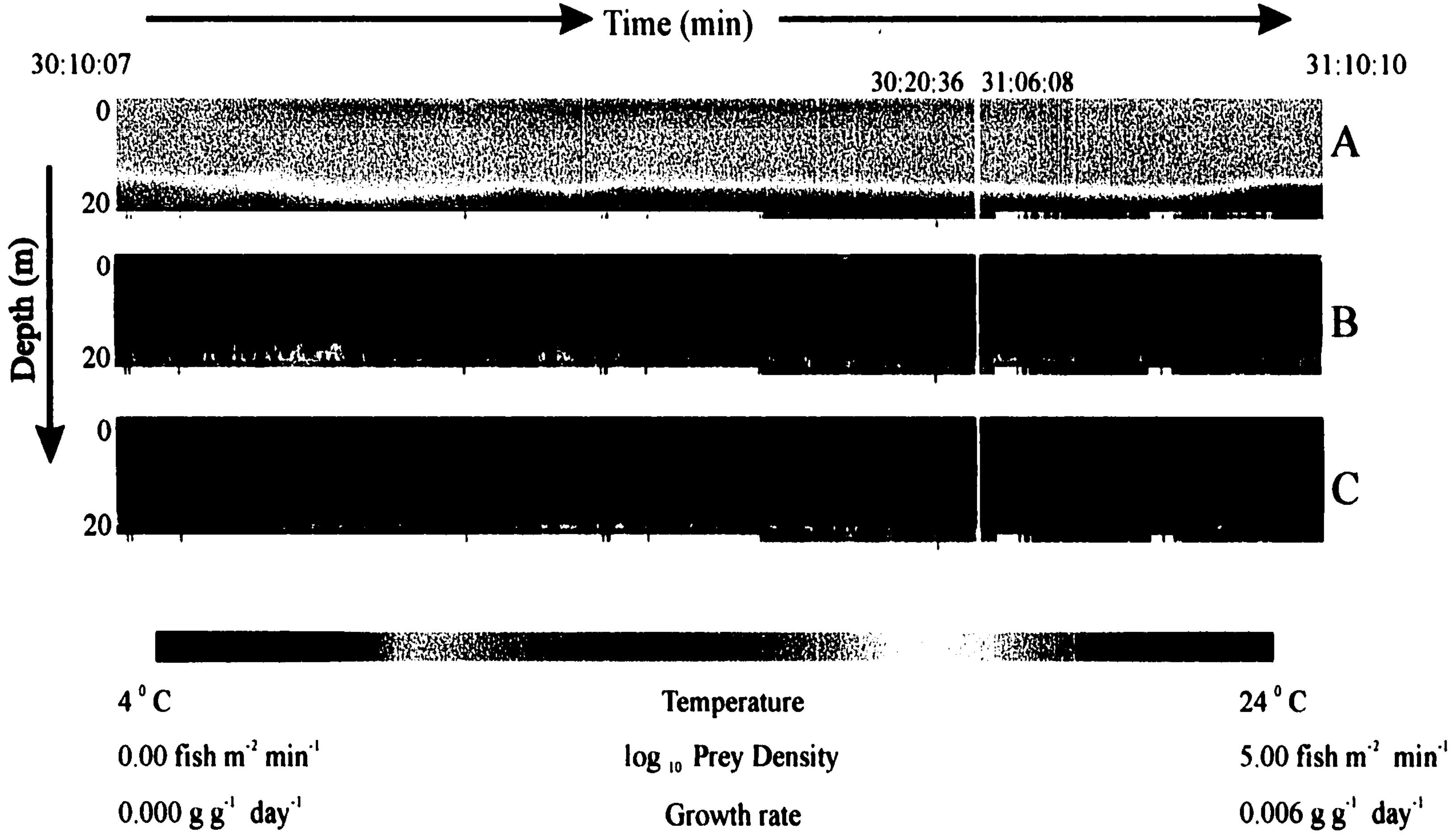

Time (min)
30:10:07
30:20:36
31:06:08
31:10:10
Depth (m)
0
20
A
B
C
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1

Figure 2.18 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dusk (*20:39-22:08*) of July 30, 1997, in western Lake Ontario.

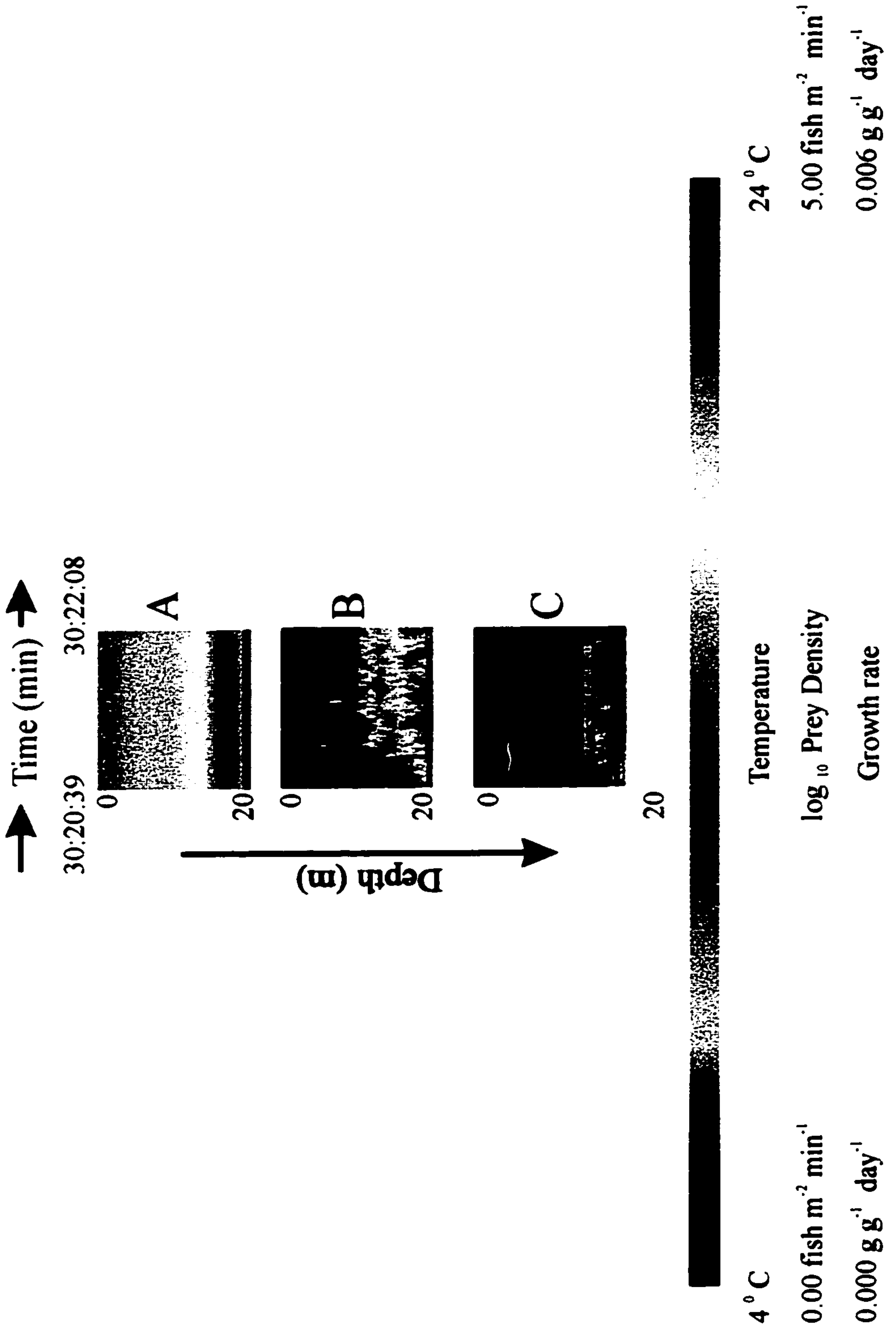

Time (min)
30:20:39
30:22:08
Depth (m)
0
20
A
B
C
Temperature
log $_{10}$ Prey Density
Growth rate
4 °C
0.00 fish m $^{-2}$ min $^{-1}$
0.000 g g $^{-1}$ day $^{-1}$
24 °C
5.00 fish m $^{-2}$ min $^{-1}$
0.006 g g $^{-1}$ day $^{-1}$

Figure 2.19 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the night (*22:11-04:13*) of July 30-31, 1997, in western Lake Ontario.

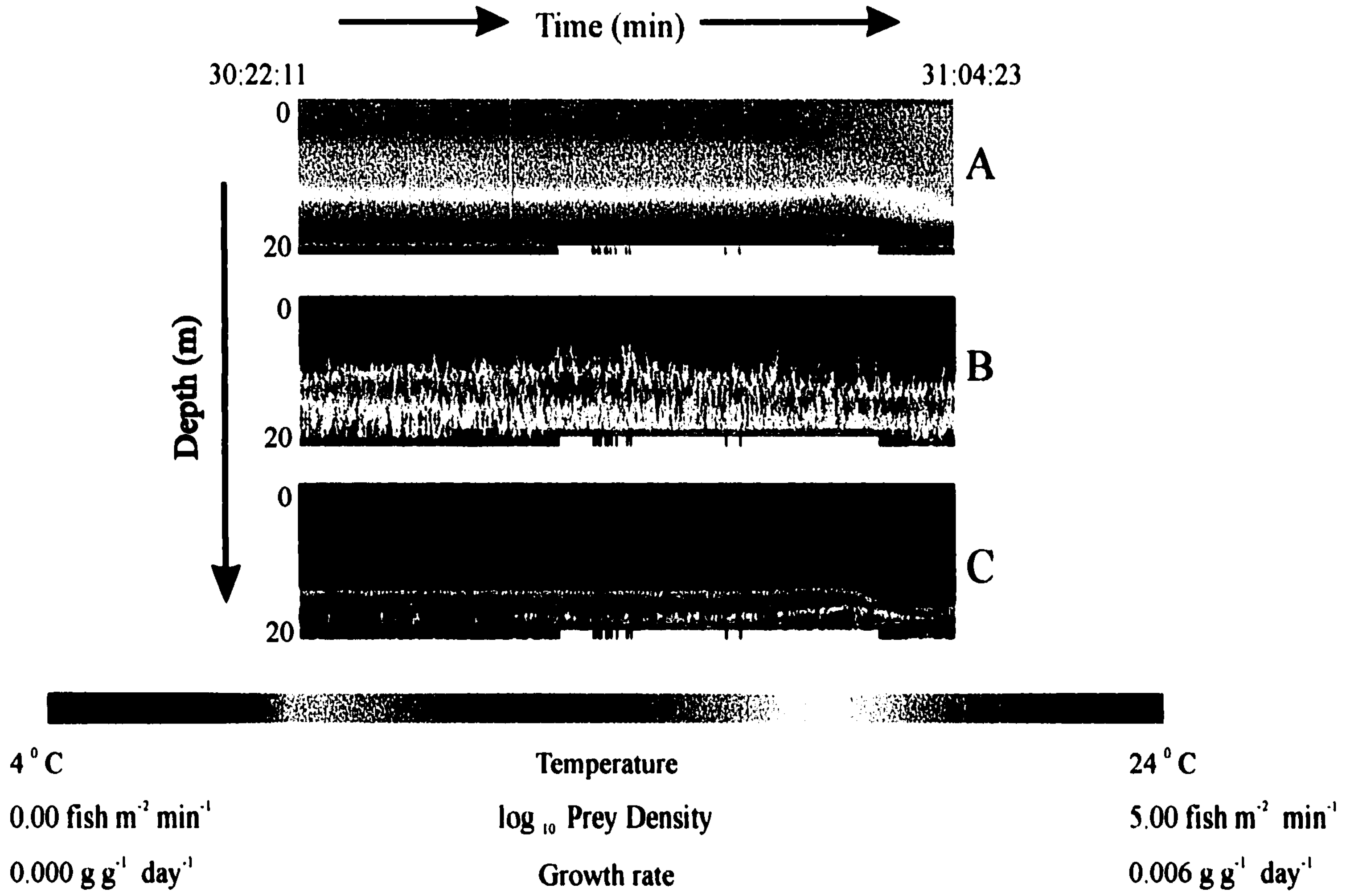

Time (min)
30:22:11
31:04:23
Depth (m)
0
20
A
0
20
B
0
20
C
4 °C
Temperature
24 °C
0.00 fish m⁻² min⁻¹
log ₁₀ Prey Density
5.00 fish m⁻² min⁻¹
0.000 g g⁻¹ day⁻¹
Growth rate
0.006 g g⁻¹ day⁻¹

Figure 2.20 —Cumulative distribution of the proportion of each time period (dawn, day, dusk, and night) supporting Chinook salmon (*Oncorhynchus tshawytscha*) growth rate potential at one location in western Lake Ontario during the July 30-31 sampling event.

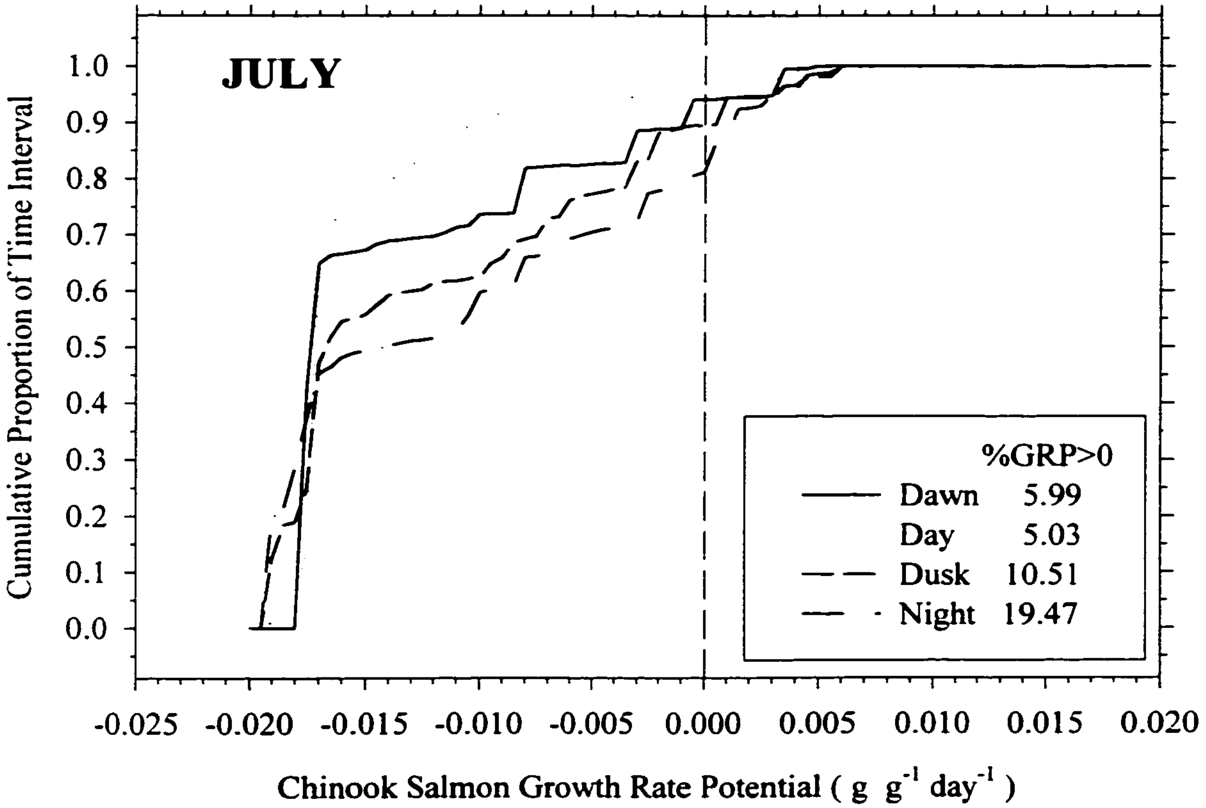

JULY
Cumulative Proportion of Time Interval
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.025
-0.020
-0.015
-0.010
-0.005
0.000
0.005
0.010
0.015
0.020
Chinook Salmon Growth Rate Potential (g g^{-1} day^{-1})
%GRP>0
Dawn 5.99
Day 5.03
Dusk 10.51
Night 19.47

Figure 2.21 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the day (*16:54-19:32*) of September 5, 1997, in western Lake Ontario.

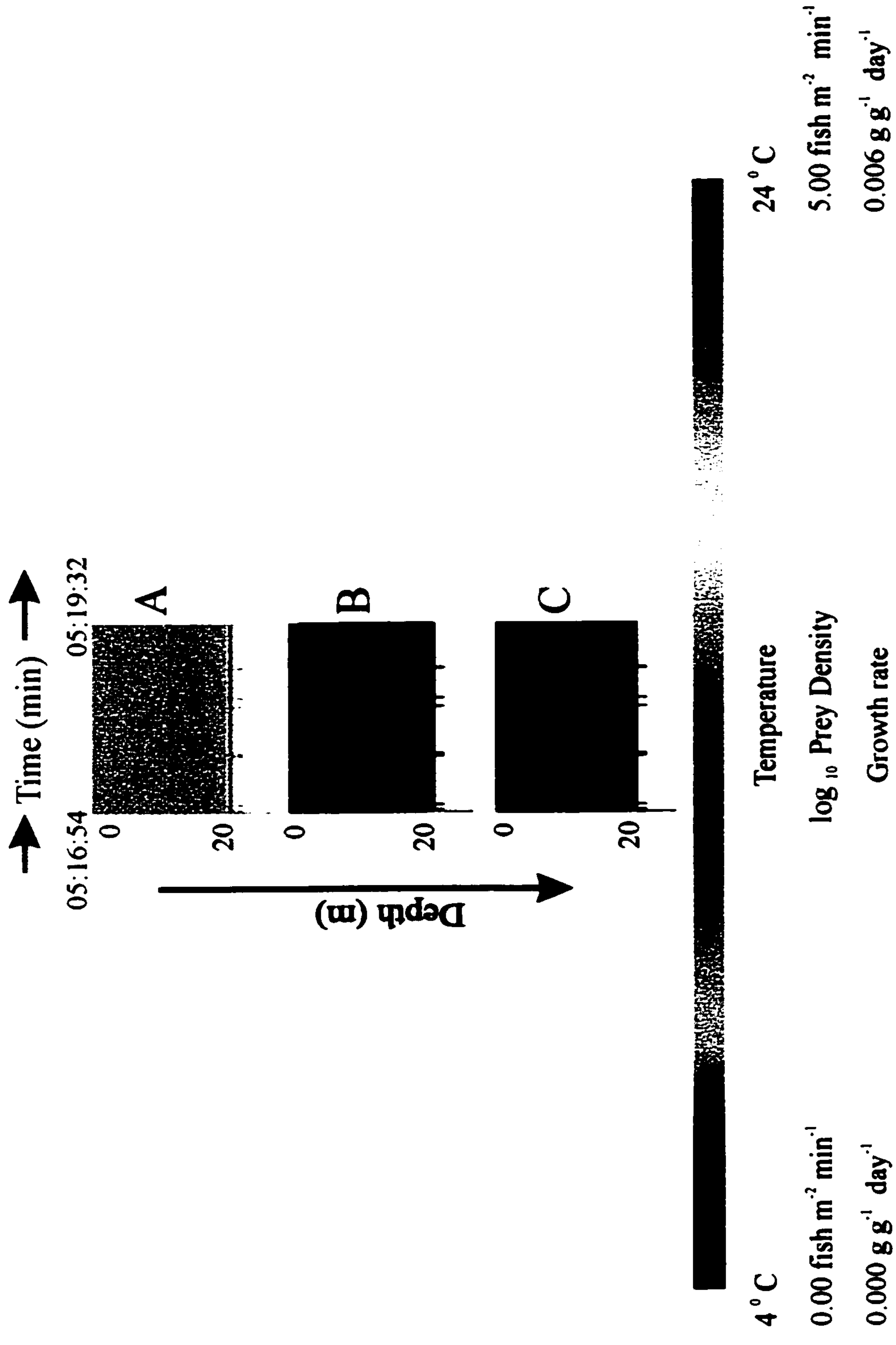

Time (min)
05:16:54
05:19:32
A
B
C
0
20
0
20
0
20
Depth (m)
Temperature
log $_{10}$ Prey Density
Growth rate
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}

Figure 2.22 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dusk (*19:48-21:15*) of September 5, 1997, in western Lake Ontario.

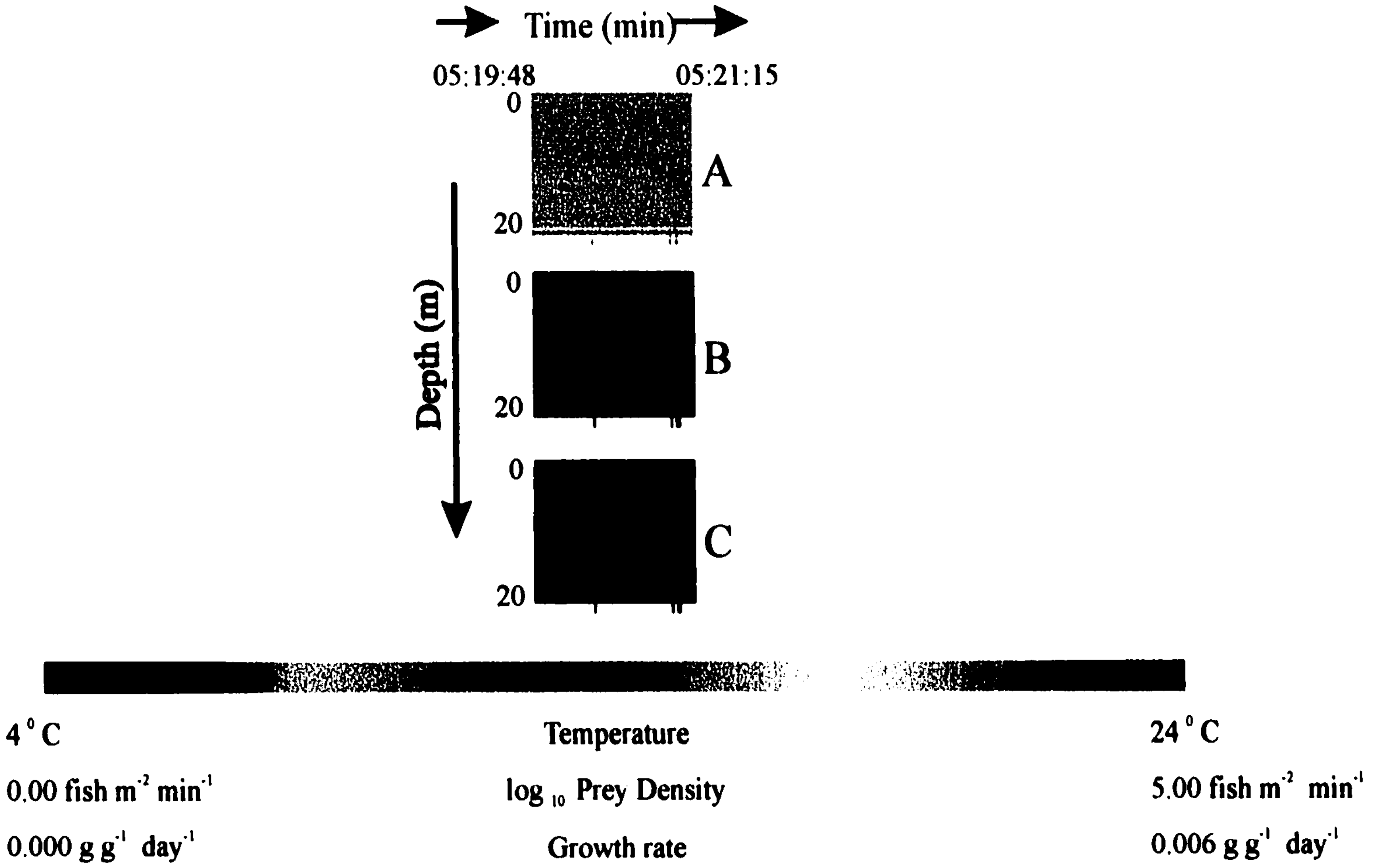

Time (min)
05:19:48
05:21:15
Depth (m)
0
20
A
B
C
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Temperature
log$_{10}$ Prey Density
Growth rate
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}

Figure 2.23 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the night (*21:17-05:03*) of September 5-6, 1997, in western Lake Ontario.

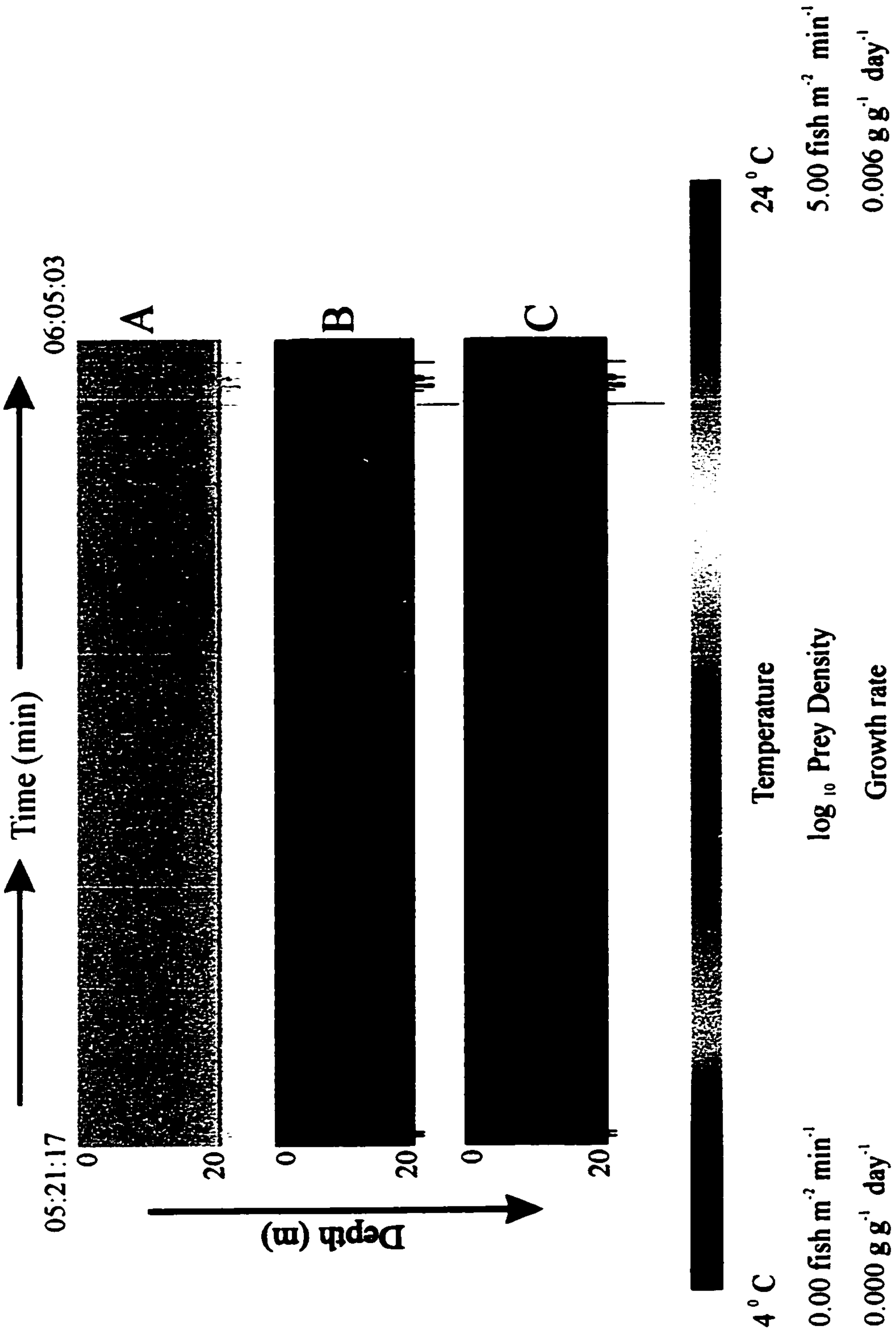

Time (min)
05:21:17
06:05:03
A
B
C
0
20
0
20
0
20
Depth (m)
4 °C
24 °C
Temperature
0.00 fish m-2 min-1
5.00 fish m-2 min-1
log10 Prey Density
0.000 g g-1 day-1
0.006 g g-1 day-1
Growth rate

Figure 2.24 —Cumulative distribution of the proportion of each time period (dawn, day, dusk, and night) supporting Chinook salmon (*Oncorhynchus tshawytscha*) growth rate potential at one location in western Lake Ontario during the September 5-6 sampling event.

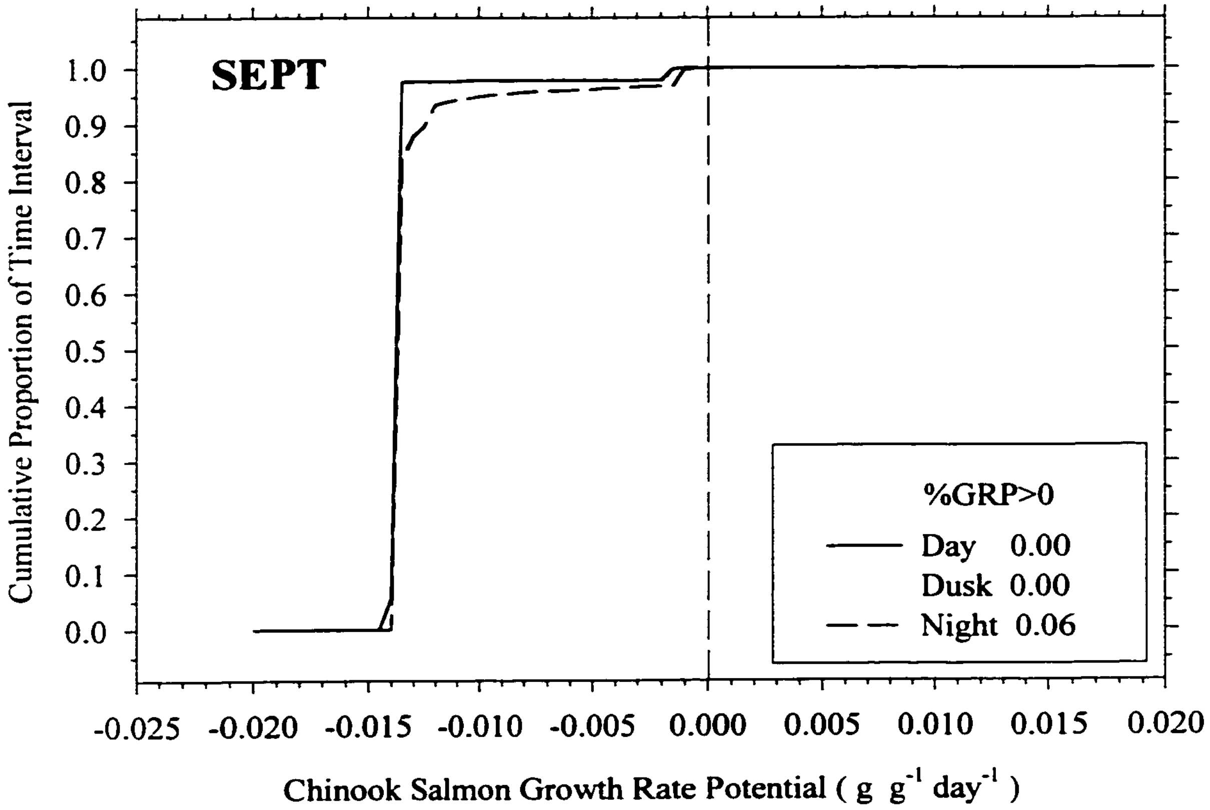

SEPT
%GRP>0
Day 0.00
Dusk 0.00
Night 0.06
Cumulative Proportion of Time Interval
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
-0.025
-0.020
-0.015
-0.010
-0.005
0.000
0.005
0.010
0.015
0.020
Chinook Salmon Growth Rate Potential (g g^{-1} day^{-1})

Figure 2.25 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dawn (*06:03-07:32*) of October 19, 1997, in western Lake Ontario.

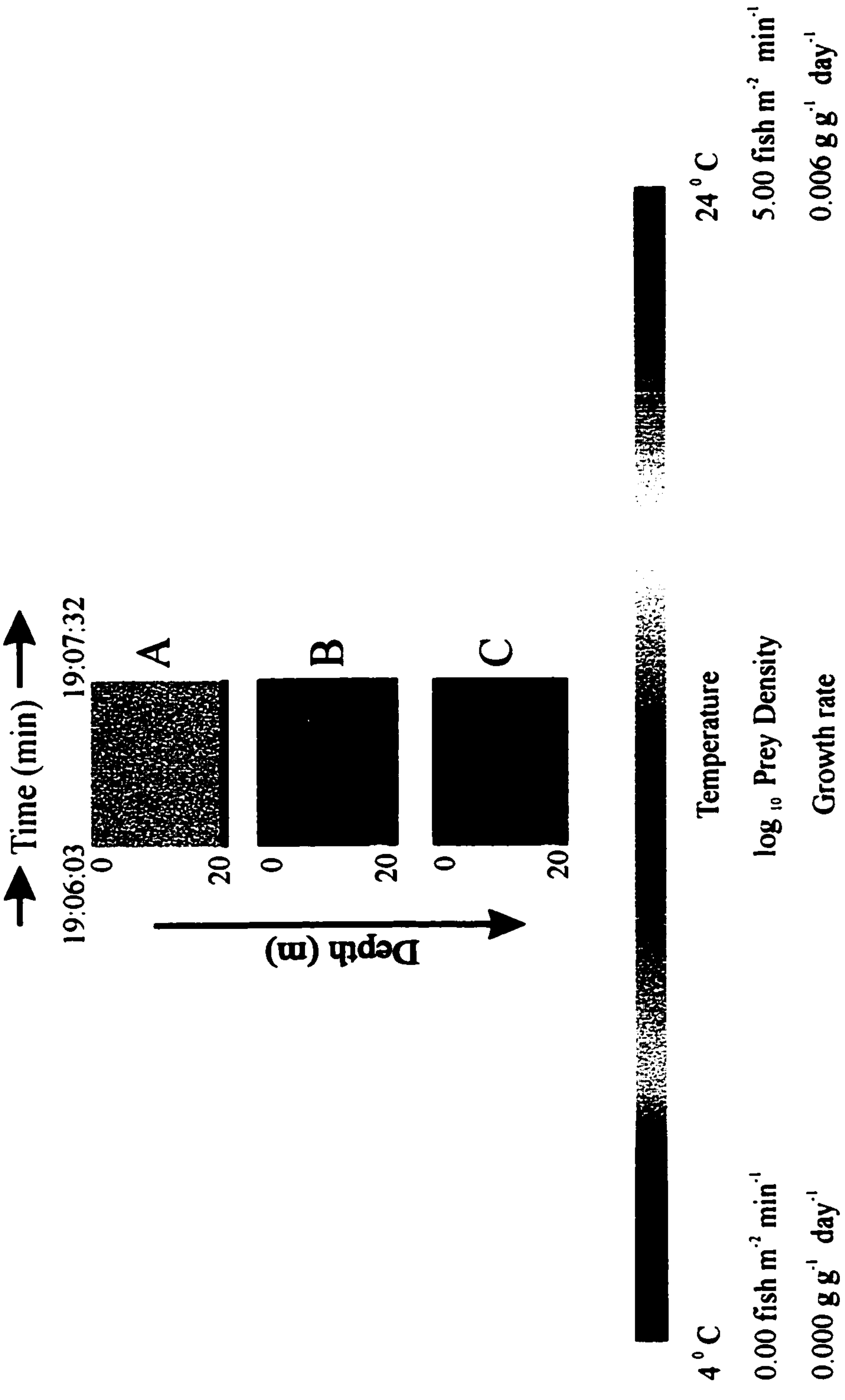

Time (min)
19:06:03
19:07:32
Depth (m)
A
B
C
0
20
0
20
0
20
Temperature
log $_{10}$ Prey Density
Growth rate
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}

Figure 2.26 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the day (*16:10-18:25 & 07:35-15:53*) of October 18-19, 1997, in western Lake Ontario.

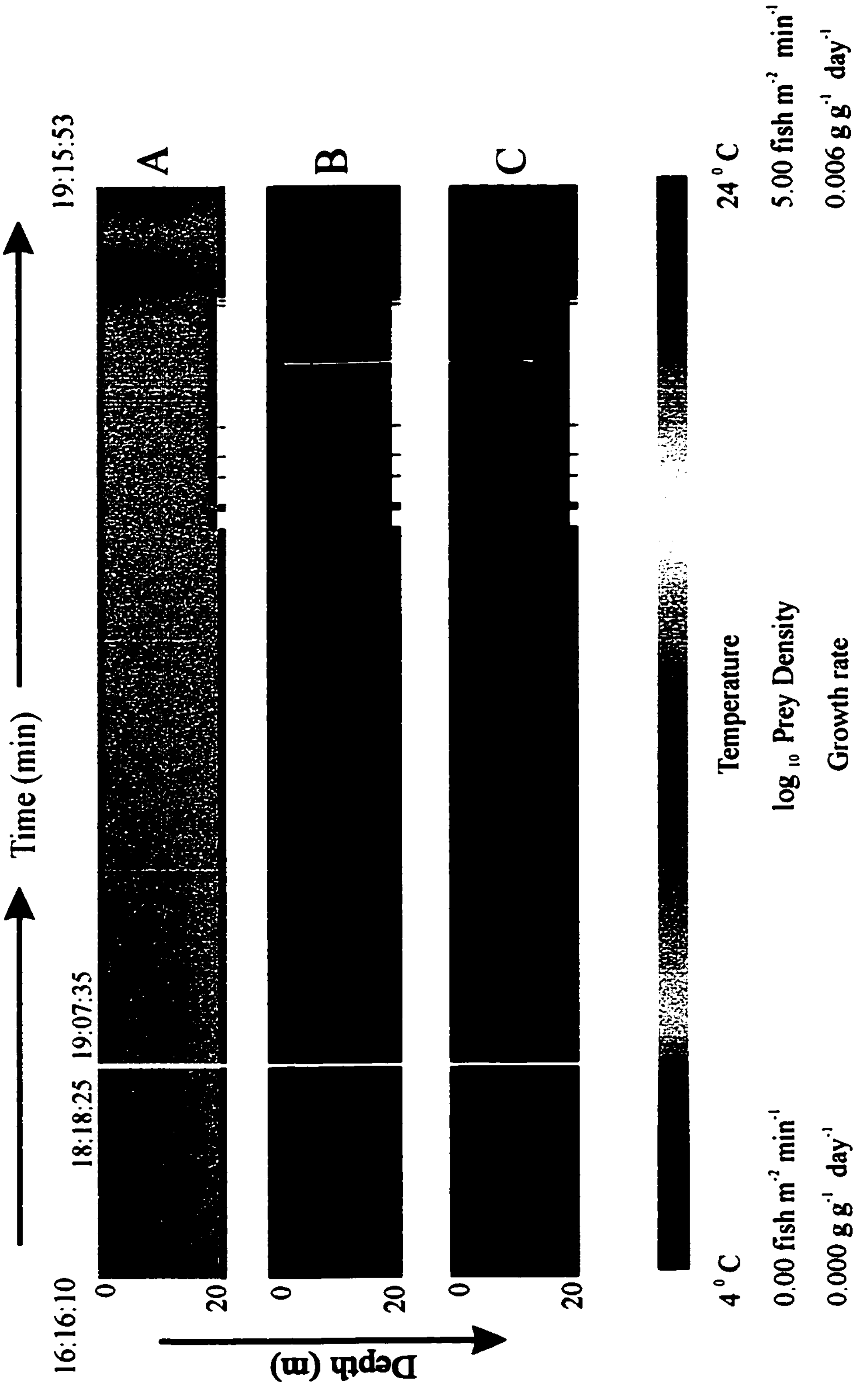

Time (min)
16:16:10
18:18:25
19:07:35
19:15:53
A
B
C
Depth (m)
0
20
0
20
0
20
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1

Figure 2.27 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the dusk (*18:27-19:57*) of October 18, 1997, in western Lake Ontario.

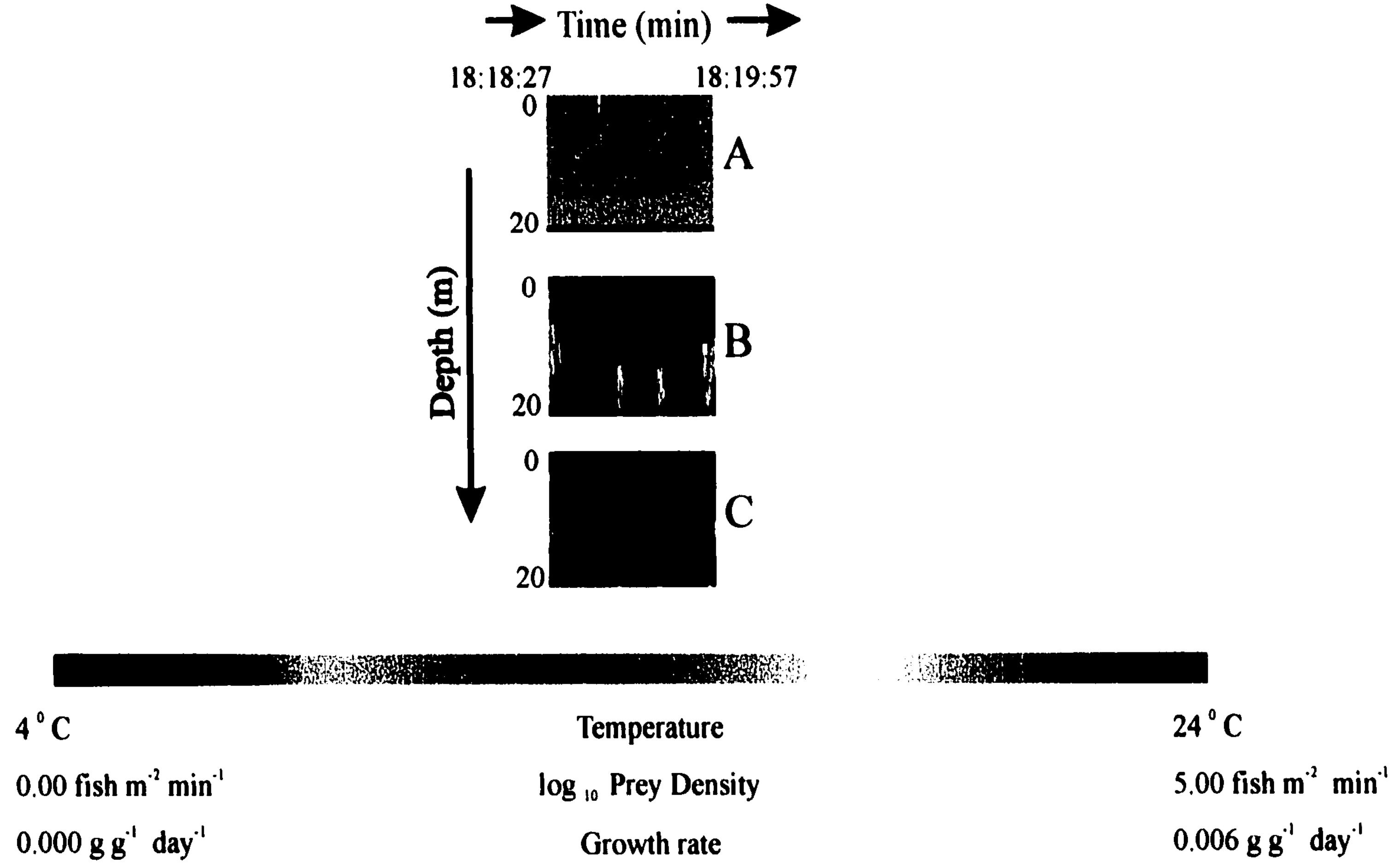

Time (min)
18:18:27
18:19:57
Depth (m)
0
20
A
0
20
B
0
20
C
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log$_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}

Figure 2.28 —The evolution of temperature (A), acoustically derived distribution of alewife (*Alosa pseudoharengus*; B), and the growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*; C) during the night (00:*26-06:01*) of October 18-19, 1997, in western Lake Ontario.

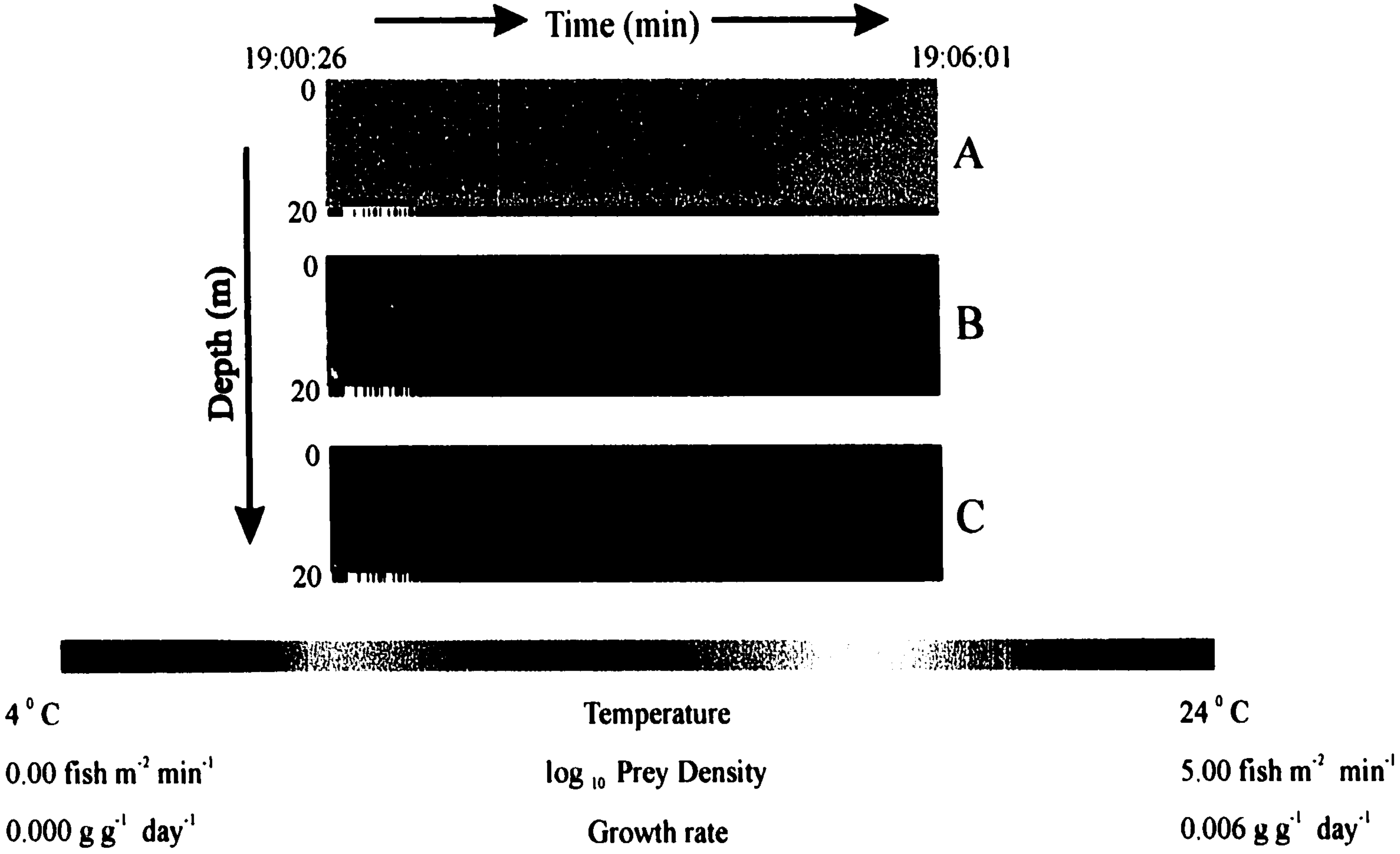

Time (min)
19:00:26
19:06:01
Depth (m)
0
20
A
0
20
B
0
20
C
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log$_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}

Figure 2.29 —Cumulative distribution of the proportion of each time period (dawn, day, dusk, and night) supporting Chinook salmon (*Oncorhynchus tshawytscha*) growth rate potential at one location in western Lake Ontario during the October 18-19 sampling event.

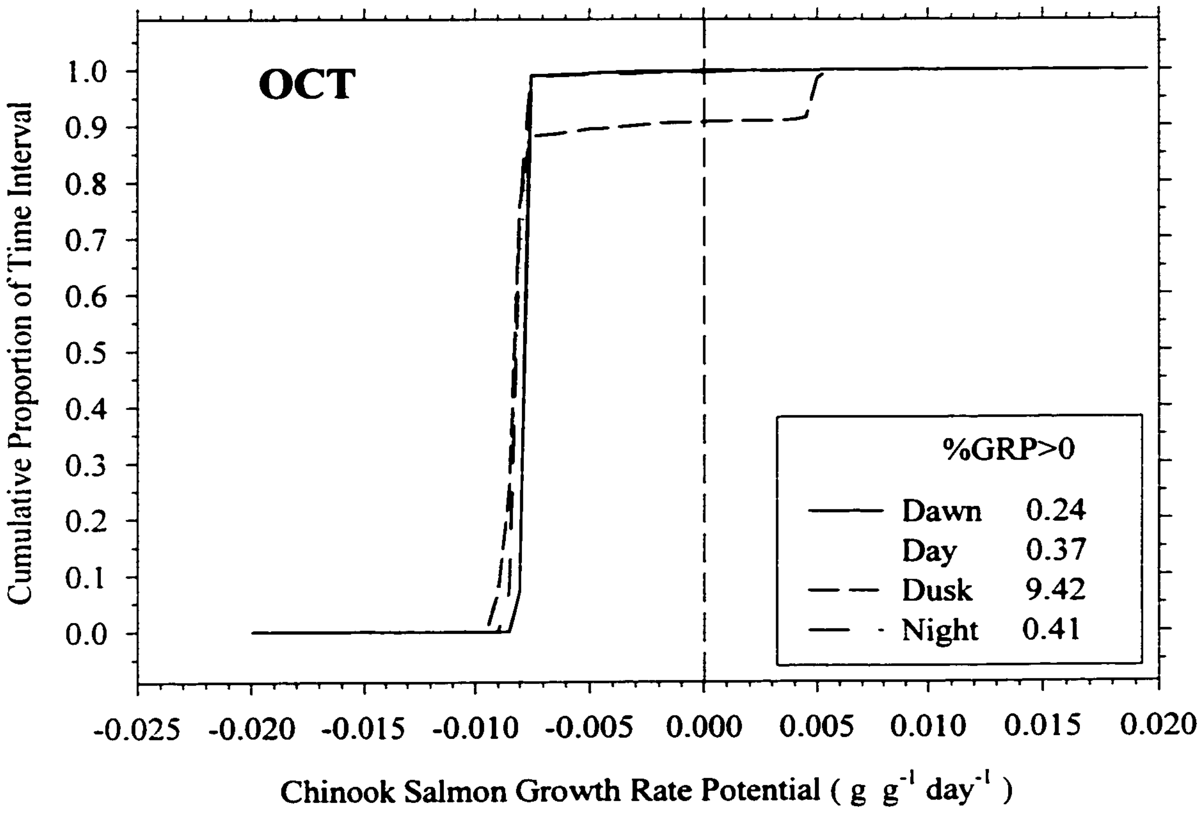

OCT
Cumulative Proportion of Time Interval
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
%GRP>0
Dawn 0.24
Day 0.37
Dusk 9.42
Night 0.41
-0.025
-0.020
-0.015
-0.010
-0.005
0.000
0.005
0.010
0.015
0.020
Chinook Salmon Growth Rate Potential (g g^{-1} day^{-1})

Figure 2.30 —Cumulative proportion of each sampling event (May, June, July, September, and October) supporting growth rate potential of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) at one location in western Lake Ontario, during the 1997 growing season.

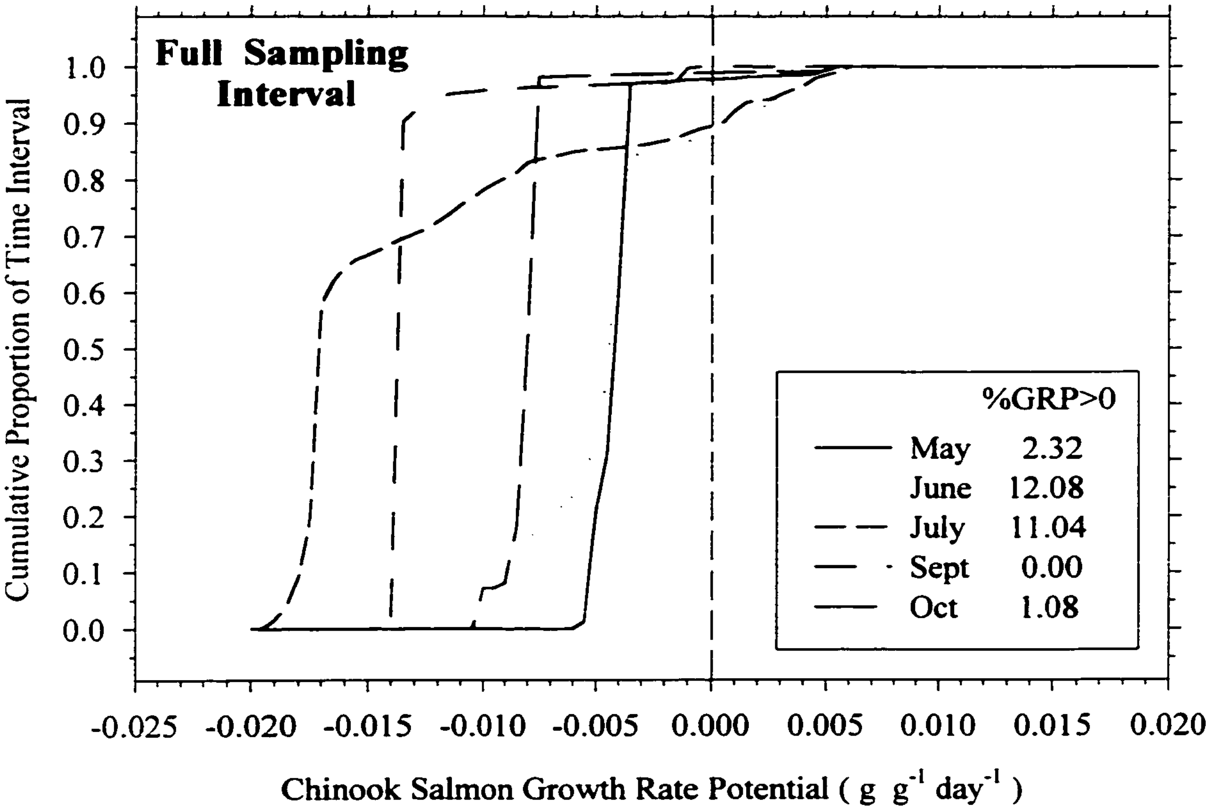

Full Sampling Interval
Cumulative Proportion of Time Interval
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.025
-0.020
-0.015
-0.010
-0.005
0.000
0.005
0.010
0.015
0.020
Chinook Salmon Growth Rate Potential (g g^{-1} day^{-1})
%GRP>0
May 2.32
June 12.08
July 11.04
Sept 0.00
Oct 1.08

Figure 2.31 — Mean temperature of water column at the stationary sampling location in western Lake Ontario during different time periods within each sampling event.

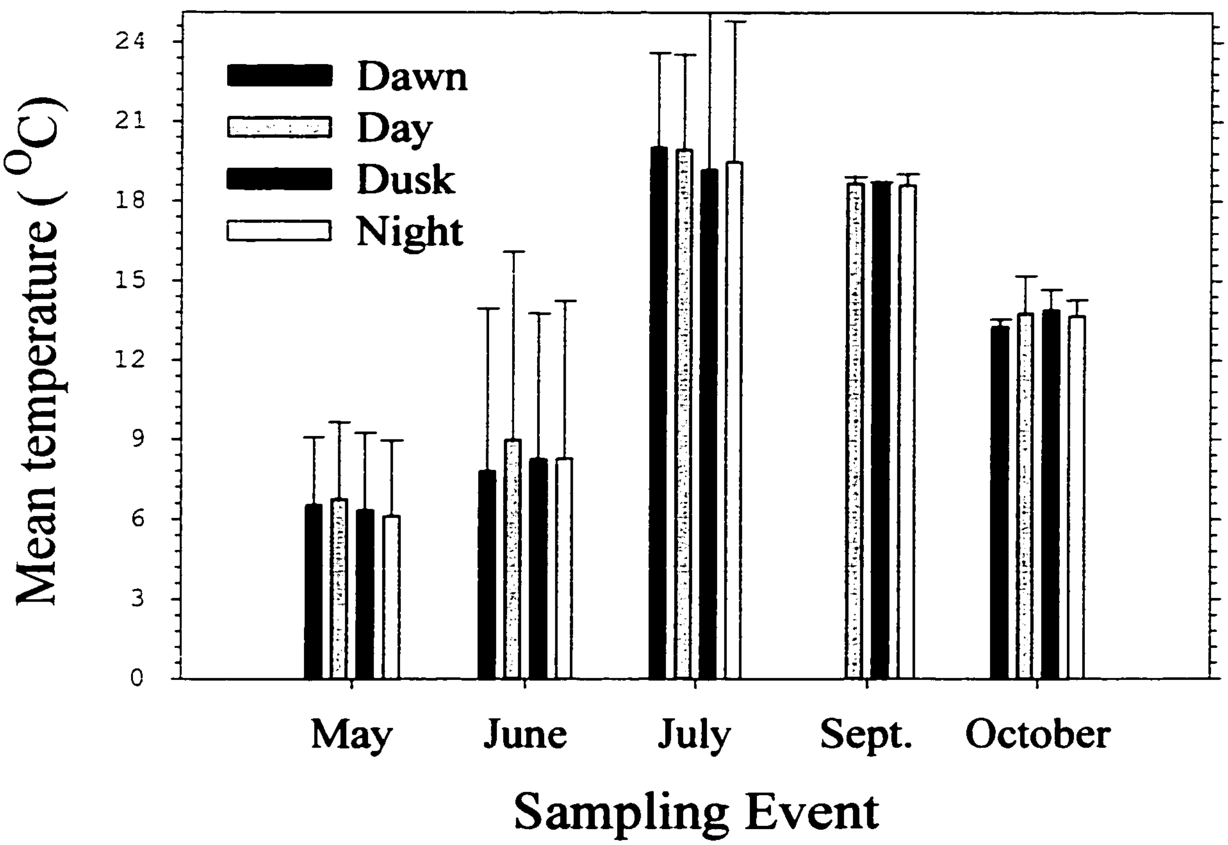

Mean temperature (^{O}C)
24
21
18
15
12
9
6
3
0
Dawn
Day
Dusk
Night
May
June
July
Sept.
October
Sampling Event

Figure 2.32 — Mean prey biomass density at the stationary sampling location in western Lake Ontario during different time periods within each sampling event.

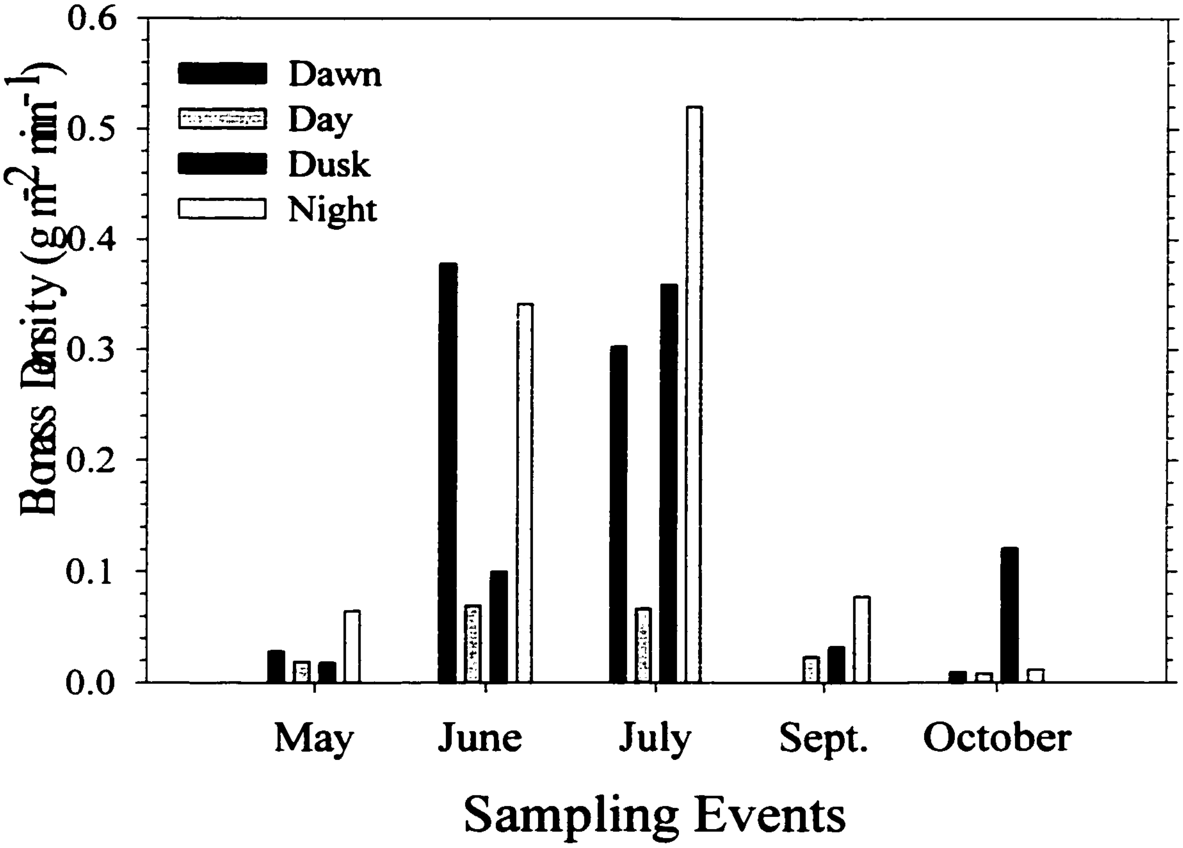

0.6
0.5
0.4
0.3
0.2
0.1
0.0
Biomass Density (g m-2 mm-1)
Dawn
Day
Dusk
Night
May
June
July
Sept.
October
Sampling Events

Table 2.3 –Kruskall-Wallis H' statistic calculated to test the differences among the average growth rate potential (GRP; g^{-1} g^{-1} day $^{-1}$) per minute, from each time section within a given sampling period. GRP data derived from acoustically collected prey density, data and temperature data entered into foraging and bioenergetic models. H' values are compared to standard tabulated χ^2 statistic for the proper sample size (Groups-1), and evaluated at the α=0.05 level of significance.

Time	Time Section	N	Groups	K-W(H_{init})	K-W(D_{corr})	Corr H'=(H/D)	χ^2 (α=0.05)
May	Dawn	91	4	4629.785	-6.108	-759.669	7.815
	Day	797					
	Dusk	91					
	Night	343					
June	Dawn	88	4	4487.808	0.999	4488.076[A]	7.815
	Day	783					
	Dusk	91					
	Night	337					
July	Dawn	101	4	5260.551	1.001	5260.687[A]	7.815
	Day	855					
	Dusk	91					
	Night	371					
Sept	Day	108	3	2088.446	0.839	2500.694[A]	5.991
	Dusk	89					
	Night	459					
Oct.	Dawn	91	4	3673.316	0.092	40017.500[A]	7.815
	Day	630					
	Dusk	91					
	Night	335					

[A] Indicates significant differences at α=0.05.

Table 2.4 –Kolmogorov-Smirnov statistic (K-S) calculated to assess significant differences among growth rate potentials of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) during different time periods of the May sampling event. K-S statistics are evaluated against the critical-D for unplanned comparison. K-S values > critical-D indicate a significant difference at the $\alpha=0.05$ level (Sokal and Rohlf 1995).

Comparing	K-S Statistic	Unplanned critical-D
Dawn vs. Day	0.0689	0.1142
Dawn vs. Dusk	0.1496	0.1530
Dawn vs. Night	0.2362^{A}	0.1217
Day vs. Dusk	0.1408^{A}	0.1142
Day vs. Night	0.2275^{A}	0.0667
Dusk vs. Night	0.0866	0.1217

^{A} Indicates significant differences at $\alpha=0.05$.

*Unplanned critical-Ds have been adjusted for multiple comparisons.

Table 2.5 –Kolmogorov-Smirnov statistic (K-S) calculated to assess significant differences among growth rate potentials of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) during different time periods within the June sampling event. K-S statistics are evaluated against the critical-D for unplanned comparison. K-S values > critical-D indicate a significant difference at the α=0.05 level (Sokal and Rohlf 1995).

Comparing	K-S Statistic	Unplanned critical-D
Dawn vs. Day	0.3873^{A}	0.1114
Dawn vs. Dusk	0.4712^{A}	0.1488
Dawn vs. Night	0.2244^{A}	0.1187
Day vs. Dusk	0.1634^{A}	0.1107
Day vs. Night	0.2676^{A}	0.0649
Dusk vs. Night	0.2468^{A}	0.1181

^{A} Indicates significant differences at α=0.05.

*Unplanned critical-Ds have been adjusted for multiple comparisons.

Table 2.6 –Kolmogorov-Smirnov statistic (K-S) calculated to assess significant differences among growth rate potentials of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) during different time periods within the July sampling event. K-S statistics are evaluated against the critical-D for unplanned comparison.K-S values > critical-D indicate a significant difference at the α=0.05 level (Sokal and Rohlf 1995).

Comparing	K-S Statistic	Unplanned critical-D
Dawn vs. Day	0.2859[A]	0.1169
Dawn vs. Dusk	0.1889[A]	0.1593
Dawn vs. Night	0.2884[A]	0.1246
Day vs. Dusk	0.2779[A]	0.1209
Day vs. Night	0.3595[A]	0.0691
Dusk vs. Night	0.1254	0.1284

[A] Indicates significant differences at α=0.05.

*Unplanned critical-Ds have been adjusted for multiple comparisons.

Table 2.7 –Kolmogorov-Smirnov statistic (K-S) calculated to assess significant differences among growth rate potentials of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) during different time periods within the September sampling event. K-S statistics are evaluated against the critical-D for unplanned comparison.

K-S values > critical-D indicate a significant difference at the $\alpha=0.05$ level (Sokal and Rohlf 1995).

Comparing	K-S Statistic	Unplanned critical-D
Day vs. Dusk	0.0552	0.1177
Day vs. Night	0.1396^A	0.0878
Dusk vs. Night	0.1305^A	0.0953

^{A} Indicates significant differences at $\alpha=0.05$.

*Unplanned critical-Ds have been adjusted for multiple comparisons.

Table 2.8 –Kolmogorov-Smirnov statistic (K-S) calculated to assess significant differences among growth rate potentials of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) during different time periods within the October sampling event. K-S statistics are evaluated against the critical-D for unplanned comparison. K-S values > critical-D indicate a significant difference at the α=0.05 level (Sokal and Rohlf 1995).

Comparing	K-S Statistic	Unplanned critical-D
Dawn vs. Day	0.5291[A]	0.1313
Dawn vs. Dusk	0.6837[A]	0.1735
Dawn vs. Night	0.6618[A]	0.1384
Day vs. Dusk	0.1546[A]	0.1313
Day vs. Night	0.1485[A]	0.0794
Dusk vs. Night	0.1833[A]	0.1384

[A] Indicates significant differences at α=0.05.

*Unplanned critical-Ds have been adjusted for multiple comparisons.

Table 2.9 –Kruskall-Wallis H' statistic calculated to test the differences among the average growth rate potential (GRP; g^{-1} g^{-1} day^{-1}) per minute, from total sampling periods. Growth rate potential data derived from acoustically collected prey density, data and temperature data entered into foraging and bioenergetic models. H' values are compared to standard tabulated χ^2 statistic for the proper sample size (Groups-1), and evaluated at the α=0.05 level of significance.

Time Section	N	Groups	K-W(H_{init})	K-W(D_{corr})	Corr H'=(H/D)	χ^2 (α=0.05)
May	1324	5	22512.958	0.351	64180.005^	9.488
June	1300					
July	1418					
Sept.	657					
Oct.	1148					

^ indicates signficant differences at α=0.05

Table 2.10 –Kolmogorov-Smirnov statistic (K-S) calculated to assess significant differences among growth rate potentials of a 512 g (300 mm) Chinook salmon (*Oncorhynchus tshawytscha*) during 5 different sampling events within the 1997 growing season. K-S statistics are evaluated against the critical-D for unplanned comparison. K-S values > critical-D indicate a significant difference at the α=0.05 level (Sokal and Rohlf 1995).

Comparing	K-S Statistic	Unplanned critical-D
May vs June	0.2581^{A}	0.0504
May vs July	0.8492^{A}	0.0522
May vs Sept.	0.9664^{A}	0.0668
May vs Oct.	0.7741^{A}	0.0515
June vs July	0.9833^{A}	0.0668
June vs Sept.	0.9535^{A}	0.0663
June vs Oct.	0.8060^{A}	0.0565
July vs Sept.	0.6764^{A}	0.0676
July vs Oct.	0.7677^{A}	0.0581
Sept. vs Oct.	0.9557^{A}	0.0714

^{A} Indicates significant differences at α=0.05.

*Unplanned critical-Ds have been adjusted for multiple comparisons.

Discussion

Temperature

The thermal structure of the water column observed during this study conforms well to both long term seasonal patterns and short term fluctuations previously reported by Boyce et al., (1991) and Simons and Schertzer (1987). The thermal structure of the water column in late May was weakly stratified. As the season progressed, stratification intensified and the overall temperature increased developing distinct thermal layers (see Figures 2.6a-2.9a; 2.11a-2.14a; 2.16a-2.19a).

By late summer (September), water temperature was uniformly warm throughout the water column (see Figures 2.21a-2.23a). The isothermal nature of the water column was the result of a severe storm giving rise to high winds providing enough energy to mix the entire water column and breaking down density dependent thermal stratification (Boyce et al., 1991; Simons and Schertzer 1987; Wetzel 1975).

In October, the water column was again essentially isothermal with only minor deviations occurring throughout the 24 hour period (see Figure 2.25a-2.28a). Absence of thermal stratification in October was indicative of the fall overturn process which typically occurs during this period of the growing season (Boyce et al., 1991; Simons and Schertzer 1987; Wetzel 1975; Vallentyne 1967).

The water column temperature data also revealed evidence of high frequency thermal structure fluctuations (generally 24 hours). For example, the water column thermal structure during both June and July showed substantial modifications within time periods shorter than 24 hours (see Figure 2.12a, 2.14a,2.17a, and 2.19a). In June, the warmer, upper thermal layers expanded encompassing more depths during the daylight hours. In July, variations in thermal layer thickness were accompanied with increased surface water temperature during the day, dusk, and night hours. Strong winds associated with storm events can substantially alter thermal structure by initiating internal seiches with hourly periodicities (Wetzel 1975; Vallentyne 1967). Sporadic upwelling or downwelling events originating from a variety of sources can further upset water column thermal structure (Boyce et al., 1991; Simons and Schertzer 1987).

Prey distribution

Alewife distribution and abundance collected during this study are in close agreement to both seasonal and daily fluctuations reported in previous studies (O'Gorman et al 1997; Urban and Brandt 1993; O'Gorman et al., 1997; Bergstedt et al., 1989; Olson et al., 1988; Janssen and Brandt 1980). The biomass density of alewife was relatively low during May, but increased substantially during the June-July period reaching a maximum in July, subsequently decreasing in September and October (Figure 2.6b-2.9b;, 2.11b-2.14b; 2.16b-2.19b; 2.21b-2.23b; 2.25b-2.28b). Seasonal fluctuations in alewife biomass density observed in this study are related to seasonal inshore-offshore migration of alewife.

O'Gorman et al.,(1987), suggested that seasonal nearshore-offshore migration patterns are due to alewife tracking the warmest available water during the early part of the growing season. This thermal tracking behaviour in alewives continues throughout the growing season until the warm waters include their thermal optima (Bergstedt et al., 1989; O'Gorman et al., 1987). Once in their thermal optimum, alewife migration toward the nearshore regions ceases.

The alewife data collected, when sorted into distinct time periods associated with diel light cycles, also revealed diel shifts in abundance and occurrence. Larger more consistent alewife abundances were observed during the night and dawn periods than during the day or dusk (see Figure 2.11b-2.14b; 2.16b-2.19b; 2.21b-2.23b). Daily shifts in alewife abundance are thought to be a function of this species engaging in diel vertical migration. Janssen and Brandt (1980), reported such a diel migration pattern for alewives in Lake Michigan. During the day, alewives tended to aggregate toward the bottom of the water column, while spending the night period in and about the thermocline. Crepuscular periods were spent migrating to and fro. Janssen and Brandt (ibid) contended that diel alewife movements in this case, reflected the diel vertical migration of their principal prey items such as mysis (*Mysis relicta)* and other microcrustacea.

Recent studies performed in Lake Ontario, reported similar shifts in alewife distribution patterns on a daily scale (Urban and Brandt 1993; Bergstedt et al., 1989; Olson et al., 1988). Urban and Brandt (1993), demonstrated an ontogenetic shift in the degree of vertical migration exhibited by alewife in this system. Younger and smaller alewives tended to migrate to more shallow depth than did larger older ones. These authors suggested that the disparity in migration between the differently sized alewives is attributable to each size selectively choosing to follow different prey items.

Appenzeller and Leggett (1995), demonstrated a similar diel vertical migration for rainbow smelt (*Osmerus mordax*) in Lake Memphremagog, Quebec. These authors explained that diel vertical migration in this species is tightly linked to the diel light conditions. Rainbow smelt exhibit anti-predatory behaviour by avoiding the pelagic area during daylight hours when predator visual acuity is maximized by increased light-levels. Clark and Levy (1988), and Levy (1991), proposed similar arguments in efforts to describe the diel shifts in juvenile sockeye salmon, and zooplankton species distributions in British Columbia lakes. Bevelhimer and Adams (1993), further suggest that diel shifts in vertical migration exhibited by many fish species is more than a mere response to shifts in light levels, or to the occurrence of predators. Rather, diel shifts in distribution are a judicious response to combinations of both biotic and abiotic stimuli present in the environment (Bevelhimer and Adams ibid). Thus, vertical daily shifts in fish distribution are not unprecedented, and can be explained by a variety of published theories.

Habitat quality

Taking into consideration the dynamic nature of temperature and alewife density at both seasonal and diel time scales, it is reasonable to anticipate that measurements of habitat quality derived from a bioenergetic combination of the former two parameters will also vary at these temporal scales of observation. Indeed, chinook growth rate potential measured in this study showed significant changes in the ability of the sampled environment to support chinook growth at both time scales.

The relatively low amount of chinook growth rate potential observed in May is probably related to the water column temperature being below chinook thermal optimum (12-16 ^{o}C), and to low occurrences of alewife in the sampling area. Many studies have demonstrated marked decreases in metabolic efficiency, cessation of growth and eventual mortality of several fish species exposed to sub-optimal temperatures (Mac 1985; Coutant 1977; Brett 1971; 1952; Javaid and Anderson 1967).

Substantial increases in growth rate potential in June and July were a function of the proportion of the water column where conditions of chinook thermal optima and prey availability were met. These corresponded well to the patterns of temperature structure and alewife migration reported above. In July, all but the cooler bottom layers had minimal chinook growth rate potential. Even at depths just above the cooler water regions, where prey were abundant, chinook growth was still limited by thermal conditions. Water temperatures in the upper thermal layers, however, were considerably higher than chinook's thermal optima suggesting that although ample prey were present in the water column, only prey densities overlapping with the cooler bottom regions contributed to chinook growth.

Similarly, the virtual absence of chinook growth rate potential in September further emphasized the importance of temperature limitations on chinook habitat quality occurring during warm periods. In September, the entire water column was uniformly warm, and above chinook thermal optimum. During these warm conditions, all prey were essentially inaccessible to chinook because of their proximity to thermally inhospitable environments. This is consistent with results obtained by Mason et al., (1995) who reported negative chinook growth rate potential in waters exceeding 20 °C in Lake Ontario during late summer of 1987. Data presented in this study shows mostly negative chinook growth rate potential occurring during September suggesting that chinook located in the water column during this particular time period would actually lose rather than gain weight (Figure 2.21-2.23).

Moderate chinook growth rate potential was observed in October suggesting a slight resurgence of favourable chinook habitat. This amelioration of chinook habitat quality however, was limited to levels comparable with those observed in May. Better thermal conditions returned in October but were concurrent with decreasing alewife abundances resulting from their autumnal offshore migration. This suggests that although better thermal conditions return during this period, chinook growth becomes limited by the amount of food resources available rather than temperature. Thus, a seasonal pattern in chinook growth rate potential and therefore, habitat quality, is observable in my data, and reflect seasonal patterns observed in both water column thermal structure, and alewife density.

Seasonal variation in growth rate potential has been reported for different species in a variety of systems (Horne et al., 1996; Mason et al., 1995; Brandt and Kirsch 1993; Goyke and Brandt 1993). Goyke and Brandt (1993), demonstrated seasonal fluctuations in chinook growth rate potential measured in Lake Ontario during 1991-1992. In their study, however, Goyke and Brandt (1993), reported maximum chinook growth rate potential occurring during the autumn rather than during the mid-summer as reported here. The discrepancy between these findings may be related to the limited spatial extent of the sampling efforts during this study. Goyke and Brandt (1993), estimated chinook growth rate potential along cross-lake transects outlining with much greater detail the inherent spatial discontinuity of both environmental condition and chinook growth rate potential occurring throughout the lake. Chinook growth rate potential measured at one specific location in the lake may be dramatically different from that measured at another, based on the prevailing structure of both biotic and abiotic conditions at each location

(Horne et al.,1996; Mason et al., 1995; Goyke and Brandt 1993; Mason and Patrick 1993; Luo and Brandt 1993). Studies encompassing larger spatial scales may resolve patterns that go unnoticed by studies of limited spatial extent such as this one. Scale dependent differences in observable patterns are an inherent characteristic of spatially complex systems (Sale 1998; Holling 1992; Levin 1992; Nero et al., 1990; Legendre and Demers 1984).

Still, both this study, and that of Goyke and Brandt (1993), demonstrated a seasonal pattern of fluctuation in the growth rate potential measured for chinook salmon in Lake Ontario. This indicates that chinook growth rate potential estimated at one time during the growing season in Lake Ontario, does not necessarily represent that occurring throughout the remainder of the growing season.

Similarly, estimates of chinook growth rate potential made during short time periods do not necessarily represent that occurring throughout an entire 24 hour period. Significant fluctuations in chinook growth rate potential were observed over different time periods within a single 24 hour period. Chinook growth rate potential occurred more often and more consistently during the night and crepuscular periods than during the day (see Figures 2.11c-2.14c; 2.16c-2.19c). This may be associated with higher densities of alewife occurring within the appropriate temperature layers of the water column during the night and crepuscular hours. The increase in alewife density during these periods is consistent with reports of alewife exhibiting diel vertical migration as described above (see Urban and Brandt 1993; Janssen and Brandt 1980). Because alewives are more dispersed within the water column at night and during crepuscular periods, the probability of these latter intersecting thermal regions conducive to chinook growth increases. Basically, alewife contribution to chinook growth is more plausible during migration and/or mid-water residency. Chinook growth rate potential therefore, is also observed to fluctuate on a diel scale.

Statistical analysis

Statistically, the differences between the temporal distributions of chinook growth rate potential calculated for each sampling event (May, June, July, September, and October), and for each time period within a sampling event (dawn, day, dusk, and night), were evaluated using the Kolmogorov-Smirnoff test. This test is used extensively to compare differences between two cumulative frequency distributions (Perry and Smith 1994; MacNeill and Brandt 1990). Recently, however, Syrjala (1996), and Greenstreet et al., (1997) suggest that the Kolmogorov-Smirnoff statistic is much too sensitive to even a small number of abnormally large differences between two distributions. This often leads to the detection of significant differences between two distributions that, aside from rare deviations, may be identical. This is especially prevalent in studies considering continuous measures of periodically changing variables such as this one, where stochastic variation in distributions are not uncommon (Syrjala 1996). This phenomenon may have operated here when comparing the differences between chinook growth rate potential calculated for different time periods. Syrjala (1996), suggests a modified Cramér-von Mises test as alternative to the Kolmogorov-Smirnoff test for demonstrating significant differences between two distributions. The modified Cramér-von Mises test averages the difference of corresponding values between two distributions from many different rotational perspectives and generally provides a more robust estimate of divergence between distributions (Greenstreet et al., 1997; Syrjala 1996). Perhaps in future applications of this model, the Cramér-von Mises test could replace the Kolmogorov-Smirnoff to yield more accurate results in terms of evaluating the difference between the distribution of growth rate potential estimated at different time periods.

Model Assumptions

The results obtained in this study are based on a variety of simplifying assumptions. Firstly, I chose to model the growth rate potential and thus habitat quality for a particular sized (300mm, 512g) chinook salmon. The habitat quality of the sampling location therefore was described in terms of the metabolic and physiological requirements for this particular sized chinook. The metabolic and physiological requirements of this particular sized chinook, however, are not necessarily the same for those of larger chinook. Thus, the growth rate potential and ultimately habitat quality of a larger chinook occurring within the same sampling environment could be radically different than that described herein.

Similarly, I also modelled chinook growth rate potential, and hence habitat quality, based only on alewife as prey assuming constant energy density. There are two potential problems associated with this procedure. Firstly, alewife consumed early during the growing season transfer the same amount of energy to chinook as those in the latter portion. Stewart and Binkowski (1986), however, demonstrate that energy density varies both ontogenetically and through seasons for alewives in Lake Michigan. It is reasonable to assume that such variations in energy density are likely to also occur in alewife in Lake

Ontario. Using a constant average energy density value does not consider changes in growth rate potential attributable to these energy density variations, and misrepresents events within the environment.

Secondly, using alewife as sole potential prey is principally a limitation associated with acoustic target discrimination (Horne and Clay 1998; Brandt 1996; Argyle 1992; Rose and Leggett 1988; MacLennan and Simmonds 1992). Although alewife consist of the majority prey items in western Lake Ontario, studies demonstrate a substantial portion of the actual prey base being composed of other species such as rainbow smelt (*Osmerus mordax*), emerald shiner (*Notropis atherinoides*), and three-spined sticklebacks (*Gasteroseus aculeatus*) (Hondorp 1998; Rand and Stewart 1998; Lantry and Schaner 1998; Urban and Brandt 1993). Considering only the energy density provided to chinook by alewives may bias actual energy density provided from a larger prey base. Perhaps a more accurate estimate of chinook growth could have been generated if the prey base was divided into proportions that closely estimated actual proportions in the lake. Each species provides unique amounts of energy density which would contribute to overall chinook growth, based on chinook affinity for each particular prey item.

Other potential sources of error are the parameter hungry foraging and bioenergetic models which are used in concert to estimate potential chinook growth. Both these models are derived using, at times, up to 30 different parameters, each with its own degree of associated uncertainty. When these parameters are combined in complex models, their uncertainties are quickly compounded, rendering the uncertainty factor for the entire model very large. This brings into question the predictive power and eventual usefulness of such parameter rich models.

Furthermore, many such bioenergetic parameters are empirically derived averages, and although these averages may serve well to describe the growth rate potential of a typical predator of a certain size, Hartman and Brandt (1993), argue that such empirically derived averaged parameters may often be very far from those calculated from individual fish. Many empirically derived bioenergetic parameters such as consumption, and activity costs are estimated in fish using in vitro and/or telemetry studies and as a consequence may be artifactual because of the increased stress levels, or artificial conditions to which fish are exposed (Adams et al., 1998; Hartman and Brandt 1993; Ney 1993). Other parameters meanwhile, are often 'borrowed' from other species whose relationship to the one under study is sometime nebulous (Ney 1993). These parameters, may therefore not necessarily reflect actual bioenergetic rates exhibited by fish within their natural environment or free from telemetric devices, and as a result, may lead to false conclusions.

Applications

Chinook growth rate potential and thus habitat quality is temporally dynamic over both short and long time scales. Depending on the time scale or 'window' at which it is observed, habitat quality is determined by transient blends of environmental conditions. In this study, temperature and climatic events dictated water column thermal structure, which exerted a predominant influence over chinook growth rate potential on a seasonal scale. Alewife distribution, meanwhile, influenced chinook growth rate potential at both seasonal and diel levels. Thus, chinook growth rate potential reflected temporal differences in the spatial arrangement of alewives and thermal structure of the sampled environment.

Single estimates of habitat quality apply only to the particular time at which they are taken, while, averages may integrate measures taken over many time intervals, but likely oversimplify important events occurring at smaller scales. Averaging conditions will also give a false impressions as to the overall ability of a particular habitat to support the growth of a particular species. For example, in this study, the relatively high habitat quality of chinook in June is predominantly a result of the ability of the environment to support chinook growth during the dawn and night periods whereas, the day and dusk periods supported little growth (Figure 2.11c-2.14c). Averaging the growth incurred in each time period for June would fail to indicate when, during this sampling event, habitat quality was appropriate to support the growth of chinook salmon.

The temporally explicit model of fish growth rate potential developed here, can accurately pinpoint notable events and fluctuations in the ability of the environment to support a particular species growth. As such, this modelling framework can be used to monitor and predict the quality of a particular habitat of interest. Such a model would be useful in evaluating stochastic changes in the forage population of recreationally important systems like Lake Ontario. Independent measurements of environmental conditions are limited without the knowledge of how these relate to each other to create habitat suitability. Excellent physical conditions can arise, and abundant prey can exist, but if both these latter fail to cooccur, the habitat will not support target species growth. This modelling framework provides mechanisms for quantifying the interconnectedness of environmental conditions with respect to fish growth. As such, the applications of this model could be extended to include monitoring the influence of stocking rates on the availability of growth conducive habitat for a stocked predator. Important stocking locations could be monitored to determine more precisely the most suitable stocking times. Supplementing these data with that of actual predator distribution could be used to run sensitivity analysis on the modelling framework itself, or to initiate predator behaviour studies of habitat selection (Goyke and Brandt 1993). Adaptation of the model to important prey species such as alewife could be used in critical spawning or nursery grounds to determine the amount of habitat available for production and recruitment of new year classes. Bioenergetic models can be modified to integrate concentration based pollutant assimilation rates for fish extending the application of this modelling framework to include toxicity influence on certain species in highly polluted areas (Morisson et al., 1997; 1996). This list is by no means exhaustive. In short, the temporally explicit model demonstrates the inherent temporal fluctuations and ephemeral nature of environmental conditions supporting growth of a specific fish, and provides a method to assess these changes on a variety of temporal scales.

References

Adams, N., D. Rondorf, S. Evans, J. Kelly, and W. Perry. 1998. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 55:781-787.

Appenzeller, A., W. Leggett. 1995. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). *Can. J. Fish. Aquat. Sci.* 52:504-511.

Argyle, R. 1992. Acoustic as a tool for the assessment of Great Lakes forage fishes. *Fish. Res.*, 14:179-96.

Bergstedt, R., and R. O'Gorman. 1989. Distributions of alewives in southeastern Lake Ontario in autumn and winter: a clue to winter mortalities. *Trans. Amer. Fish. Soc.* 118:687-92.

Bevelhimer, M., and S. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka. Can J. Fish Aquat. Sci.* 50:2336-49.

Bodwitch, N. 1982. American Practical Navigator. Vol 2. An Epitome of Navigation. Defence Mapping Agency, Hydrographic/Topographic Center, Washington, D.C.

Boyce, F., W. Schertzer, P. Hamblin, and C. Murthy. 1991. Physical behaviour of Lake Ontario with reference to contaminant pathways and climate change. *Can. J. Fish. Aquat. Sci.* 48:1517-28.

Brandt, S. 1996. Acoustic assessment of fish abundance and distribution. Chapter 13 in Fisheries Technologies. 2nd ed. B. Murphy, and D. Willis eds. American Fisheries Society publication. Bethesda. Maryland.

Brandt, S. 1993. Effect of thermal fronts on fish growth: a bioenergetics evaluation of food and temperature. *Estuaries*. 16(1):142-59.

Brandt, S., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Trans. Amer. Fish. Soc.* 122:845-69.

Brandt, S., D. Mason, and E. Patrick. 1992. Spatially-explicit models of fish growth rate. *Fisheries*. 17(2):23-35.

Brandt, S., and six co-authors. 1991 .Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 48:894-908.

Brett, J. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zoologist.* 11:99-113.

Brett, J. 1952. Temperature tolerance in young pacific salmon, genus *Oncorhynchus*. *J. Fish. Res. Bd. Can.* 9(6):265-309.

Carpenter, S., and P. Leavitt. 1991. Temporal variation in a paleolimnological record arising from a trophic cascade. *Ecology*. 72(1):277-85.

Clark, C., and D. Levy. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. *Am. Nat.* 131(2):271-90.

Coutant, C.1977. Compilation of temperature preference data. *J. Fish. Res. Bd. Can.* 34:739-45.

Elrod, J., and R. O'Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979-1987. *Trans. Amer. Fish. Soc.* 120:290-302.

Frank, K., and W. Leggett. 1983. Survival value of an opportunistic life-stage transition in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 40:1442-48.

Frank, K., and W. Leggett. 1982a. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*), and its application to the match/mismatch hypothesis. *Can. J. Fish. Aquat. Sci.* 39:691-99.

Frank, K., and W. Leggett. 1982b. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 39:991-1003.

Frank, K., and W. Leggett.1981. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 38:215-23.

Goyke, A., and S. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. Trans. Amer. Fish. Soc. 122:870-83.

Greenstreet, S., I. Tuck, G. Grewar, E. Armstrong, D. Reid, and P. Wright. 1997. An assessment of the acoustic survey technique. RoxAnn, as a means of mapping seabed habitat. ICES Journal of Marine Science. 54:939-59.

Hartman, K., and S. Brandt. 1993. Systematic sources of bias in a bioenergetics model: examples of age-0 striped bass. Trans Amer. Fish. Soc. 122:912-26.

Hewett, S., and B. Johnson. 1992. A generalized bioenergetics model of fish growth for microcomputers, version 2.0. University of Wisconsin Sea Grant Institute. Madison, WI.

Holling, C. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. 62(4):447-502.

Hondorp, D. 1998. Spatial distributions of planktivorous fish and zooplankton in western Lake Ontario: Implications for fish thermal ecology, fish bioenergetics modelling and trophic interactions. M. Sc. Thesis. State University of New York College at Buffalo. Buffalo, NY.

Hondorp, D., and S. Brandt. 1996. Spatially-explicit models of fish growth rate: tools for assessing habitat quality. *Great Lakes Res. Rev.* 2(2):11-19.

Horne, J., and C. Clay. 1998. Sonar systems and aquatic organisms: matching equipment and model parameters. *Can. J. Fish. Aquat. Sci.* 55:1296-1306.

Horne, J., J. Jech, and S. Brandt. 1996. Spatial modelling of aquatic habitat from a fish's perspective. http://www.ncgia.ucsb.edu/conf/SANTA_FE_CD-ROM/sf_papers/horne_john/hornpap.html.

Janssen, J., and S. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 37:177-84.

Jassby, A., T. Powell, and C. Goldman. 1990. Interannual fluctuations in primary production: direct physical effects and the trophic cascade at Castle Lake, California. *Limnol. Oceanogr.* 35(5):1021-38.

Javaid, M., and J. Anderson. 1967. Influence of starvation on selected temperature of some salmonids. *J. Fish. Res. Bd. Can.* 24(7):1515-19.

Jech, J., and J. Luo. 1998. Digital Echo Visualization and Information System (DEVIS) for processing spatially-explicit fisheries acoustic data. Submitted manuscript, *Fisheries Oceanography.*

Jones, M., J. Koonce, and R. O'Gorman. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. *Trans. Amer. Fish. Soc.* 122:1002-18.

Kitchell, J., D. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Bd. Can.* 34:1922-35.

Lantry, B., and T. Schaner. 1998. The status of the pelagic preyfish in Lake Ontario, 1997. *In* Lake Ontario Fisheries Unit 1998 Annual Report Section 6. NewYork State Department of Environmental Conservation.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. *Rapp. P. -v. Réun. Cons. int. Explor. Mer.* 173:212-30.

Legendre, L., and S. Demers. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.* 41:2-19.

Levin, S. 1992. The problem of patterns and scale in ecology. *Ecology.* 73(6):1943-67.

Levy, D. 1991. Acoustic analysis of diel vertical migration behavior of *Mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. *Can. J. Fish. Aquat. Sci.* 48:67-72.

Luo, J., and S. Brandt. 1993. Bay anchovy *Anchoa mitchilli* production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. *Mar. Ecol. Progr. Ser.* 98:223-36.

Mac, M. 1985. Effects of ration size on preferred temperature of lake charr *Salvelinus namaycush. Environmental Biology of Fishes.* 14(2-3):227-31.

MacLennan, D., and E. Simmonds. 1992. Fisheries acoustics. Chapman and Hall, London.

MacNeill, D., and S. Brandt. 1990. Ontogenetic shifts in gill-raker morphology and predicted prey capture efficiency of the alewife *Alosa pseudoharengus. Copeia.* 1990(1):164-71.

Mason, D., and S. Brandt. 1996. Effects of spatial scale and foraging efficiency on the predictions made by spatially-explicit models of fish growth rate potential. *Environmental Biology of Fishes.* 45:283-98.

Mason, D., A. Goyke, and S. Brandt. 1995. A spatially explicit bioenergetics measure of habitat quality for adult salmonines: Comparison between Lakes Michigan and Ontario. *Can. J. Fish. Aquat. Sci.* 52:1572-83.

Mason, D., and E. Patrick. 1993. A model for the space-time dependence of feeding for pelagic fish populations. *Trans. Amer. Fish. Soc.* 122:884-901.

May, R. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature.* 269:471-77.

Mc Eadie, J., and A. Keast. 1984. Resource heterogeneity and fish species diversity in lakes. *Can. J. Zool.* 62:1689-95.

Mixter, G. 1966. Primers of Navigation. 6th edition. Van Nostrand, Reinhold.

Morisson, H., F. Gobas, R. Lazar, M. Whittle, and D. Haffner. 1997. Development and verification of a benthic/pelagic food web bioaccumulation model for PCB congeners in western Lake Erie. *Environ. Sci. Technol.* 31:3267-73.

Morisson, H., F. Gobas, R. Lazar, and D. Haffner. 1996. Development and verification of a bioaccumulation model for organic contaminants in benthic invertebrates. *Environ. Sci. Technol.* 30:3377-84.

Nero, R., J. Magnuson, S. Brandt, T. Stanton, and J. Jech. 1990 . Finescale biological patchiness of 70 kHz acoustic scattering at the edge of the Gulf Stream—EchoFront 85. *Deep-Sea Research.* 37(6):999-1016.

Ney, J. 1993. Bioenergetics modelling today: growing pains on the cutting edge. *Trans. Amer. Fish. Soc.* 122:736-48.

O'Gorman, R., O. Johannsson, and C. Schneider. 1997. Age and growth of alewives in the changing pelagia of lake Ontario, 1978-1992. *Trans. Am. Fish. Soc.* 126:112-26.

O'Gorman, R., R. Bergstedt, and T. Eckert. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978-84. *Can. J. Fish. Aquat. Sci.* 44(Suppl.2):390-403.

O'Gorman, R., and C. Schneider. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. *Trans. Amer. Fish. Soc.* 115:1-14.

Olson, R., J. Winter, D. Nettles, and J. Haynes. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. *Trans. Am. Fish. Soc.* 117:552-59

Pearson, S., M. Turner, L. Wallace, and W. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecological Applications.* 5(3):744-55.

Perry, R., and S. Smith. 1994. Identifying habitat associations of marine fishes using survey data: an application to the northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 51:589-602.

Rand, P., and D. Stewart. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 55:318-27.

Rand, P., B. Lantry, R. O'Gorman, R. Owens, and D. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978-1990: Implications of salmonine energetics. *Trans. Am. Fish. Soc.* 123:519-34.

Rose, G., and W. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. *Ecology*. 71(1):33-43.

Rose, G., and W. Leggett. 1988. Hydroacoustic signal classification of fish schools by species. *Can. J. Fish. Aquat. Sci.* 45:597-604.

Rudstam, L., and eleven other authors. 1996. A review of the current status of Lake Ontario's pelagic fish community. Report of 1996 Lake Ontario technical panel. *Great Lakes Res. Rev.* 2(2):4-10.

Sale, P. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Australian Journal of Ecology*. 23:202-08.

Schneider, C., and T. Schaner. 1994. The status of pelagic prey stocks in Lake Ontario in 1993. *In* Lake Ontario Fisheries Unit 1994 Annual Report. New York State Department of Environmental Conservation.

Simons, T., and W. Schertzer. 1987. Stratification, currents, upwelling in Lake Ontario, summer 1982. *Can. J. Fish. Aquat. Sci.* 44:2047-58.

Sokal, R., and F. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Company, New York, NY.

Steele, J. 1985. A comparison of terrestrial and marine ecological systems. *Nature*. 313:355-58.

Stewart, D., and M. Iberra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. *Can J. Fish. Aquat. Sci.* 48:909-22.

Stewart, D., and F. Binkowski. 1986. Dynamics of consumption and food conservation by Lake Michigan alewives: An energetics-modelling synthesis. *Trans. Amer. Fish. Soc.* 115:643-59.

Stewart, D., D. Weininger, D. Rottiers, T. Edsall. 1983. An energetics model for lake trout, (*Salvelinus namaycush*): Application to the Lake Michigan population. *Can. J. Fish. Aquat. Sci.* 40:681-98.

Stewart, D., J. Kitchell, and L. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Amer. Fish. Soc.* 110:751-63.

Stewart, T., M. Rawson, and J. Bowlby. 1998. Managing the chinook fishery. *Great Lakes Res. Rev.* 3(2):32-34.

Stewart, T., and T. Schaner. 1998. Alewife and their role in structuring the Lake Ontario fish community. *Great Lakes Res. Rev.* 3(2):28-31.

Stommel, H. 1963. Varieties of oceanographic experience. *Science*. 139:572-76.

Syrjala, S. 1996. A statistical test for a difference between the spatial distributions of two populations. *Ecology*. 77(1):75-80.

Turner, M. 1998. Landscape ecology: Living in a mosaic. In Ecology. S. Dodson, T. Allen, S. Carpenter, A. Ives, R. Jeanne, J. Kitchell, N. Langston, and M. Turner. Oxford University Press. Oxford, England.

Tyler, J. 1998. A users guide for growth rate potential map maker version 2.0. Cooperative Institute for Limnology and Ecosystem Research. University of Michigan. Ann Arbor, MI.

Urban, T., and S. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. *Environmental Biology of Fishes*. 36:359-72.

Vallentyne, J. 1967. Principles of modern limnology. *American Scientist*. XX:218-44.

Wetzel, R. 1975. Limnology. W. B. Saunders Company, Toronto.

Zar, J. 1984. Biostatistical Analysis 2nd edition. Prentice Hall, Engelwood Cliffs, NJ.

CHAPTER III: The relative importance of environmental conditions regulating chinook (*Oncorhynchus tshawytscha*) habitat preference over time, in western Lake Ontario.

Introduction

Fish distributions within aquatic ecosystems are governed by a myriad of environmental conditions such as: temperature, prey availability, refuge areas, dissolved oxygen levels, and others (Hondorp 1998; Gadomski and Barfoot 1998; Levin et al., 1997; Eklöv and Presson 1996; Gregory and Levings 1996; Burke 1995; Levin 1994; Mason and Patrick 1993; Levy 1991; 1990; Clark and Levy 1988; Crowder and Magnuson 1983; Janssen and Brandt 1980; Brett 1971;1952; Wells 1968). Previous studies attempting to describe fish distribution within aquatic environments typically focus on the influence of one particular condition on the variability in fish distributions and abundances. These types of studies have demonstrated important relationships between key environmental conditions and species-specific distributions within aquatic ecosystems. For example, Brett (1971; 1952) demonstrated the importance of temperature in mitigating physiological and metabolic rates of several salmonid species, and showed that these fish will often distribute themselves in thermal regions which optimize physiological and metabolic efficiency. Janssen and Brandt (1980), as well as many others, demonstrated that distributional patterns of several fish species frequently correspond closely to aggregations of their preferred prey.

More recent studies of fish distribution attempt to consider more judicious combinations of environmental conditions influencing species distribution such as temperature and prey, or predation pressure and refuge availability (Levin et al., 1997;

Eklöv and Presson 1996; Levin 1994; Goyke and Brandt 1993; Levy 1991; Crowder and Magnuson 1983). Although these latter add more realism to the description of fish distributional patterns, little has been done to quantify the degree of influence of environmental conditions acting synergistically to dictate fish distribution.

A major impediment to determining the relative importance of environmental conditions is the sheer number of factors that can potentially influence species distribution. Species distribution within their environments represents a compilation of individual responses to all environmental stimuli present, and attempting to account for the influence of all stimuli is beyond the scope of present ecological understanding (Hondorp 1998; Mäki-Petäys et al., 1997; Krebs and Kacelnik 1993). As such, the best one can hope to achieve is the determination of the relative importance of environmental conditions being monitored.

Although more recent studies address the combined influence of several environmental stimuli, more often than not, studies of species distributional patterns fail to demonstrate the intrinsic temporal dynamics of environmental conditions dictating these patterns through time. Environmental conditions are inherently transient, and trying to correlate species distribution to any set of environmental conditions without taking into consideration this transient nature, leads to little more than 'snap-shot' interpretations of species distributional behaviour (Hastings 1998; Mäki-Petäys et al., 1997; Post et al., 1995; Krebs and Kacelnik 1993; Mason and Patrick 1993; Holling 1992; see also chapter II).

To complicate matters, the particular needs of a species within these dynamic environments are also inherently transient, and many organisms volitionally modify their distributions based on the ability of these environments to meet these specific needs (Svensson 1999; Nisikawa and Nakano 1998; Gregory and Levings 1996; Haila et al., 1996; Wallis de Vries Schippers 1994). This has been termed state-dependent habitat selection or preference (Jones et al., 1999; Krebs and Kacelnik 1993).

Combreau and Smith (1997), described such state dependent habitat preferences for houbara bustards (*Chlamydotis undalata* Jacquin) in the Mahazat as-Sayd reserve, Saudi Arabia. During the day, this bird species typically clusters in vegetation covered areas of the reserve decreasing its susceptibility to areal predation, and finding shelter from the hot, dry conditions. At night, cooler conditions allow the houbara to move to the edge of covered areas to forage and replenish much needed moisture. On very dark nights, on the other hand, houbara roost in wide open expanses to minimize encounters with terrestrial predators. This demonstrates that the houbara change their distribution over time within the reserve, based on their predominant habitat requirements at the time (temperature, food, and predator avoidance), and on the ability of the environment to fulfill these requirements.

Shifts in species distributional patterns can be attributed to two fundamental types of influences. The first type involves the environmental conditions to which species are exposed, and the second type is species-specific habitat requirements within these environments. Variability in species distributional patterns exists because both environmental conditions and species-specific habitat requirements change through time. Conceptually, species distributional patterns can be related to environmental conditions by the strength or magnitude of certain habitat requirements.

Shifts in distributional patterns can occur on a variety of temporal scales. The houbara bustard example above demonstrates changes occurring on a daily time scale while other shifts can occur over much larger temporal scales. Gregory and Levings (1996), suggest that juvenile chinook salmon *(Oncorhynchus tshawytscha)* change their habitat selection based on ontogenetic shifts in habitat requirements. As chinook increase in size, they become bolder and spend more time foraging within a habitat rather than seeking refuge. Gregory and Levings (1996), contend that, as these fish become larger, their perceived threat to predation decreases allowing them to focus more on foraging and less on predator avoidance. As such, their distribution changes from areas of moderate food levels and high refugia to areas of greater food abundance and less refugia. In this case, the relative importance of predation pressure and food availability, as influential factors of juvenile chinook distribution changes over time.

Moreover, the relative importance of environmental conditions influencing species distribution can also vary depending on the time scale of observation (Svensson 1999; Combreau and Smith 1997; Turner 1997; Haila et al., 1996; Wallis de Vries and Schippers 1994). Mäki-Petäys et al., (1997), for example, demonstrated that water flow velocity best described the distribution and habitat preference of brown trout (*Salmo trutta*) in the River Kuusinkijoki, in northern Finland both on an annual and seasonal scale. However, the distribution of trout in this system was also well described by in stream vegetation cover, but only during the autumn season. The importance of in stream vegetation to trout distribution throughout the year seemed marginal, while its impact at a smaller seasonal scale was more pronounced (Mäki-Petäys et al., 1997). The influence of specific environmental conditions, and the scale of observation are, therefore, intimately related (Sale 1998; Levin 1992; Holling 1992; Legendre and Demers 1984; Harris 1980). Yet, many ecological studies fail to recognize this relationship while attempting to characterize observable distributional patterns.

In this chapter, I use a sophisticated, high resolution, hydroacoustic sampling technique to quantify fish distributions at a single sampling station in western Lake Ontario at two time scales. Environmental parameters, namely; Temperature, prey density and chinook growth rate potential (see chapter II) are monitored along with chinook salmon distribution during different periods within a day (fine scale), and during different sampling events within a growing season (coarse scale) to determine the relative importance of different environmental conditions to chinook habitat preference. The collection of these data allowed for the evaluation of three working hypotheses. Firstly, if chinook were behaviourally thermoregulating during a particular time period, then a high degree of association would be expected between their actual distribution, and regions of the water column containing their thermal preferenda. Secondly, if chinook were exhibiting prey-taxis, or attempting to maximize food intake, there ought to be a higher association with regions of the water column encompassing high prey densities. Finally, if chinook were attempting to maximize growth, it would be anticipated that their distribution be more highly associated with regions of the water column supporting the most intense growth rates. All three above mentioned hypotheses make the implicit assumption that chinook distribution within the water column is indicative, and a measure, of habitat preference.

I contend that the relative importance of temperature, prey distribution, and available growth to chinook distribution in western Lake Ontario will not only vary over time, but also at different temporal scales of observation.

Methods

Acoustic Sampling

A detailed description of data collection procedures for this portion of my study have been previously described in chapter II (see chapter II; methods). Acoustic data was collected continuously at one location in south-western Lake Ontario over 5 separate sampling events during the 1997 growing season (Figure 3.1). Sampling events occurred on May 27-28, June 19-20, July 30-31, September 5-6, and October 18-19, 1997. Each sampling event was anticipated to last 24 hours, but the September and October sampling events were abridged due to inclement weather conditions, and data contamination by artificial light.

Fish acoustic data were collected using a downward facing, 120 kHz, scientific echo-sounder equipped with a split-beam transducer (Simrad® EY500). The transducer was mounted to a stable platform designed to keep the device in a near-perfect vertical position, and de-couple the transducer form the surface action of the water. The generated acoustic signal was characterized by a pulse length of 0.3 ms, and pulse repetition rate of 2 pulses s^{-1}. The acoustic signal was corrected for spreading and absorption in water, and recorded to magneto-optical disk. Before the start of each sampling event, the acoustic system parameters and performance were evaluated with software provided by the manufacturer. A standard, tungsten carbide, reference sphere of known target strength (-40.4 dB) was suspended under the transducer at various depth to calibrate the acoustic system. The difference between recorded and actual target strength of the standard was used as a correction factor for the collected acoustic data.

In the laboratory, acoustic data were transferred to permanent CD-ROM medium, and echo-integrated using digital echo integration and visualization software (DEVIS; Jech and Luo 1998). Echo-integration converts echoes received from individual targets within the acoustic beam to measures of relative fish abundances within an insonofied volume of water. The speed of sound in water (approximately 1500 m s^{-1}) allows for targets within the acoustic beam to be insonofied many times, generating a distribution of echoes, or target strengths, for each target. Dividing the relative fish abundance in an insonofied volume by the mean target strength yields a measure of absolute fish density in the insonofied volume of water (Jech and Luo 1998; Brandt 1996). Absolute fish density data were then resolved into 2-dimensional representations of the water column using time and depth as indices. These procedures separated the acoustic data into cells of 1 min by 1 m (see results).

Individual acoustic targets were converted to measures of fish length (L) using a target strength—fish length relationship derived by Schneider and Schaner (1994) for Lake Ontario species (Figure 3.2). Individual fish targets were then separated by size into predator and prey items.

As described in the previous chapter, all prey items in this study were considered alewives as these are the predominant planktivores in the Lake Ontario system (O'Gorman et al., 1997; 1987). Trawls conducted routinely over the last 8 years, along the south shore of Lake Ontario by the New York Department of Environmental Conservation (NYDEC) revealed a maximum alewife size above 180 mm only in 1990. Since 1990, alewife maximum size has been consistently below the 180 mm mark (Figure

3.3). Therefore, I conservatively used 180 mm as a threshold below which all targets were considered alewife.

In addition, chinook salmon was selected to represent salmonids in this study because it accounts for upwards of 40 % of the salmonid predators stocked into the Lake Ontario system annually (O'Gorman et al., 1997; Goyke and Brandt 1993). Chinook are considered the most voracious, and impose the strongest predation pressure on alewives of all top-predator species in this system (Stewart et al., 1998; Mason and Brandt 1996; Goyke and Brandt 1993; Brandt et al., 1991; Stewart et al., 1981).

Segregating fish into size classes using fish lengths converted from acoustic target strengths is sometimes tenuous, especially when considering the degree of variability in target strength for any given fish target. Target strength of an individual fish is dependent on its behaviour, orientation, as well as the morphology and aspect of its swimbladder within the acoustic beam (Horne and Clay 1998; Brandt 1996; Clay and Horne 1994; MacLennan and Simmonds 1992). Fish occurring at a peculiar aspect or orientation can sometimes reflect less sound than a same sized fish occurring at a more normal aspect within the acoustic beam. Similarly, small fish perpendicular to the propagated acoustic wave can reflect more sound than a larger fish occurring at an odd angle (Horne and Clay 1998; Brandt 1996; Horne and Clay 1994; MacLennan and Simmonds 1992). This variation in the reflected sound from a particular target can lead to misinterpretation of actual fish length. To minimize the inclusion of large alewife as small chinook, and/or small chinook as large alewives, only acoustic targets generating fish lengths ≥ 300 mm were considered chinook salmon. Acoustic targets yielding fish length > 180 mm, but <

300 mm were excluded from further analysis (Figure 3.4). Both alewife and chinook densities were resolved into 2-dimensional matrices of the environment indexed by time and depths.

Time Period Formation

Both prey and predator fish densities collected during a particular sampling event (24 hour period) were further partitioned into four distinct time period associated with diel light intensity cycle during a typical 24 hour period, namely; dawn, day, dusk, and night. The formation of these time periods was achieved as per chapter II . Briefly, exact sunrise and sunset time were obtained from the National Weather Service (NWS) working in cooperation with the United States Astrological & Naval Time Department. Sunrise-Sunset time were obtained for respective sampling dates taken for the topographical latitude and longitude corresponding to Buffalo New York, USA, set on eastern standard time. One hour was added to the listed times to account for daylight savings. Because sunrise and sunset are not instantaneous, 1.5 hours was added to sunset to form the dusk period, while the same was subtracted from the sunrise time to create the dawn period. This was based on the assumption that sunrise and sunset times provided by the NWS correspond to the exact time the sun broke the horizon (Bodwitch 1982; Mixter 1966). All daylight hours not included in dawn or dusk constituted the day, while all dark hours between dusk and dawn formed the night period.

Temperature sampling

The protocol for temperature sampling has been previously described in chapter II. During each sampling event, water temperature profiles were collected by dropping a

Seabird, SBE 19-03, conductivity, temperature, and depth (CTD) profiler to near-bottom depths and setting it to record depth and temperature every half second as it made its ascent to the surface. Temperature profiles were generated by dividing the water column into 1m depth cells each of which was characterized by the median of water temperatures collected within that cell. For each sampling event, a water temperature profile was collected immediately upon arrival on station and repeated every hour thereafter. The use of one hour intervals is justified as it has been demonstrated that fluctuations in the thermal regime of the water column at smaller temporal scales is negligible (Boyce et al.,1991). Water column temperature within each depth cell was resolved per minute by using linear interpolation between each hourly CTD cast. This allowed the temperature data to be manipulated into a 2 dimensional matrix indexed by time in minutes and depth in metres, similar to that of the acoustic data. To evaluate the thermoregulation hypothesis, temperature data were then ranked according to their proximity to empirically derived physiological optimum for chinook salmon (12-16 °C; Goyke and Brandt 1993; Stewart and Iberra 1991). Once in a 2 dimensional representation of the water column, the optimal temperature data were split into their respective time periods as per the acoustic data (see time formation above).

Chinook Growth Rate Potential

For each time period within a sampling event (daily scale), and for each sampling event within the sampling season (seasonal scale), temperature and alewife density data were used as input variables in the temporally explicit model of fish growth rates. The temporally explicit model, developed in chapter II, incorporates both water temperature, and alewife density into a combination of foraging and bioenergetic models to generate 2 dimensional representations of the water column outlining potential fish production and growth (for model description see chapter II). In essence, the temporally explicit model divides the time series data into a matrix of cells each indexed by time and depth. Each cell is considered homogenous, characterized by a particular temperature and prey density. Temperature and prey density are used as input parameters, first in the foraging sub-model which delimits the amount of prey available to a particular sized predator. Results of the foraging sub-model, and temperature values for each cell are then entered into a bioenergetic sub-model which describes the potential consumption, respiration, egestion, excretion, and ultimately growth of a particular sized, species-specific, predator within each cell, according to the following formula:

$$G=C-(R+F+U) \tag{1}$$

Where, G = growth
C = consumption
R = respiration, and metabolism
F = egestion
U = excretion

Components in the above formula (C,R,F,and U) are described in more detail in the previous chapter (see chapter II; methods—model development). Although each cell is considered homogenous, it is distinct from all other cells in the matrix, creating a mosaic representation of predator growth rate potential of the sampled environment, through time (Figure 3.5). I used this modelling framework to describe the growth rate potential of a 512 g, 300 mm, chinook salmon at my sampling location throughout all time periods within a single sampling event, and throughout all sampling events within the growing season.

Statistical Analysis

To quantify the relative importance of the three environmental conditions monitored to chinook distribution, I performed three standard Pearson correlation analyses comparing the actual chinook distribution matrix to the matrix of each individual environmental condition, specifically; optimal chinook temperature, alewife density, and chinook growth rate potential. Assessing the standard significance (p-value) of such Pearson correlations becomes problematic as the nature of the data collection and manipulation procedures violate two of the associated p-value assumptions. In order to evaluate the standard associated p-value of a Pearson correlation, samples must be independent from one another, and follow a Gaussian distribution (Sokal and Rolf 1995; Zar 1984). The time-relatedness of the data collected during this study violates the independence assumption, and not all of the environmental data adhere to Gaussian patterns. Thus, the violation of the above assumptions prevents the parametric evaluation of the Pearson correlation analysis between two matrices.

To circumvent the obstacles preventing the evaluation of significance for the Pearson correlation analysis of paired matrices, I performed 10 000 Mantel randomization iterations of the Pearson correlation test (Jackson and Somers 1989). The Mantel randomization technique is similar to the 'boot-strapping' and/or 'Monte Carlo' techniques, and allows the evaluation of the correlation without adherence to parametric assumptions (Jackson and Somers 1989; Jackson pers. comm; University of Toronto).

During each time period within a sampling event (dawn, day, dusk, and night), and during each sampling event within the growing season (May, June, July, September, and October), initial Pearson correlation analysis were run between the matrix of actual chinook distribution, and the matrix of each individual environmental condition to establish initial correlation coefficients (r_{ini}). Once the initial correlation coefficients were calculated, the actual chinook distribution matrix was held constant while each environmental condition matrix was randomized. After randomization, new correlation coefficients were calculated and recorded for each individual comparison. The randomization step was permutated 10 000 times, and generated a normal distribution of correlation coefficients for each comparison, namely; actual chinook distribution and empirically derived optimal temperatures, actual chinook distribution and prey density, and actual chinook distribution and chinook growth rate potential. The significance of each initial correlation coefficient (r_{ini}) obtained for each comparison was assessed using the following formula:

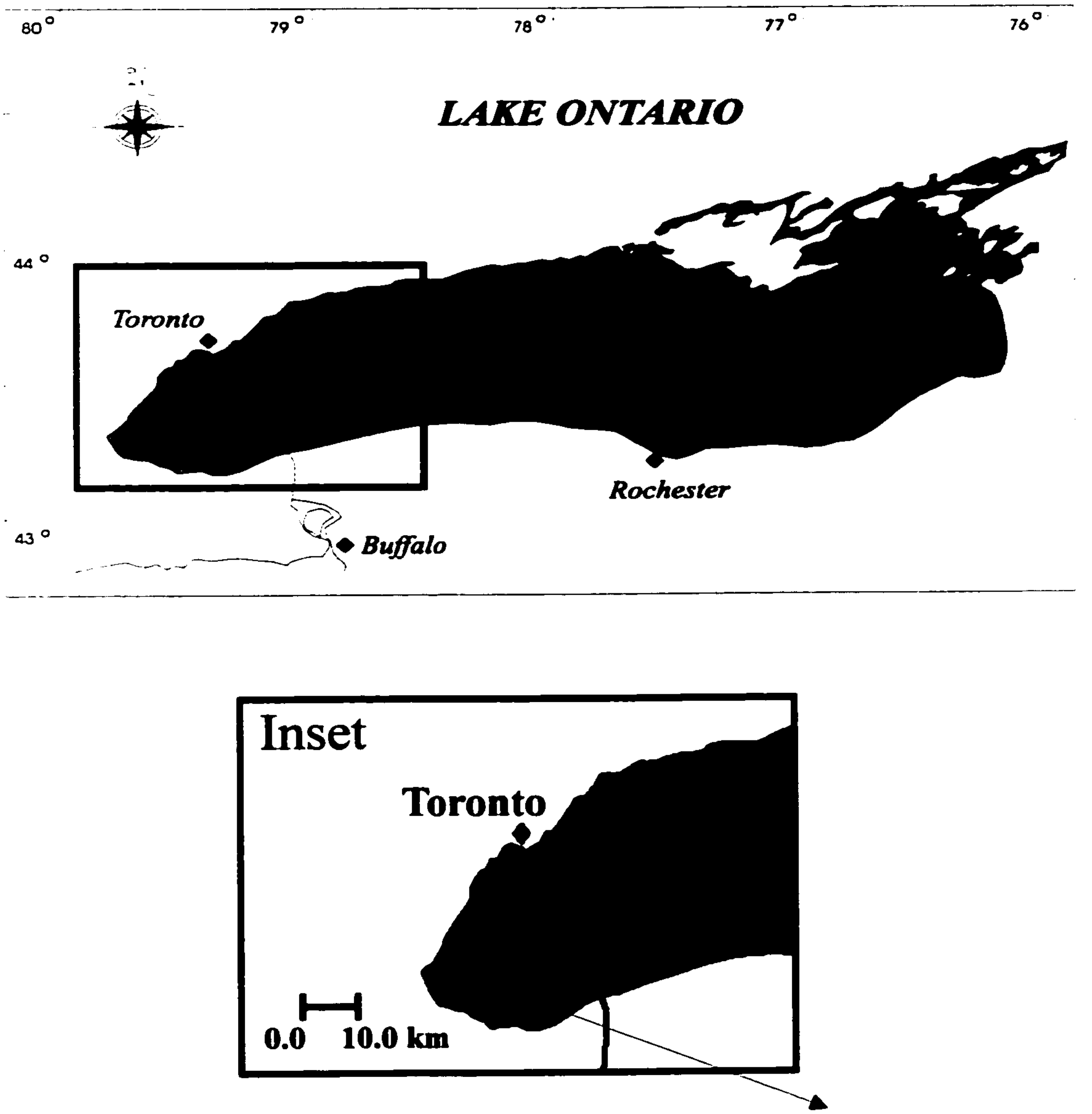
$$p = \frac{1 + (r_n)}{r_t} \qquad (2)$$

Where, p = significance of initial correlation coefficient (p-value).
r_n = the number of randomized correlation coefficient ≥ the initial correlation coefficient.
r_t = total number of randomization permutations.

The number of randomization permutations was determined *apriori* based on the desire to minimize type I errors, and because of computing limitations. The formula described above was used to determine how likely the initial correlation coefficient (r_{ini}), or the association between selected matrices, is likely to occur by chance alone (Jackson and Somers 1989).

Relative importance of monitored environmental condition to actual chinook distribution during a particular time interval, was assessed by ranking the resulting significant initial correlation coefficients (r_{ini}) by size. The environmental condition with the highest degree of association was assigned the top rank and was deemed the most important descriptor of actual chinook distribution, and habitat preference during that particular time interval. Other environmental conditions with smaller degrees of association were considered less important and ranked as such. All statistical analysis were accomplished using software specifically designed for manipulating large data sets, and for performing the aforementioned tests. The software was written in Interactive Data Language (IDL®; Research Systems Inc.) and evaluated all statistics at the $\alpha=0.05$ level of confidence.

Figure 3.1 — Stationary sampling location in western Lake Ontario.



Stationary sampling position
43°13.28'N 079°18.00'W

Figure 3.2 — Acoustic target strength-fish length relationship derived for Lake Ontario fish species allowing echo-integrated target backscatter to be converted to fish length (adapted from Schneider and Schaner 1994).

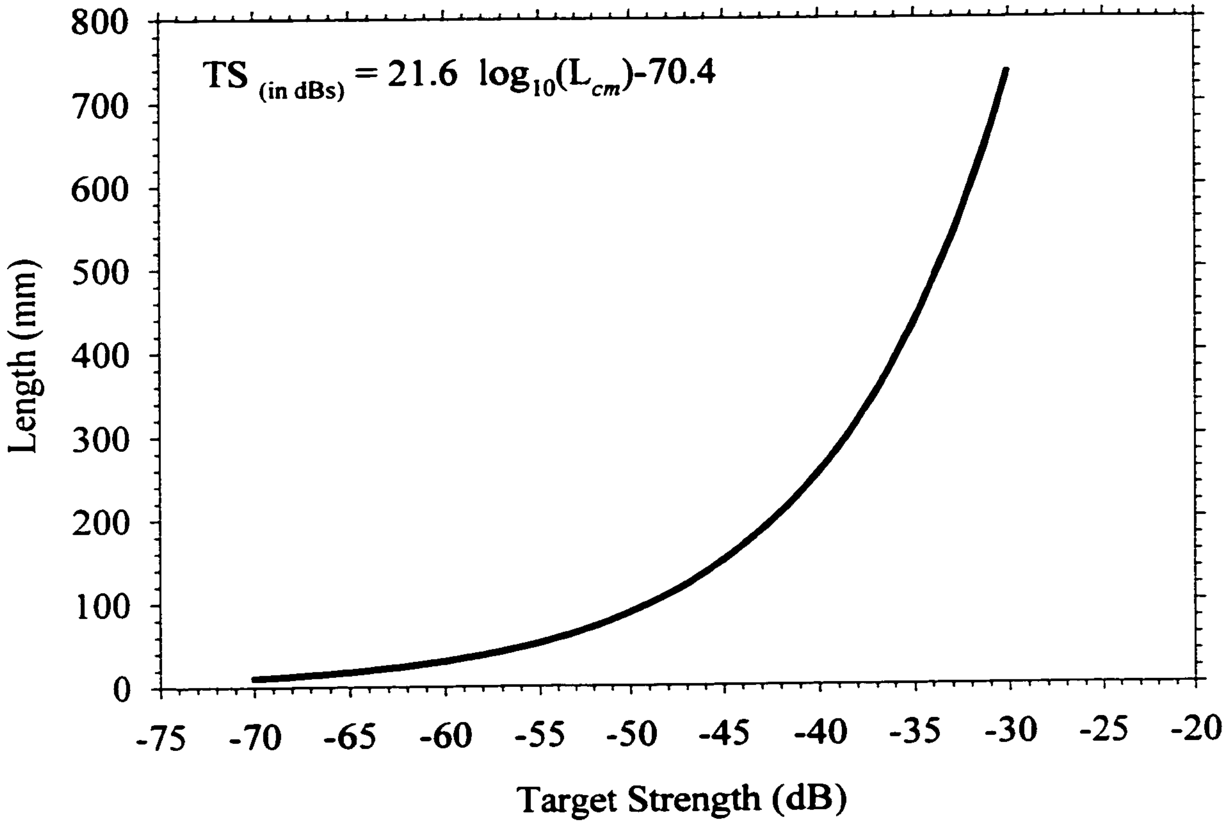

$TS_{(\text{in dBs})} = 21.6 \log_{10}(L_{cm}) - 70.4$
Length (mm)
800
700
600
500
400
300
200
100
0
-75
-70
-65
-60
-55
-50
-45
-40
-35
-30
-25
-20
Target Strength (dB)

Figure 3.3 — Maximum alewife (*Alosa pseudoharengus*) length (mm) in Lake Ontario from 1990-1997 sampling years. Dashed line indicates the maximum length set for this study. Data adapted from New York State Department of Environmental Conservation, and the Ontario Ministry of Natural Resources, Lake Ontario Management Unit historical data.

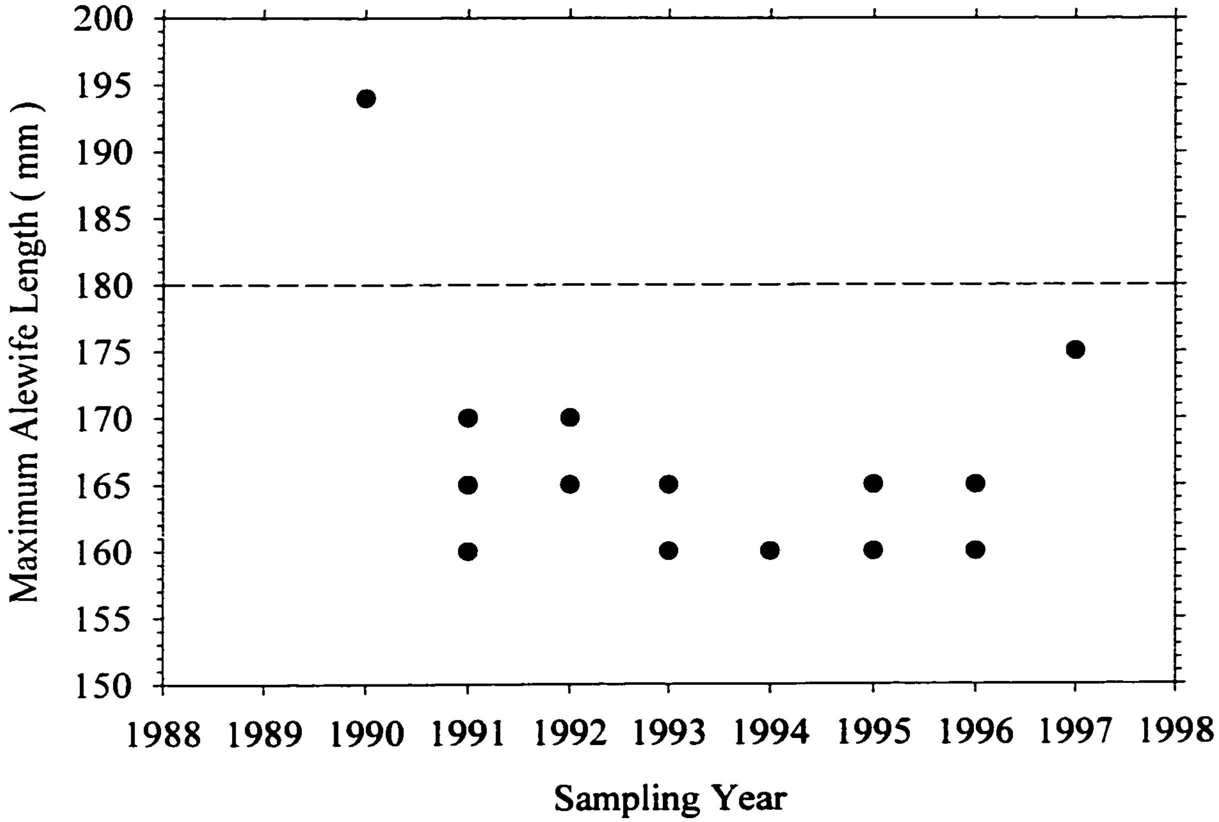

Maximum Alewife Length (mm)
200
195
190
185
180
175
170
165
160
155
150
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
Sampling Year

Figure 3.4 — Frequency distribution of fish length (in mm) converted from acoustic targets collected during all 5 stationary sampling events conducted throughout the 1997 growing season in western Lake Ontario. Shaded area represents the ambiguous acoustic data removed from further analysis, minimizing the consideration of large prey items as small predators, and small predators as large prey. Fish lengths to the left of the shaded area (≤180mm) are considered prey (alewife), while those to the right (≥300 mm) are considered predators (chinook).

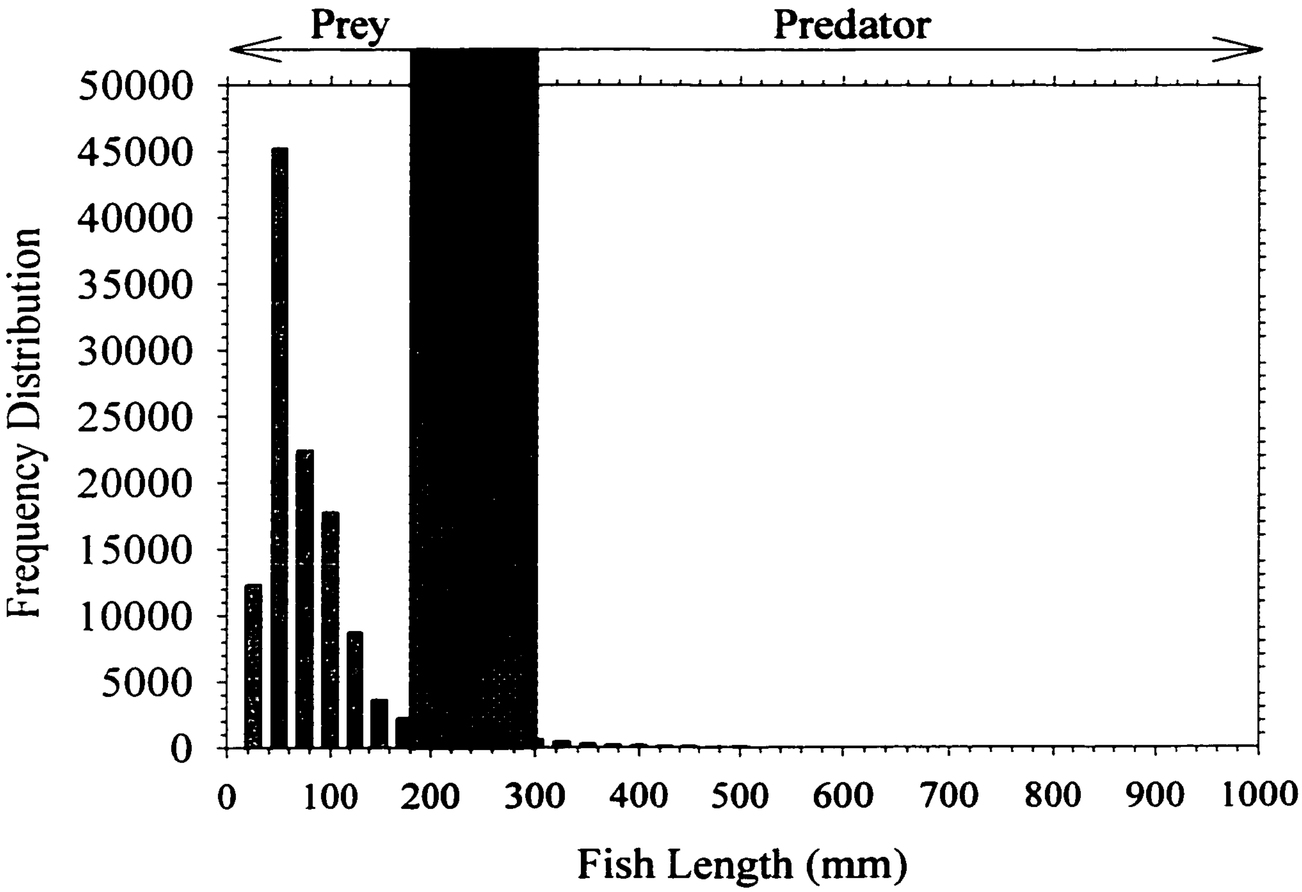
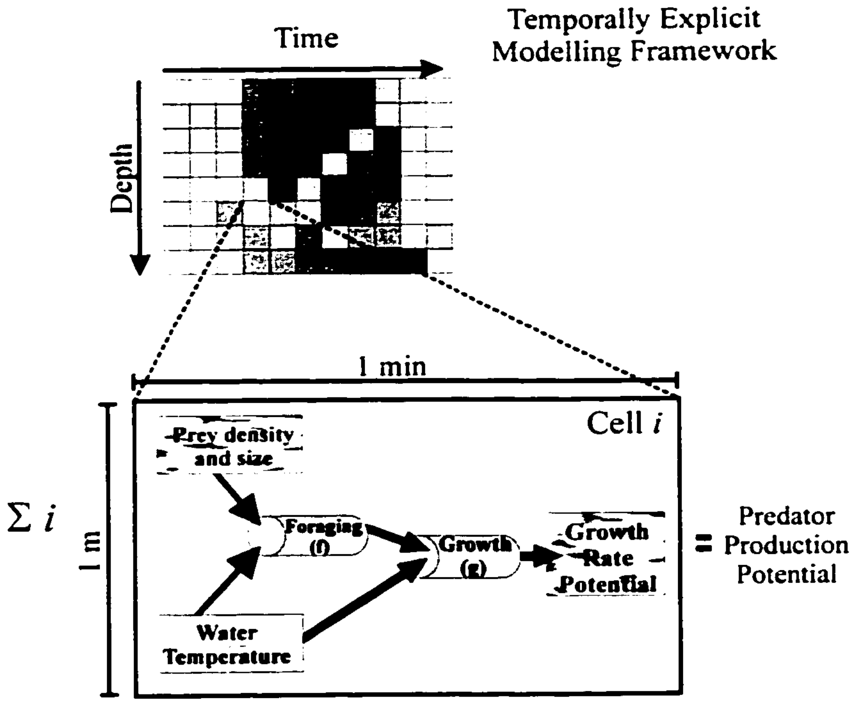

Prey
Predator
50000
45000
40000
35000
30000
25000
20000
15000
10000
5000
0
Frequency Distribution
0
100
200
300
400
500
600
700
800
900
1000
Fish Length (mm)

Figure 3.5 — Conceptualization of the temporally explicit modelling framework, dividing the sampled environment into unitary cells indexed by time and depth. Each cell ($Cell_i$) is characterised by a particular suite of environmental conditions which are entered into foraging (f) and growth (g) sub-models which determine species-specific, predator production within that cell. Conditions within each cell are updated every time interval (1 min) and provide temporal evaluation of predator potential production within each cell. The production measured in all cells (Σ all $Cell_i$ s) demonstrates the evolution of potential predator production within the sampled environment over time (adapted from Brandt and Kirsch 1993).


Time
Temporally Explicit Modelling Framework
Depth
1 min
Cell *i*
Prey density and size
Foraging (f)
Growth (g)
Growth Rate Potential
Water Temperature
Σ *i*
1 m
= Predator Production Potential

Results

May 27-28

May Dawn 04:13-05:42

During the dawn period, chinook salmon distribution was strongly correlated with chinook growth rate potential. Actual chinook distribution was positively correlated to alewife density, but to a lesser extent than with growth rate potential. Actual chinook distribution, however, failed to show any association to empirically derived chinook optimal temperatures. These results indicate that chinook growth rate potential was the most important environmental condition describing chinook distribution during this time period, and that chinook salmon were selecting their habitat in terms of growth maximization (Figure 3.6; Table 3.1).

May Day 18:51-20:41 & 05:45-18:01

Very few chinook were observed during the day period. Nevertheless, all environmental conditions monitored proved to be positively correlated with actual chinook distribution. Prey (alewife) density exhibited the highest association, followed by chinook growth rate potential. Chinook optimal temperatures, meanwhile, exhibited the weakest association. As such, alewife density best described actual chinook distribution indicating that chinook were exhibiting prey-taxis. Habitat preference was based on prey availability rather than on growth potential or thermal preference (Figure 3.7; Table 3.1).

May Dusk 20:44-22:13

Chinook were absent from the water column during the dusk period. This absence of chinook yielded zero correlations with all monitored environmental conditions preventing the determination of their relative importance in terms of chinook habitat preference (Figure 3.8; Table 3.1).

May Night 22:15-04:10

Actual chinook distribution during the night, was most highly correlated with chinook optimal temperatures, followed closely by growth rate potential. Actual chinook distribution was also positively correlated with alewife density, but to a lesser degree than either chinook optimal temperatures, or growth rate potential. During the night, chinook optimal temperatures were the best descriptor of actual chinook distribution, indicating that chinook were behaviourally thermoregulating and selecting their habitat based on temperature preference rather than growth maximization or prey availability (Figure 3.9; Table 3.1).

June 19-20

June Dawn 04:10-05:36

During the dawn, actual chinook distribution was positively correlated with all three environmental conditions monitored. Chinook growth rate potential, however, was the most highly correlated environmental condition. As chinook growth rate potential best described actual chinook distribution, chinook salmon selected their habitat in order to maximize growth rather than to optimize prey availability or thermal exposure (Figure 3.10; Table 3.2).

June Day 08:09-20:58 & 05:38-05:49

Similarly, during the day, the order of association for the three environmental conditions monitored, and actual chinook distribution, did not change from that occurring during dawn (see above). Although all three environmental conditions were correlated to actual chinook distribution, chinook growth rate potential displayed the highest correlation, followed closely by that of alewife density. Chinook optimal temperatures had the weakest correlation, well below those of both chinook growth rate potential and alewife density. Again, chinook growth rate potential was the most important environmental condition monitored in terms of describing actual chinook distribution (Figure 3.11; Table 3.2).

June dusk 21:01-22:30

The absence of chinook in the water column during the dusk period prevented the evaluation of the relative importance of the monitored environmental conditions to actual chinook habitat preference. The lack of chinook generated zero correlations for all monitored environmental conditions rendering it impossible to rank their relative degree of association (Figure 3.12; Table 3.2).

June Night 22:33-04:07

Both chinook optimal temperatures and growth rate potential exhibited very similar degrees of association with actual chinook distribution during the night period. Chinook optimal temperatures, however, had a slightly higher association than growth rate potential. The degree of association between alewife density and actual chinook distribution, meanwhile, was relatively low. The highest association between chinook optimal temperatures and actual chinook distribution indicated that chinook salmon were behaviourally thermoregulating, and selecting their habitat based on the availability of their thermal preference rather than on alewife availability, or growth potential (Figure 3.13; Table 3.2).

July 30-31

July Dawn 04:26-06:45

During dawn, only chinook growth rate potential and alewife density were significantly correlated to actual chinook distribution. Although fairly close in their degree of association with actual chinook distribution, chinook growth rate potential exhibited a higher correlation than alewife density, indicating that chinook were selecting their habitat in order to maximize growth instead of alewife availability (Figure 3.14; Table 3.3).

July Day 10:07-20:36 & 06:08-10:10

Similarly, chinook growth rate potential exhibited the highest correlation with actual chinook distribution during the day period in July. Chinook optimal temperatures were also correlated to actual chinook distribution, but to a lesser degree than growth rate potential. Alewife density, however, exhibited no association with actual chinook distribution. Throughout all daylight hours in July, chinook growth rate potential best described actual chinook distribution indicating that chinook selected their habitat based on growth maximization rather than alewife availability or thermal preference (Figure 3.15; Table 3.3).

July Dusk 20:39-22:08

Chinook growth rate potential was the only environmental condition correlated to actual chinook distribution during the dusk period in July. All other environmental conditions monitored yielded no association to actual chinook distribution (Figure 3.16; Table 3.3).

July Night 22:11-04:23

Chinook growth rate potential exhibited the highest correlation with actual chinook distribution during the night period. Alewife density was also positively correlated to actual chinook distribution but relatively less than that measured with growth rate potential. Chinook optimal temperatures, however, failed to show any association with actual chinook distribution. Chinook distribution was best described by chinook growth rate potential, and chinook selected their habitat in order to optimize growth rather than maximize alewife availability or optimize thermal exposure (Figure 3.17; Table 3.3).

September 5-6

September Day 16:54-19:32

During the short day period sampled in September, chinook growth rate potential showed the highest, and the only positive correlation with actual chinook distribution. Both chinook optimal temperatures, and alewife density exhibited weaker, negative correlations with actual chinook distribution. Throughout the short day period, actual chinook distribution was best described by chinook growth rate potential indicating that chinook were selecting their habitat based on growth maximization instead of either thermal preference or alewife availability (Figure 3.18; Table 3.4).

September Dusk 19:48-21:15

Chinook were not observed in the water column during the dusk period. The lack of chinook produced zero correlations with all monitored environmental conditions and inhibited the assessment of their relative importance on chinook habitat preference (Figure 3.19: Table 3.4).

September Night 21:17-05:03

Chinook optimal temperatures was the only environmental condition exhibiting a significant correlation with actual chinook distribution during the night period. Neither chinook growth rate potential nor alewife density displayed any association with actual chinook distribution. Chinook habitat preference during this particular time period was best described by behavioural thermoregulation rather than growth potential or prey-taxis (Figure 3.20; Table 3.4).

October 18-19

October Dawn 06:03-07:32 & October Day 16:10-18:25 & 07:35-15:53

Actual chinook distribution was non-existent during both the dawn and day periods, yielding zero correlation with all monitored environmental conditions. The zero correlations prevented the determination of the relative importance of the monitored environmental conditions to chinook habitat preference (Figure 3.21,3.22; Table 3.5).

October Dusk 18:27-19:57

During the dusk period, both optimal temperatures and alewife density exhibited no association with actual chinook distribution. Conversely, chinook growth rate potential generated a significantly positive correlation with actual chinook distribution, indicating that chinook were selecting their habitat based on growth optimization rather than maximizing alewife availability, or optimizing thermal exposure (Figure 3.23; Table 3.5).

October Night 00:26-06:01

No significant correlations were observed between any of the three environmental conditions monitored and actual chinook distribution during the night period. All assessed associations were either not significant, or yielded zero correlation, rendering the determination of the relative importance of the monitored environmental conditions to chinook habitat preference unfeasible (Figure 3.24; Table 3.5).

Sampling Season Synopsis

Performing a similar analysis on all sampling events (May, June, July, September, and October) revealed very different trends in chinook habitat preference. During May, alewife density and chinook growth rate potential displayed analogous correlations with actual chinook distribution. Chinook optimal temperatures exhibited a significant positive correlation with actual chinook distribution, but it was substantially smaller than that of either alewife density or chinook growth rate potential. Chinook exhibited prey-taxis and selected their habitat based on prey availability during the 24 hour period, rather than growth potential or thermal preference (Figure 3.6-3.9; Table 3.6).

During June, all monitored environmental conditions exhibited a significant correlation with actual chinook distribution. Chinook growth rate potential, however, showed the highest degree of association with actual chinook distribution, followed by alewife density and chinook optimal temperatures. Of the three monitored environmental conditions, chinook growth rate potential best described actual chinook distribution, throughout the entire June sampling event. This indicated that chinook selected their habitat based on optimal growth conditions more so than in terms of alewife availability, or thermal preference (Figures 3.10-3.13; Table 3.6).

Unexpectedly in July, although chinook growth rate potential proved to be the best descriptor of actual chinook distribution during all time periods (Dawn, Day, Dusk, and Night), chinook optimal temperatures exhibited the highest correlation when considering the 24 hour sampling period as a whole. Chinook growth rate potential had a comparable, but slightly smaller correlation with actual chinook distribution than chinook optimal temperatures, while alewife density did not show any association. Overall, chinook optimal temperatures were the best descriptor of actual chinook distribution during July, indicating that overall, chinook selected their habitat more in terms of thermal preference than in terms of growth, or alewife availability (Figures 3.14-3.17; Table 3.6).

None of the monitored environmental conditions were significantly correlated to actual chinook distribution when evaluating associations using the entire September sampling event. The lack of association between all environmental conditions and actual chinook distribution impeded the determination of the relative importance of these conditions to chinook habitat preference during this sampling period (Figures 3.18-3.20; Table 3.6).

When considering the entire October sampling period, chinook growth rate potential exhibited the highest correlation with actual chinook distribution. To a lesser extent, alewife density was also positively correlated to actual chinook distribution, while chinook optimal temperatures showed no association. Chinook growth rate potential was therefore, the best descriptor of chinook habitat preference during the entire October sampling event, demonstrating that chinook selected their habitat based on growth maximization rather than alewife availability, or thermal preference (Figures 3.21-3.24; Table 3.6).

Figure 3.6 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dawn (*04:13-05:42*) of May 28, 1997 in western Lake Ontario.

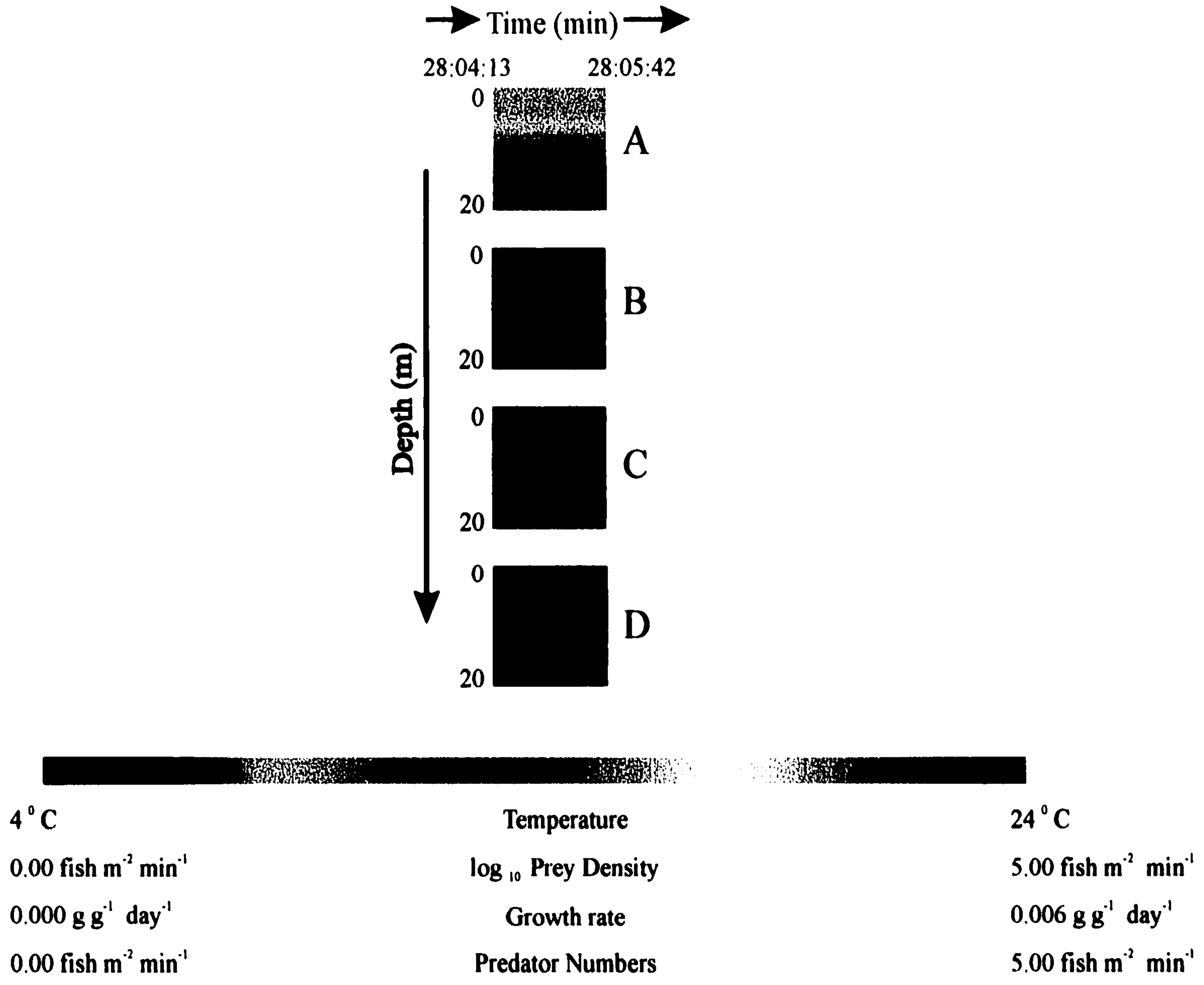
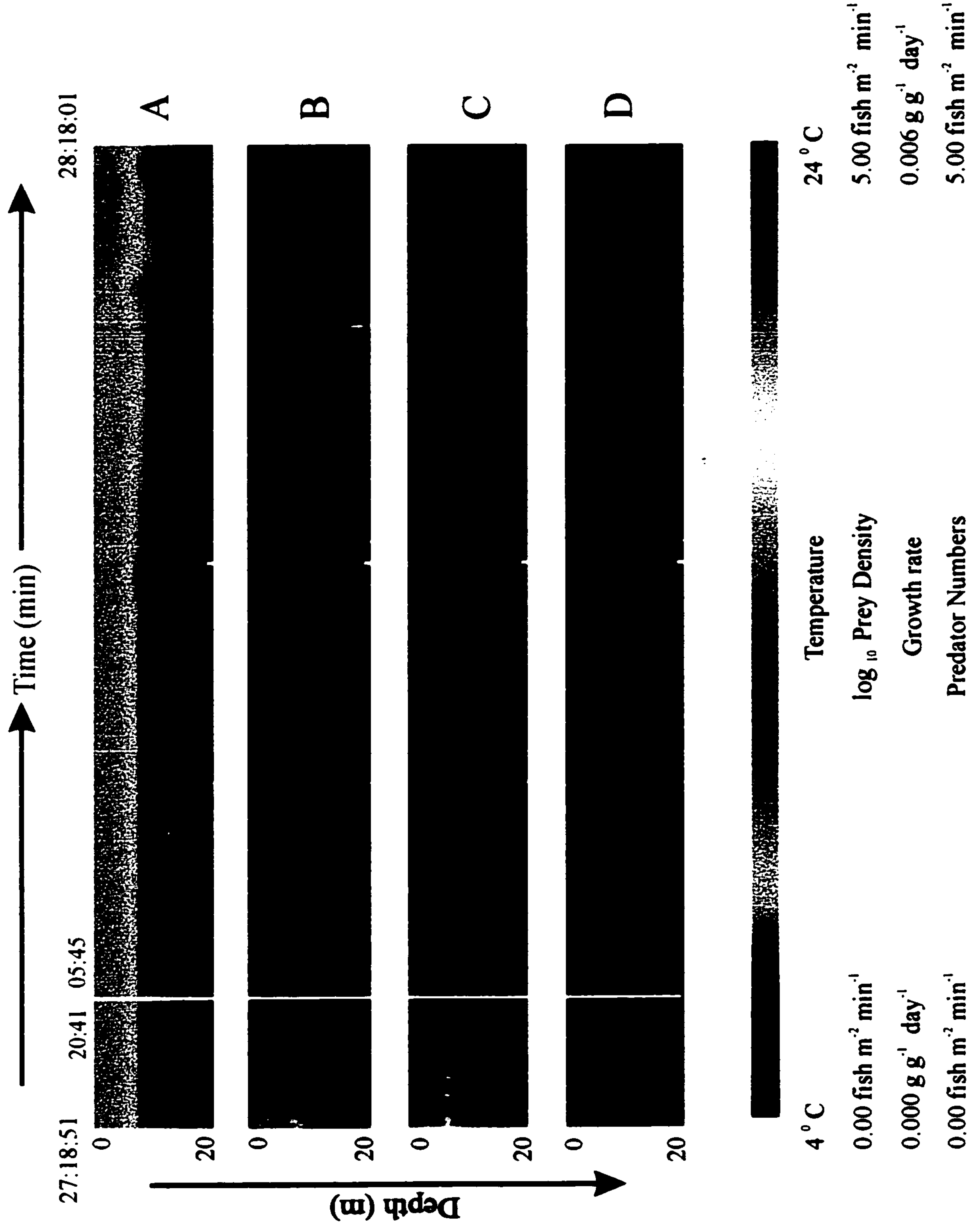

Time (min)
28:04:13
28:05:42
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log $_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Predator Numbers
5.00 fish m^{-2} min^{-1}

Figure 3.7 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the day (*18:51-20:41 & 05:45-18:01*) of May 27-28, 1997 in western Lake Ontario.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Depth (m)
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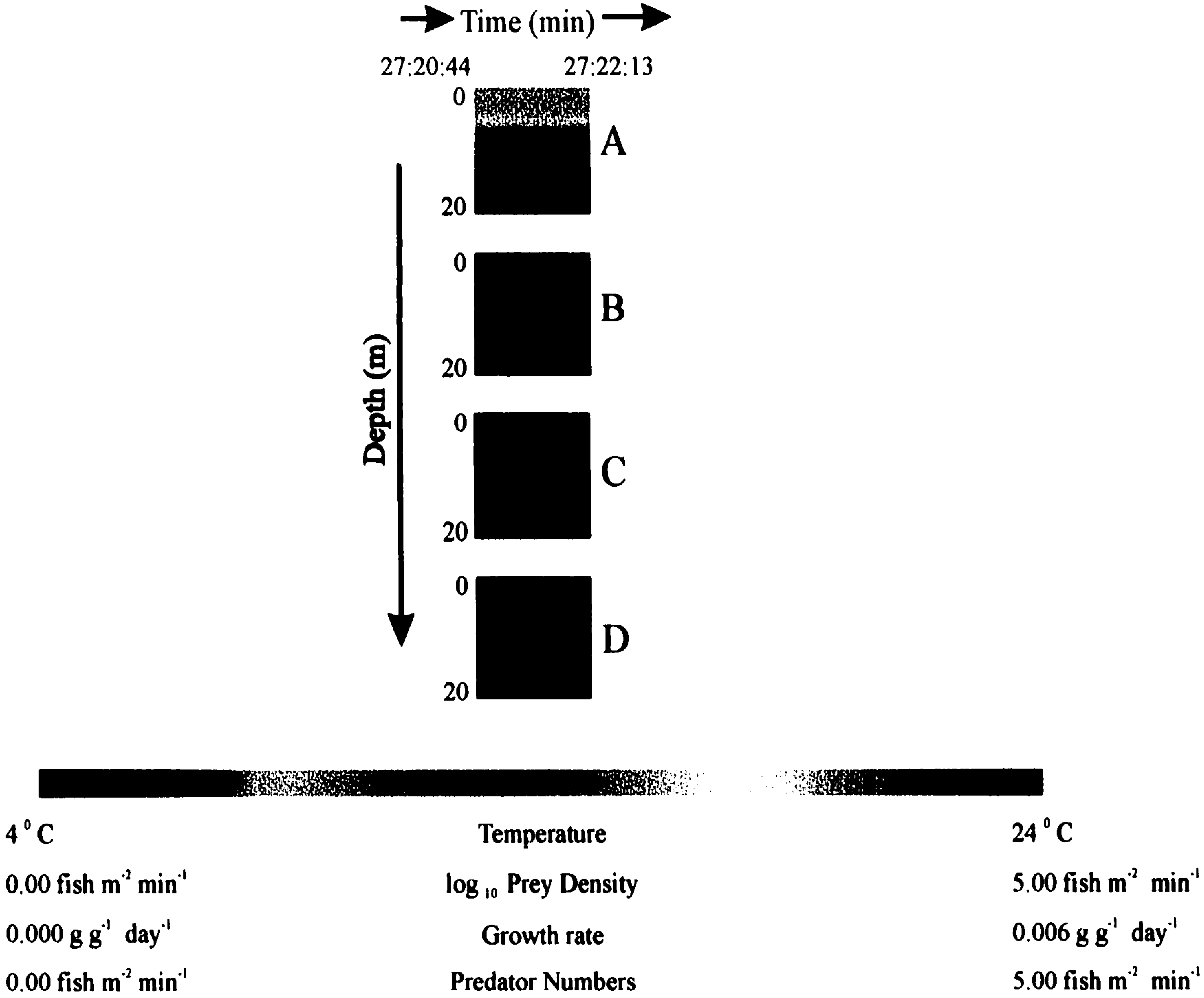
20:41
05:45
28:18:01
A
B
C
D
0
20
0
20
0
20
0
20
4 °C
24 °C
Temperature
log₁₀ Prey Density
Growth rate
Predator Numbers
0.00 fish m-2 min-1
5.00 fish m-2 min-1
0.000 g g-1 day-1
0.006 g g-1 day-1
0.00 fish m-2 min-1
5.00 fish m-2 min-1

Figure 3.8 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dusk (*20:44-22:13*) of May 27, 1997 in western Lake Ontario.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27:22:13
Depth (m)
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20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.9 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the night (*22:15-04:10*) of May 27-28, 1997 in western Lake Ontario.

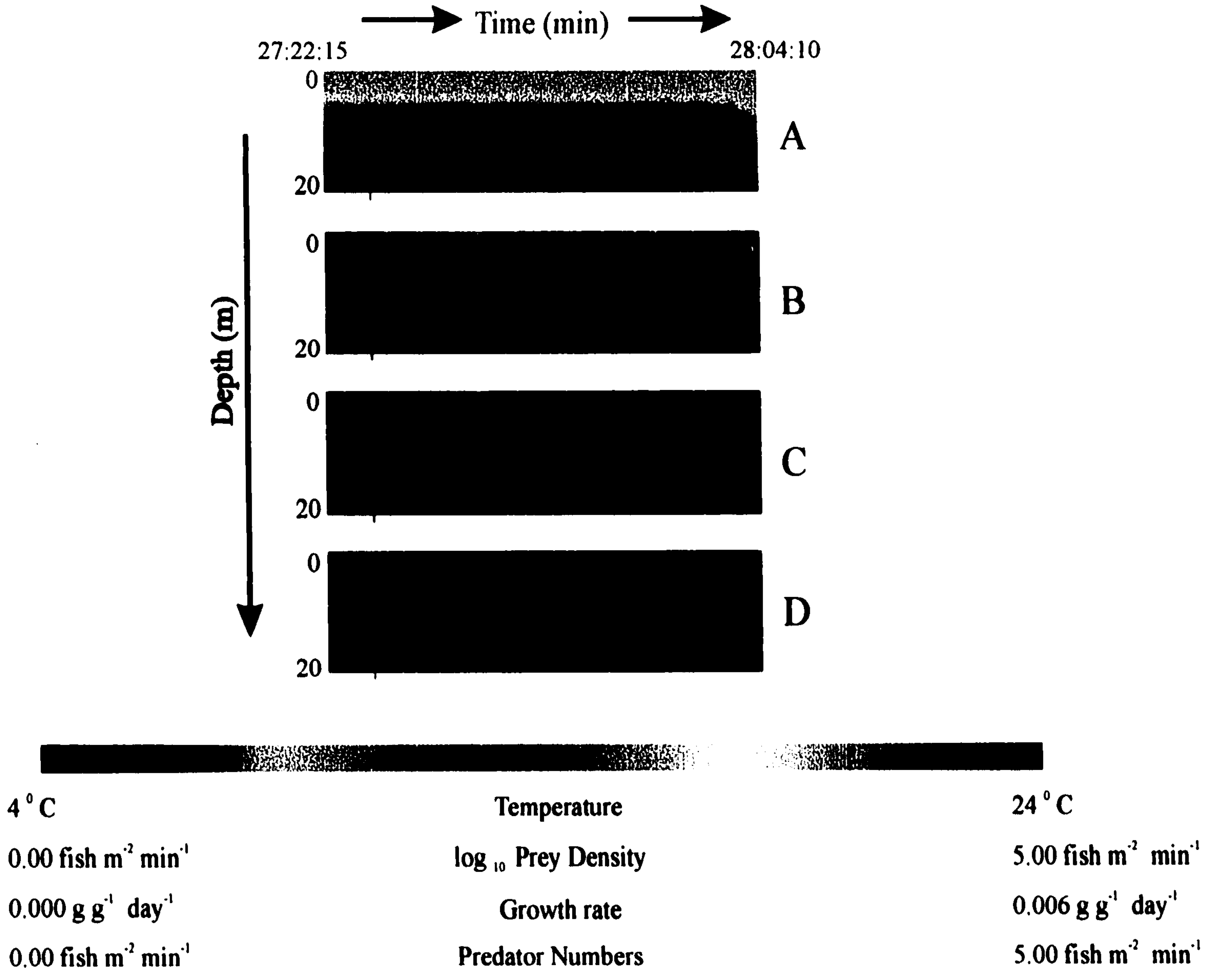

Time (min)
27:22:15
28:04:10
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.10 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dawn (*04:10-05:36*) of June 20, 1997 in western Lake Ontario.

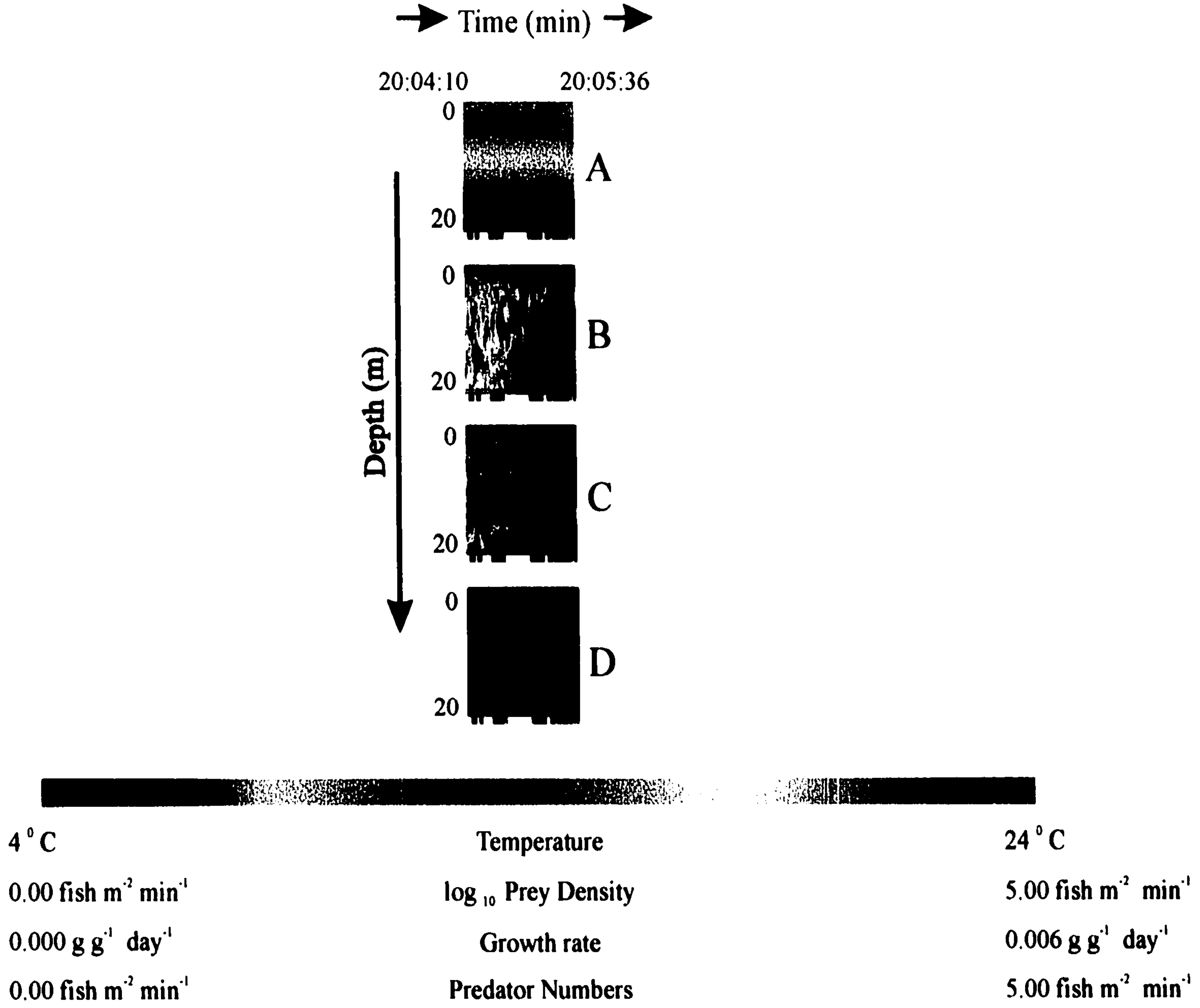

Time (min)
20:04:10
20:05:36
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.11 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the day (*08:09-20:58 & 05:38-05:49*) of June 19-20, 1997 in western Lake Ontario.

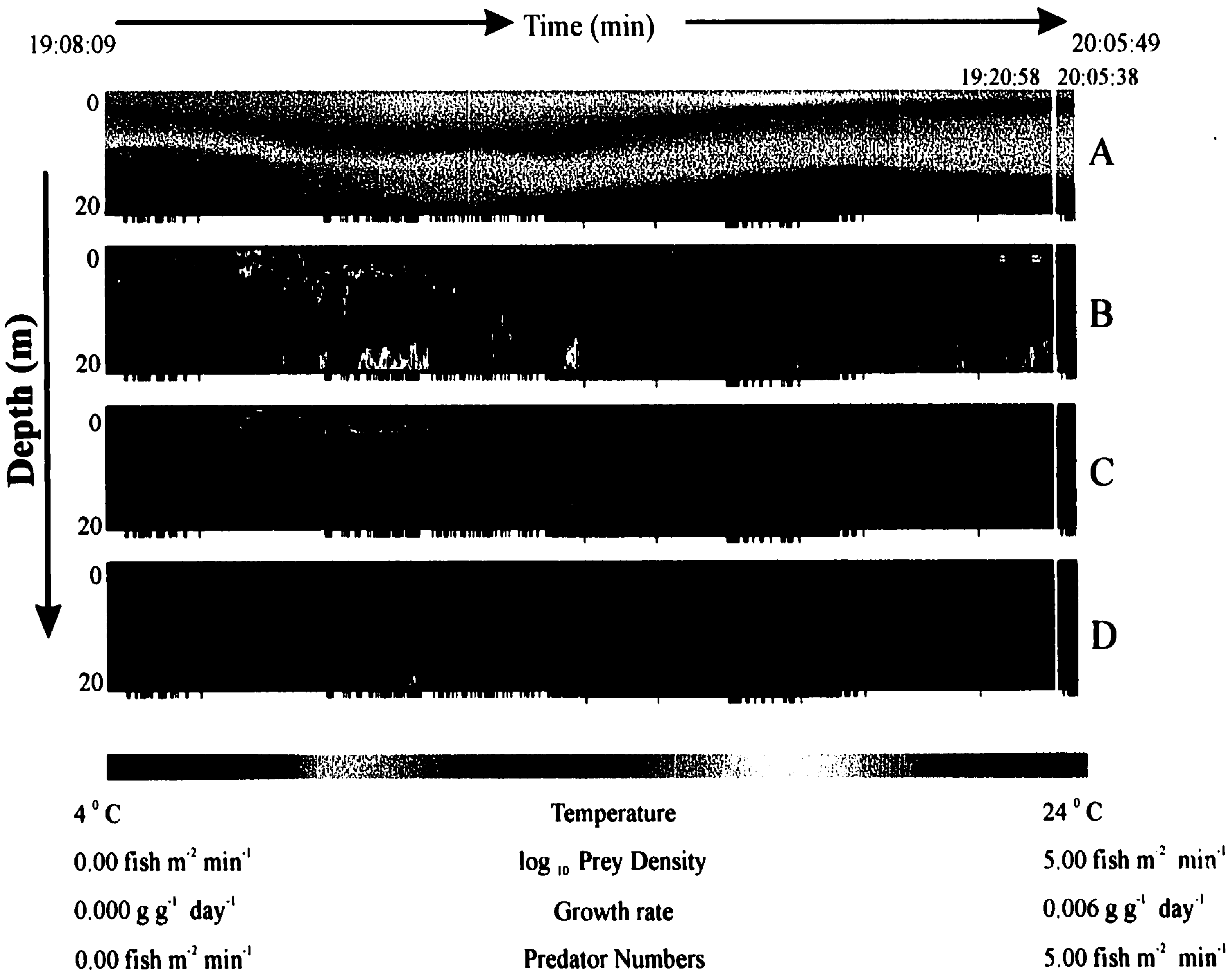

Time (min)
19:08:09
20:05:49
19:20:58
20:05:38
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.12 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dusk (*21:01-22:30*) of June 19, 1997 in western Lake Ontario.

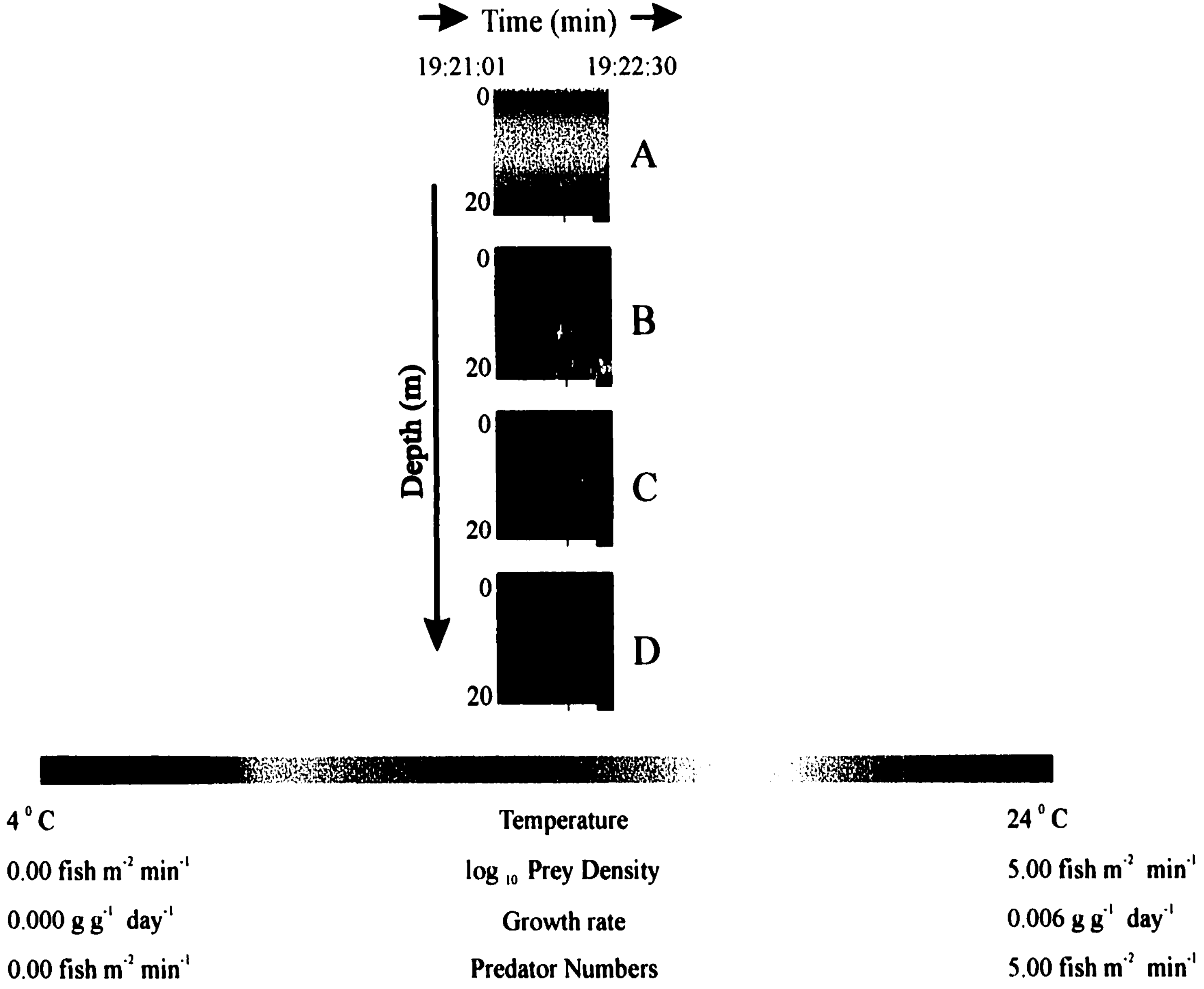

Time (min)
19:21:01
19:22:30
Depth (m)
0
20
A
B
C
D
4 °C
0.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Temperature
log$_{10}$ Prey Density
Growth rate
Predator Numbers
24 °C
5.00 fish m^{-2} min^{-1}
0.006 g g^{-1} day^{-1}
5.00 fish m^{-2} min^{-1}

Figure 3.13 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the night (*22:33-04:07*) of June 19-20, 1997 in western Lake Ontario.

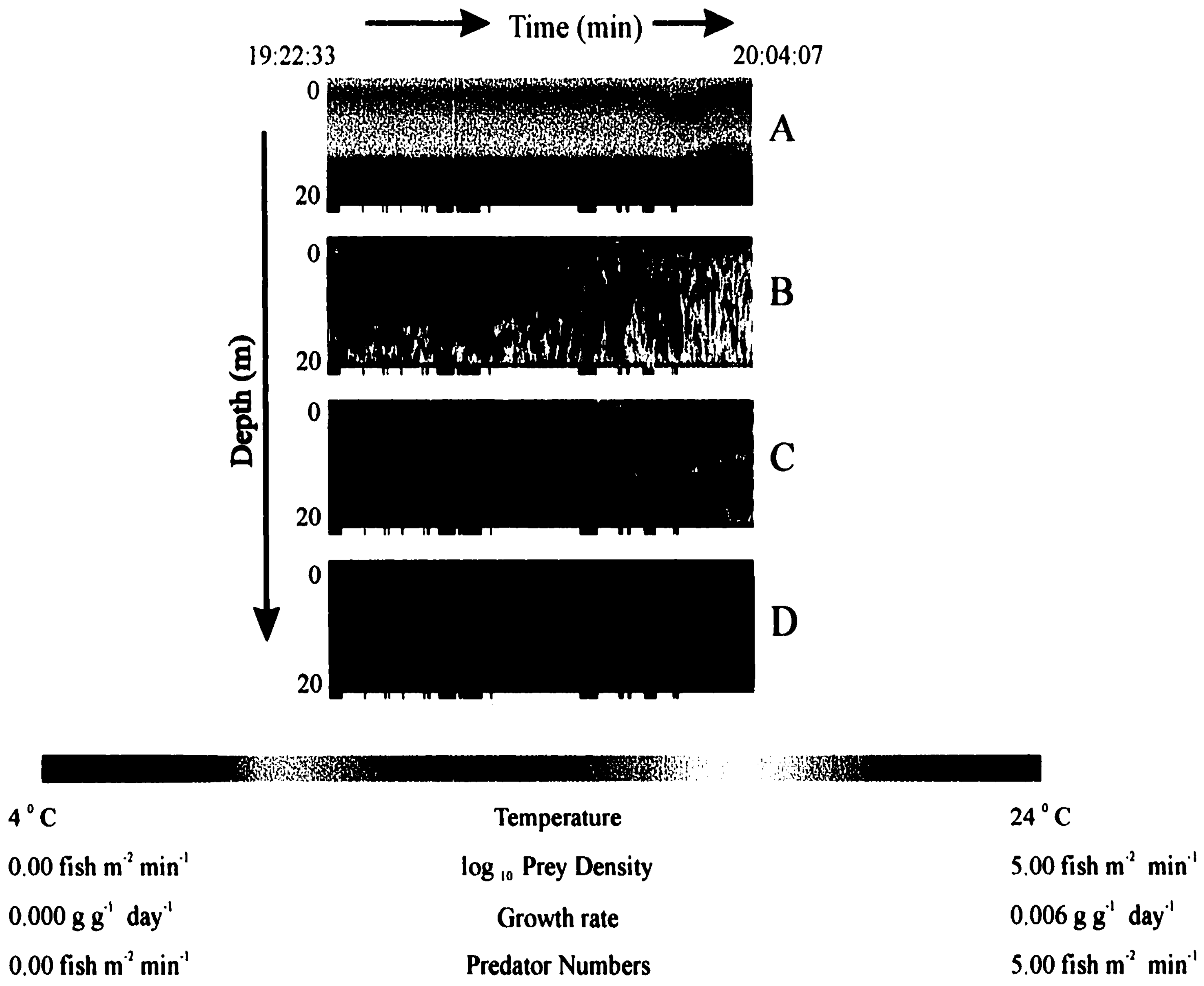
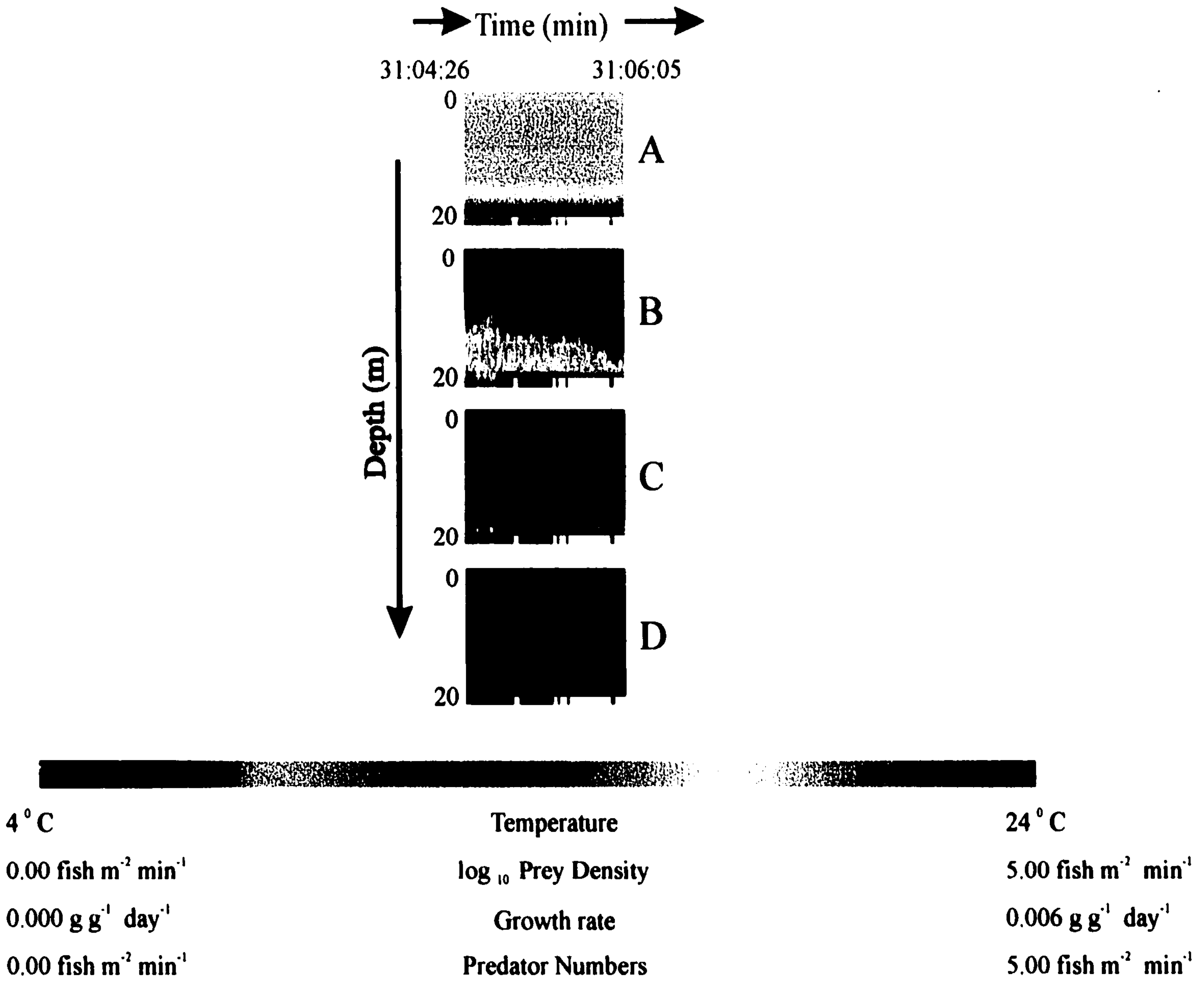

Time (min)
19:22:33
20:04:07
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log$_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Predator Numbers
5.00 fish m^{-2} min^{-1}

Figure 3.14 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dawn (*04:26-06:05*) of July 31, 1997 in western Lake Ontario.


Time (min)
31:04:26
31:06:05
Depth (m)
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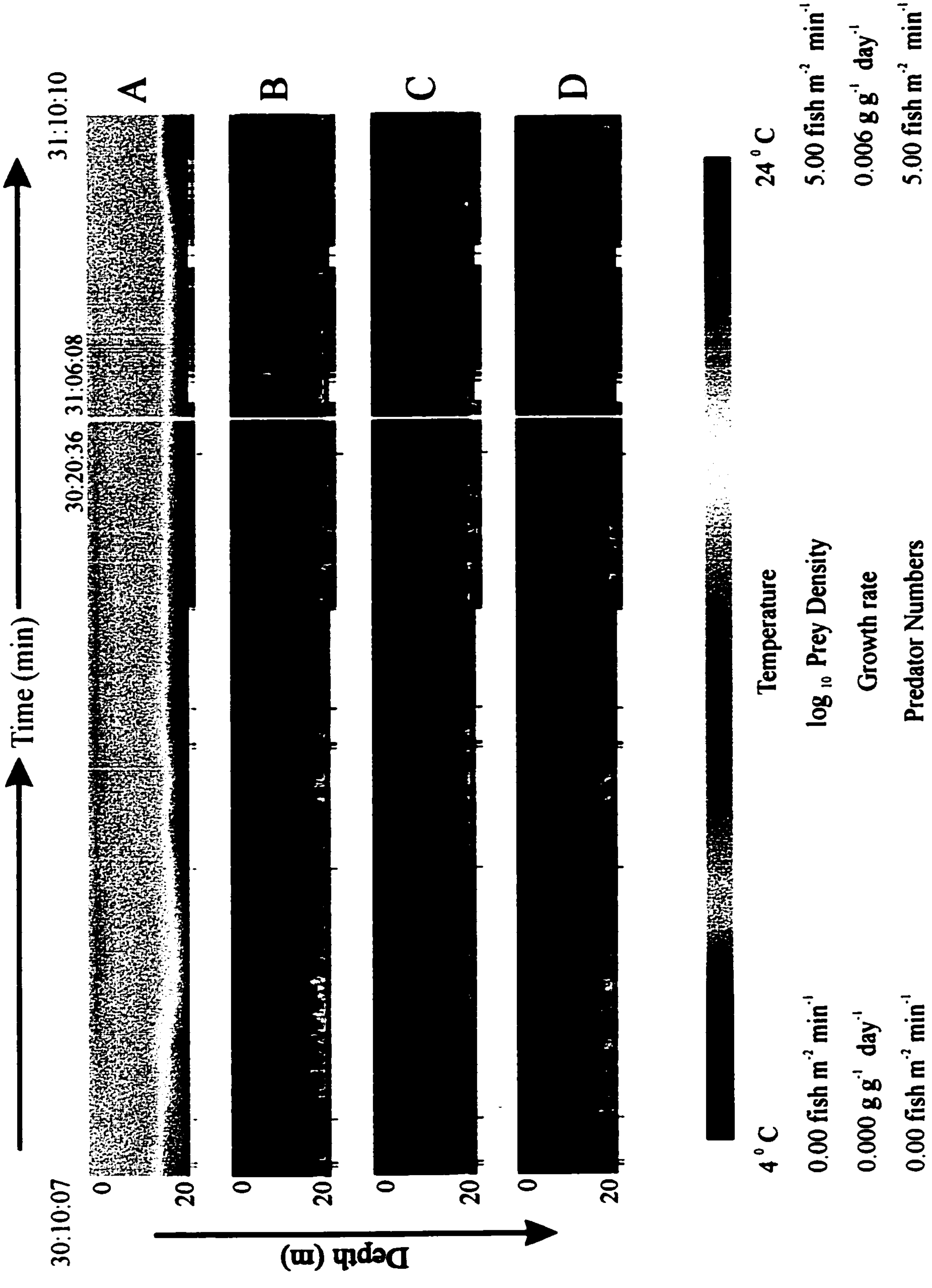
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.15 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the day (*10:07-20:36 & 06:08-10:10*) of July 30-31, 1997 in western Lake Ontario.


Time (min)
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31:06:08
31:10:10
Depth (m)
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20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log$_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Predator Numbers
5.00 fish m^{-2} min^{-1}

Figure 3.16 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dusk (*20:39-22:08*) of July 30, 1997 in western Lake Ontario.

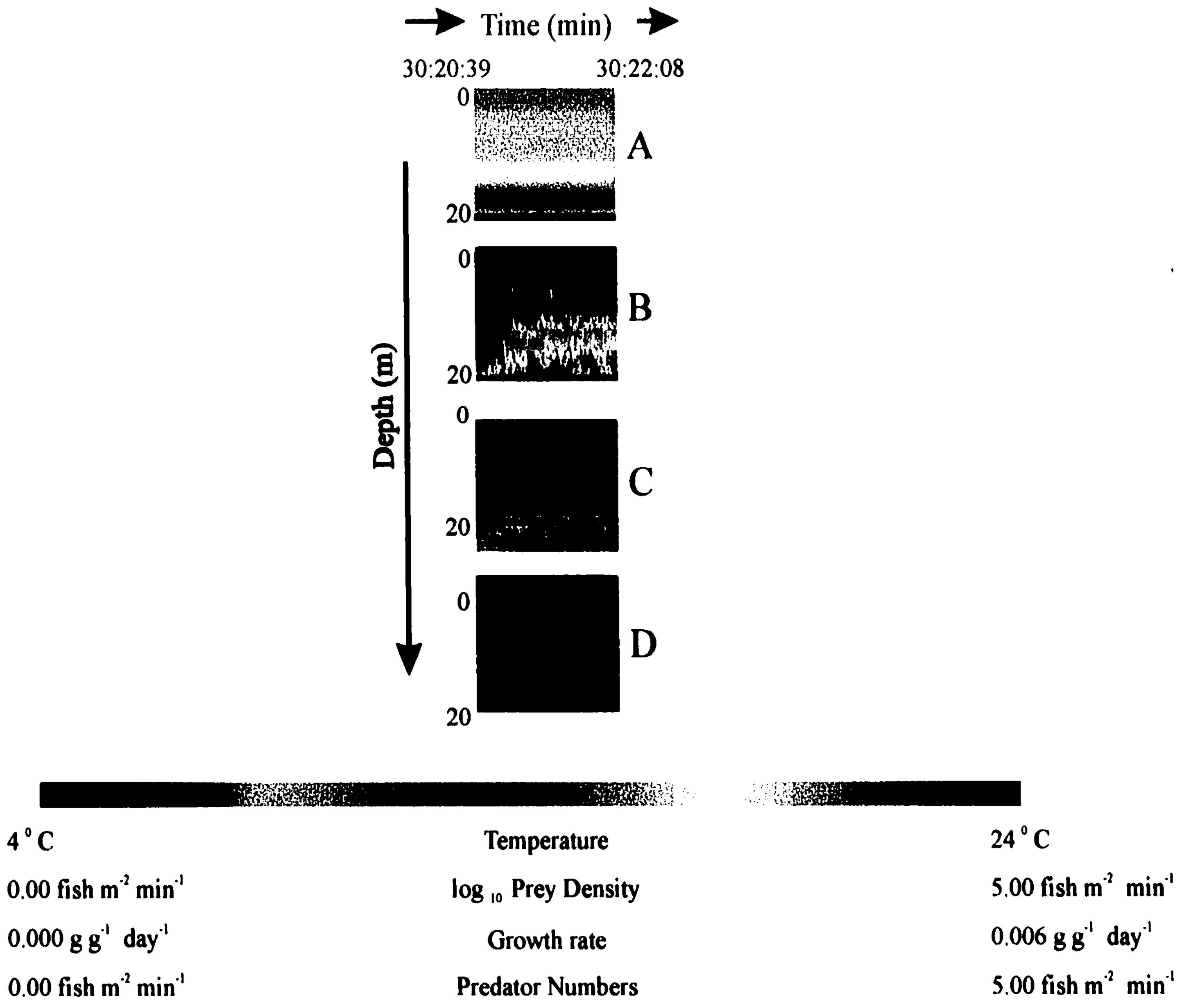
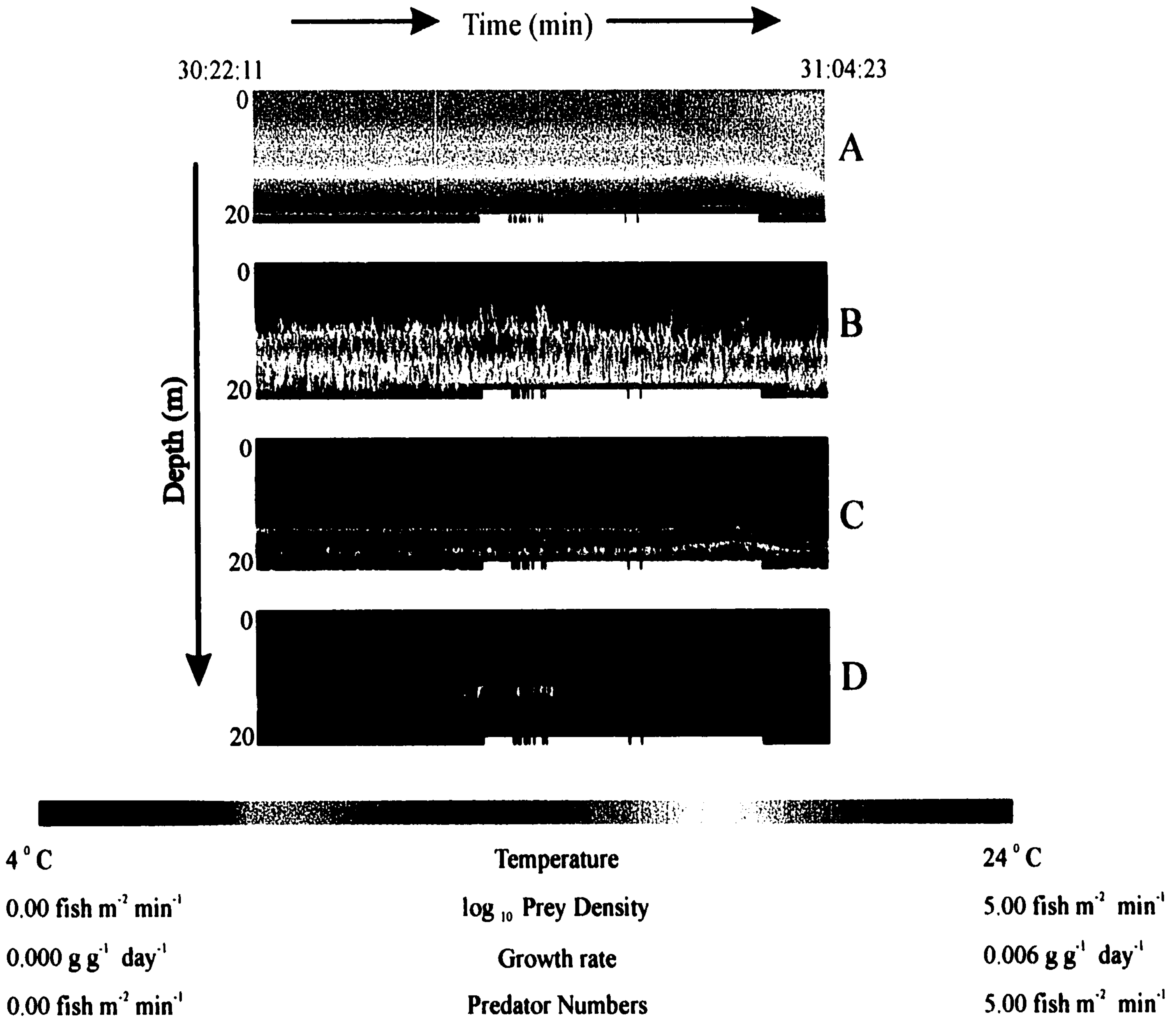

Time (min)
30:20:39
30:22:08
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log $_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Predator Numbers
5.00 fish m^{-2} min^{-1}

Figure 3.17 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the night (*22:11-04:23*) of July 30-31, 1997 in western Lake Ontario.


Time (min)
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31:04:23
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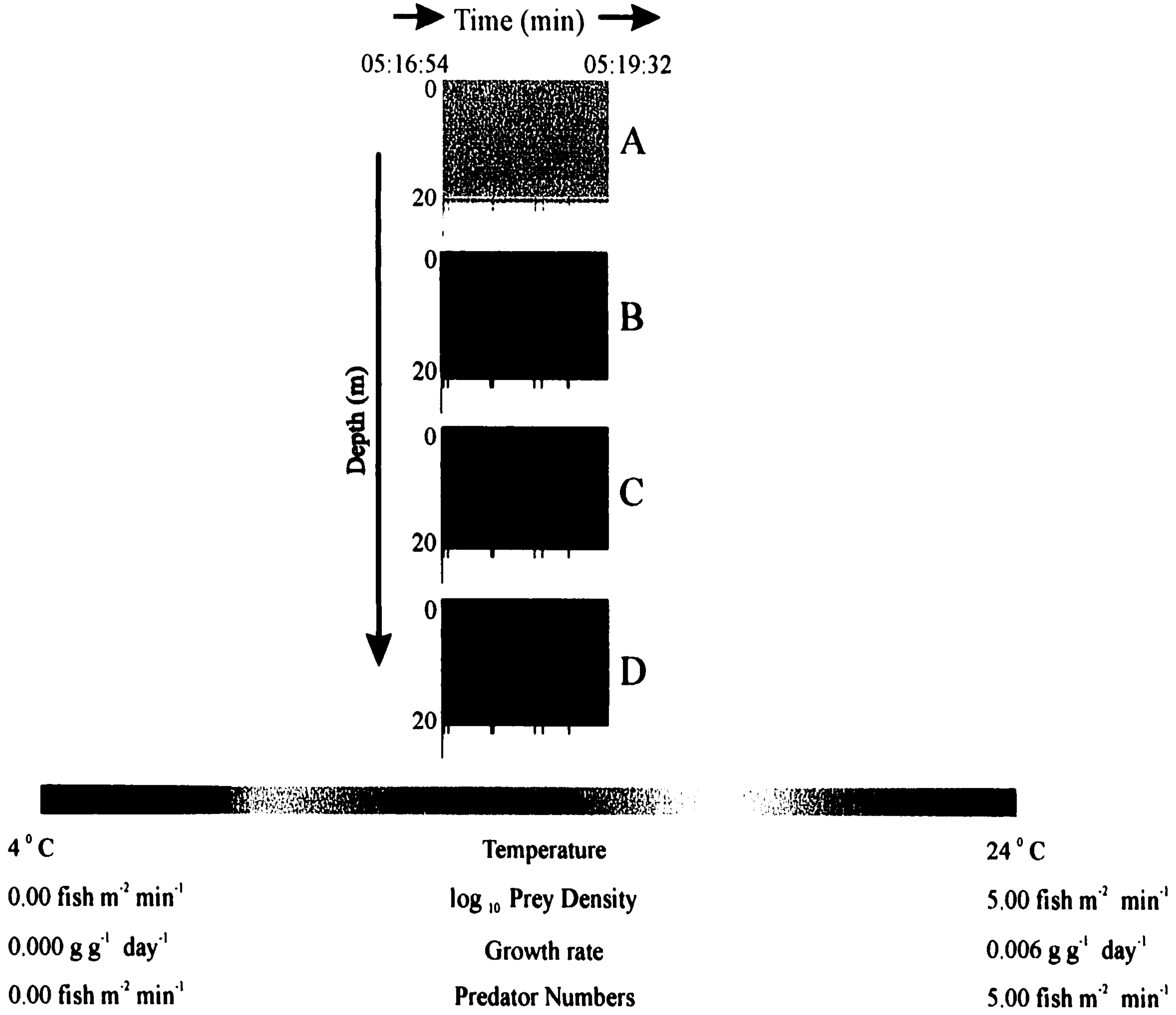
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.18 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the day (*16:54-19:32*) of September 5, 1997 in western Lake Ontario.


Time (min)
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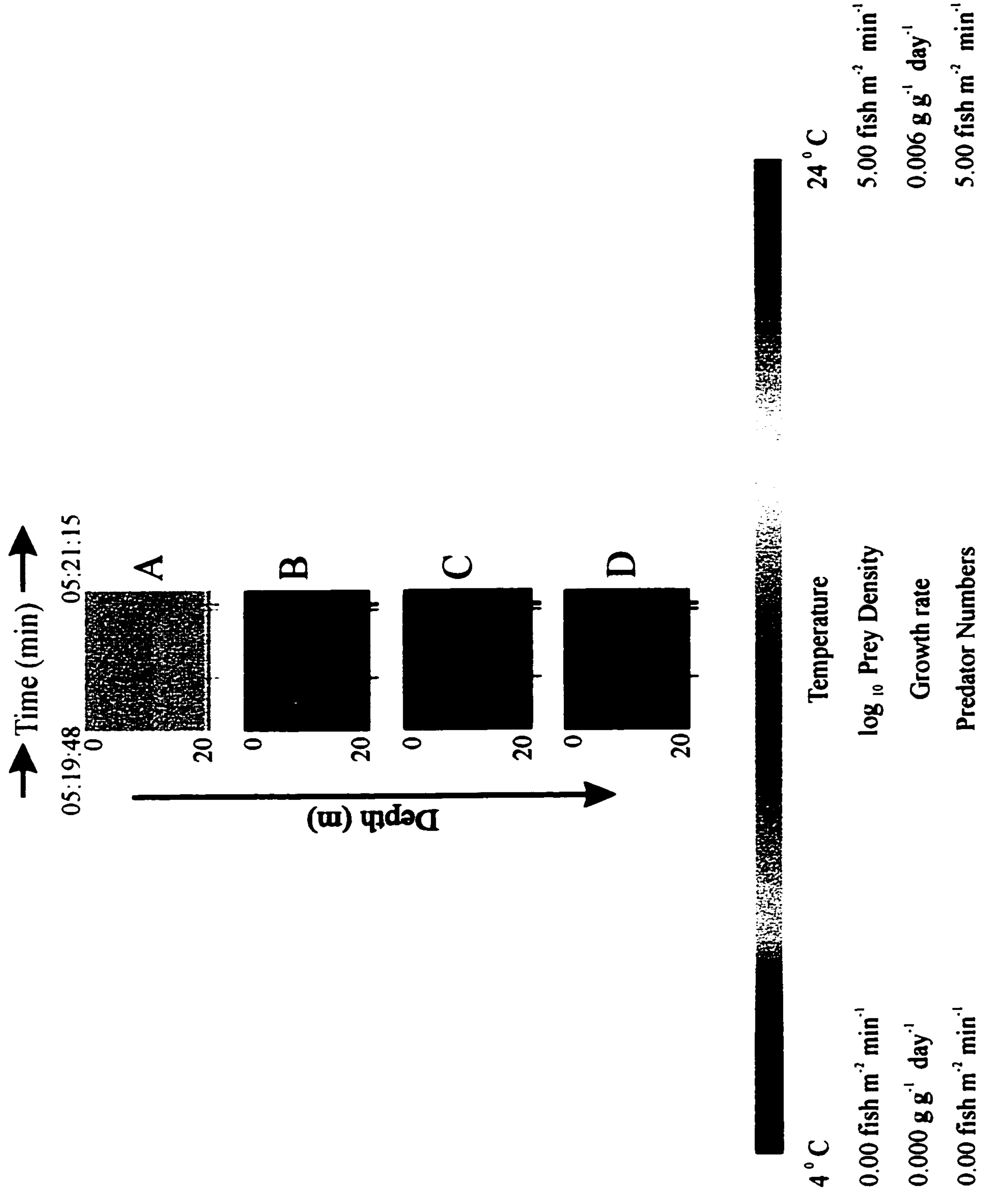
05:19:32
0
20
A
B
C
D
Depth (m)
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log$_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Predator Numbers
5.00 fish m^{-2} min^{-1}

Figure 3.19 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dusk (*19:48-21:15*) of September 5, 1997 in western Lake Ontario.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05:21:15
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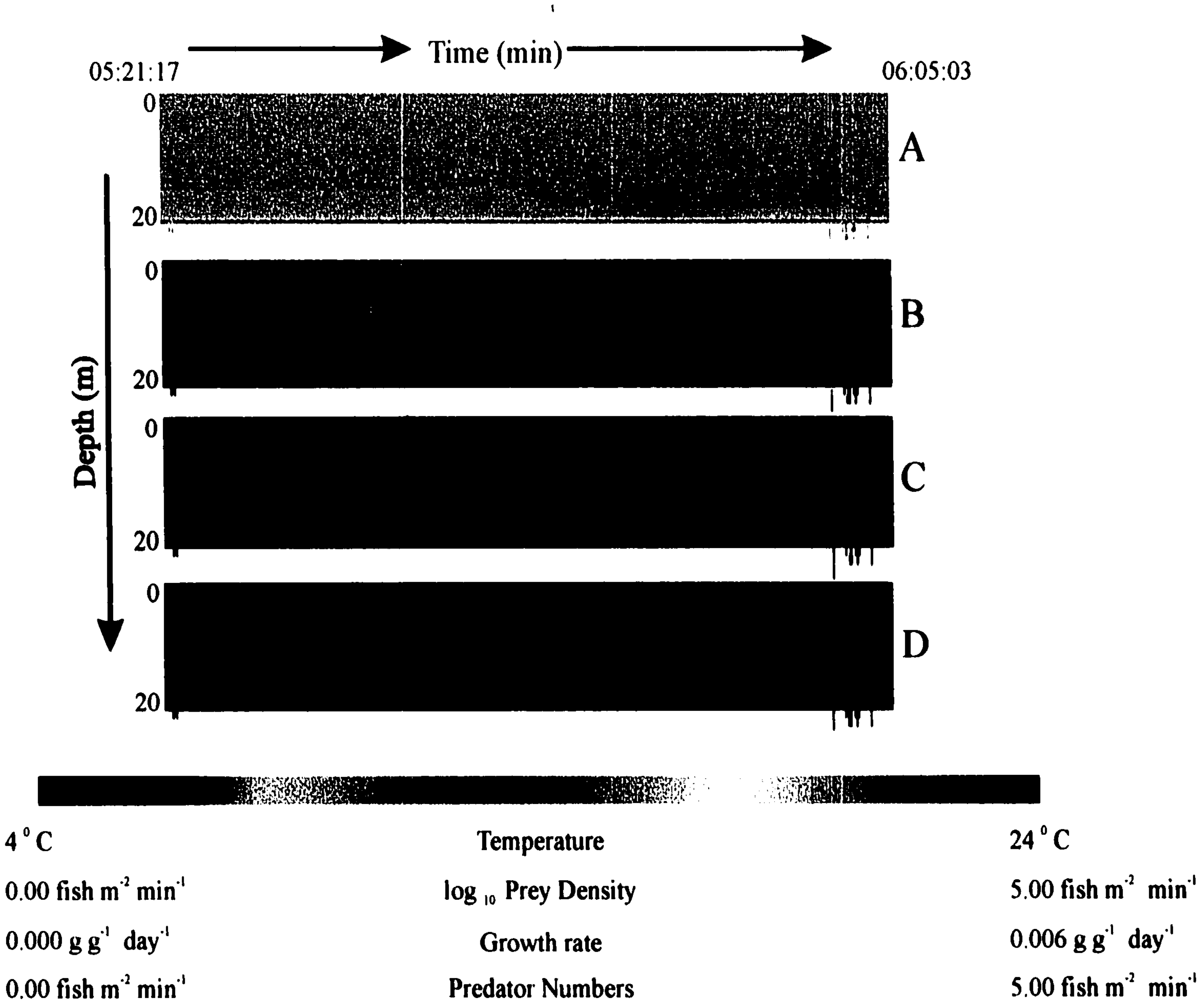
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.20 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the night (*21:17-05:03*) of September 5-6, 1997 in western Lake Ontario.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06:05:03
Depth (m)
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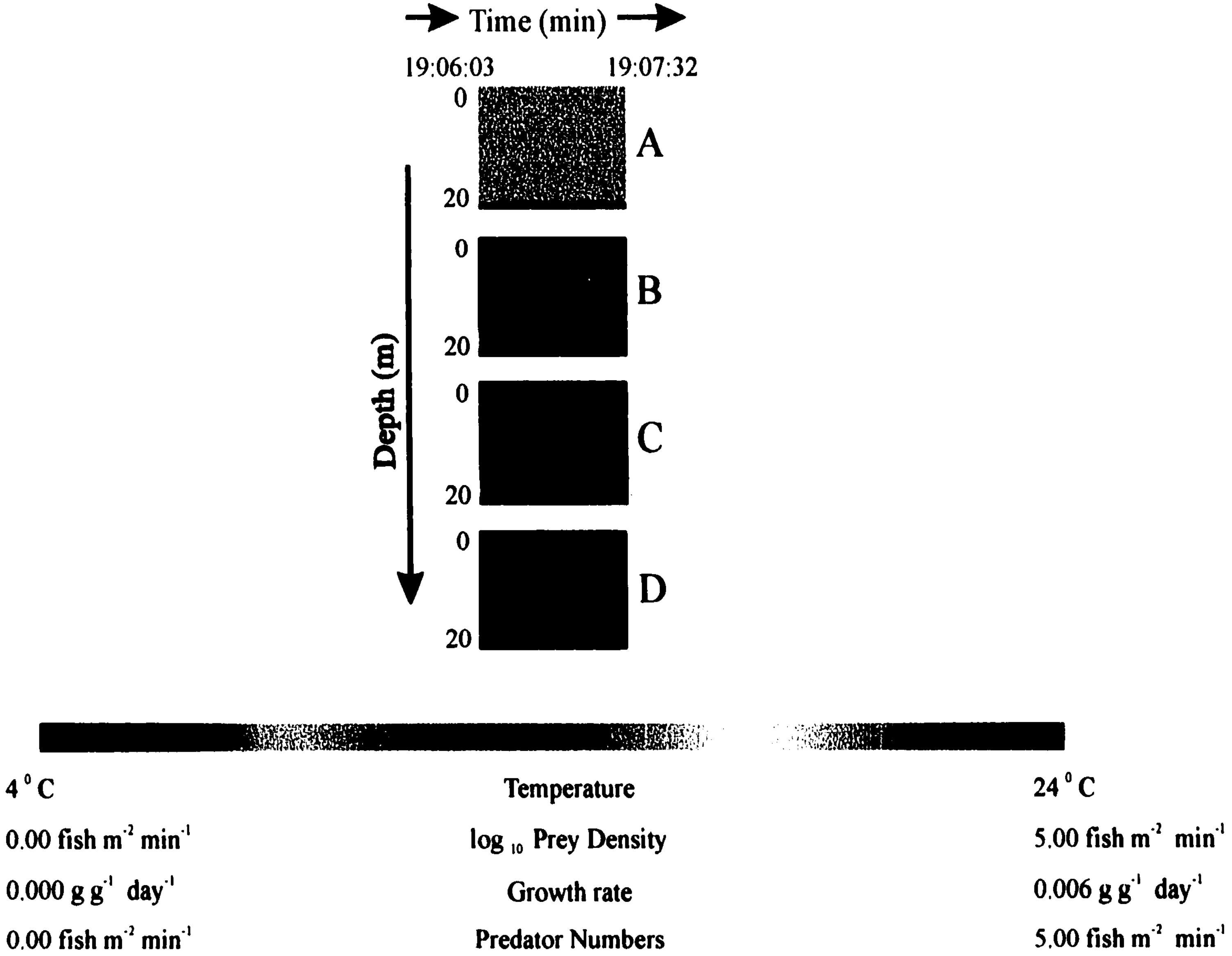
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m⁻² min⁻¹
log 10 Prey Density
5.00 fish m⁻² min⁻¹
0.000 g g⁻¹ day⁻¹
Growth rate
0.006 g g⁻¹ day⁻¹
0.00 fish m⁻² min⁻¹
Predator Numbers
5.00 fish m⁻² min⁻¹

Figure 3.21 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dawn (*06:03-07:32*) of October 19, 1997 in western Lake Ontario.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19:07:32
Depth (m)
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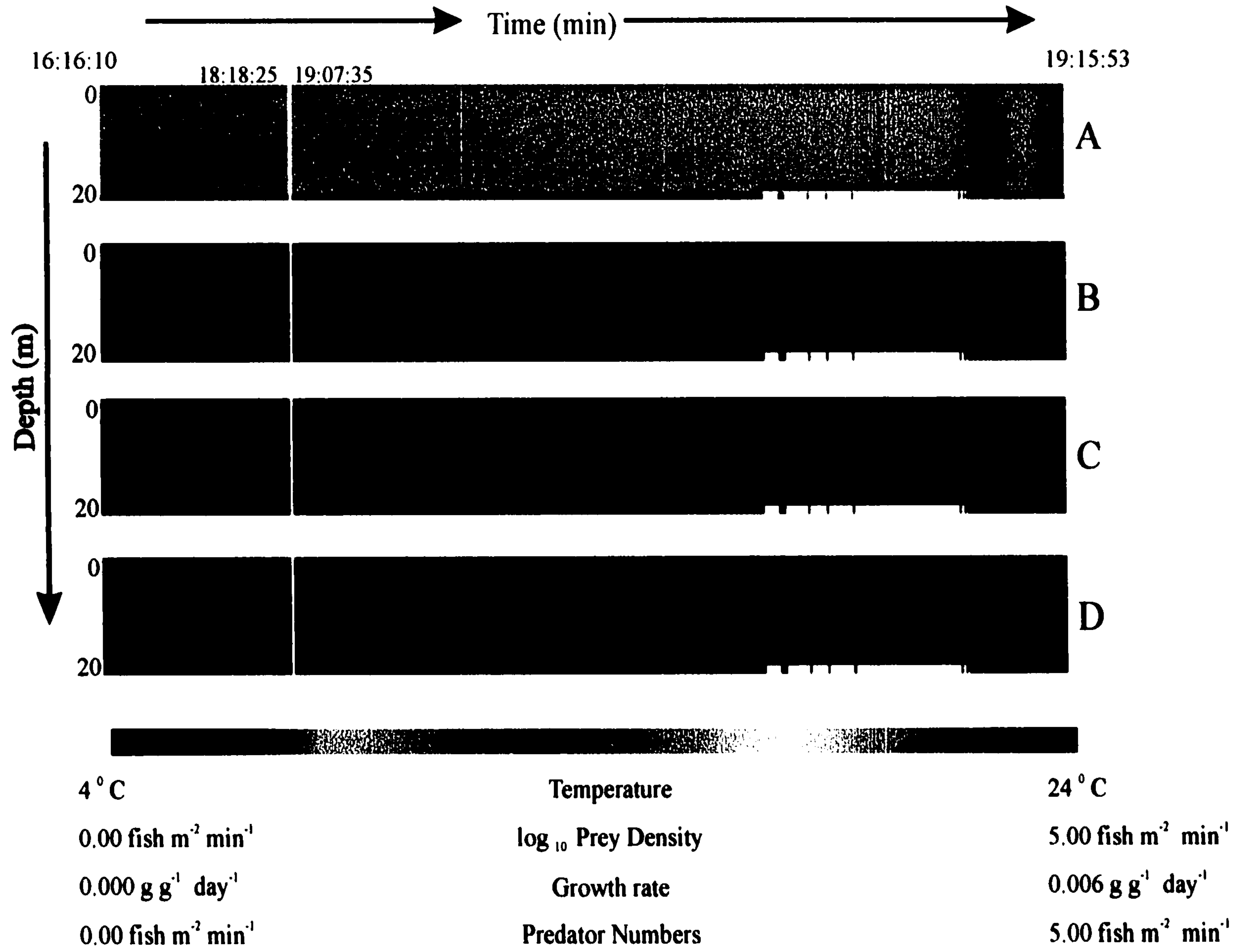
20
A
B
C
D
4 °C
0.00 fish m-2 min-1
0.000 g g-1 day-1
0.00 fish m-2 min-1
Temperature
log 10 Prey Density
Growth rate
Predator Numbers
24 °C
5.00 fish m-2 min-1
0.006 g g-1 day-1
5.00 fish m-2 min-1

Figure 3.22 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the day (*16:10-18:25 & 07:35-15:53*) of October 18-19, 1997 in western Lake Ontario.


Time (min)
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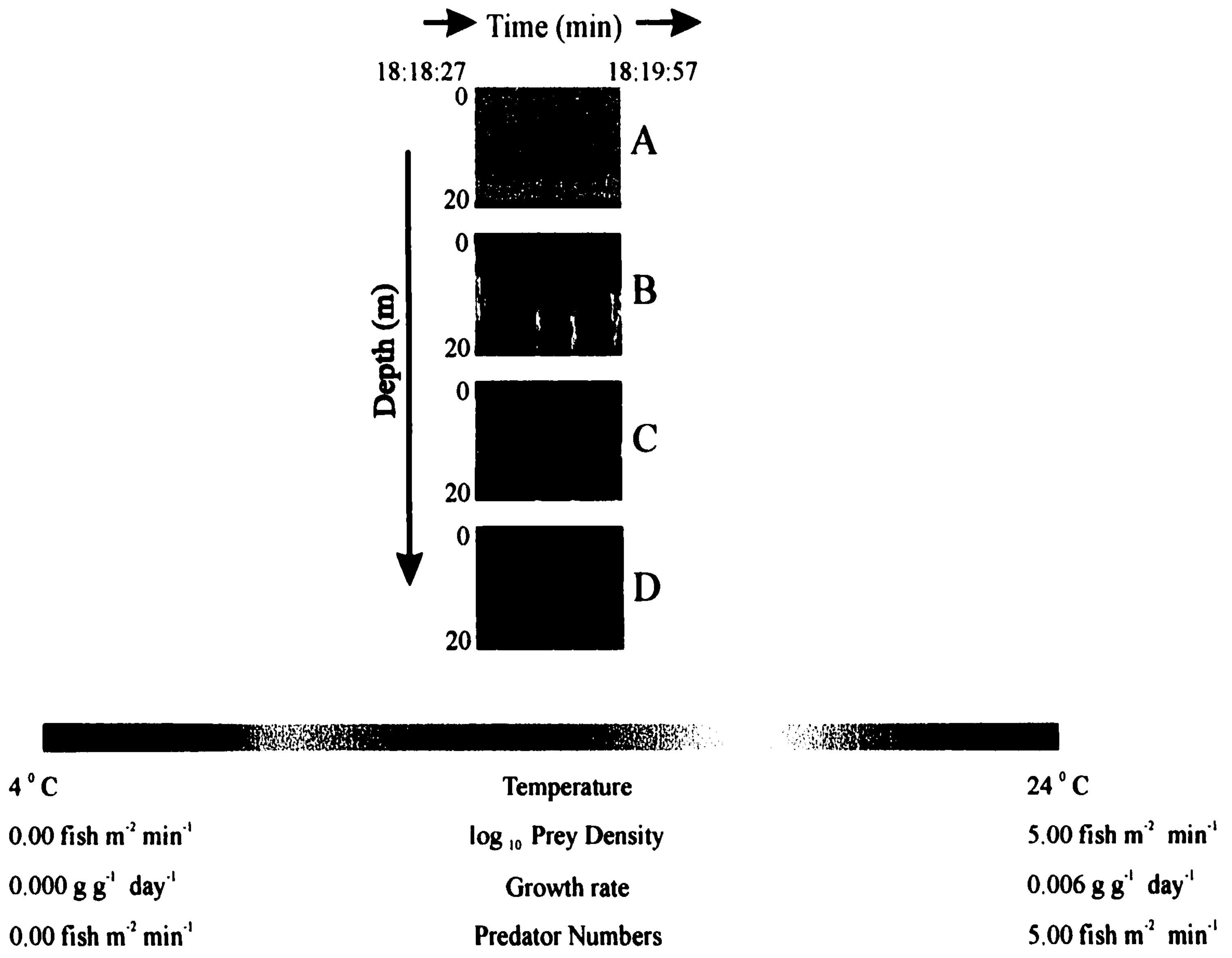
18:18:25
19:07:35
19:15:53
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Figure 3.23 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the dusk (*18:27-19:57*) of October 18, 1997 in western Lake Ontario.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18:19:57
Depth (m)
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m^{-2} min^{-1}
log $_{10}$ Prey Density
5.00 fish m^{-2} min^{-1}
0.000 g g^{-1} day^{-1}
Growth rate
0.006 g g^{-1} day^{-1}
0.00 fish m^{-2} min^{-1}
Predator Numbers
5.00 fish m^{-2} min^{-1}

Figure 3.24 — The evolution of temperature (A), acoustically derived distribution of prey (alewife; *Alosa pseudoharengus*; B), growth rate potential of a 512 g (300mm) chinook salmon (*Oncorhynchus tschwytcha*; C), and acoustically derived chinook distribution (D) during the night (*00:26-06:01*) of October 19, 1997 in western Lake Ontario.

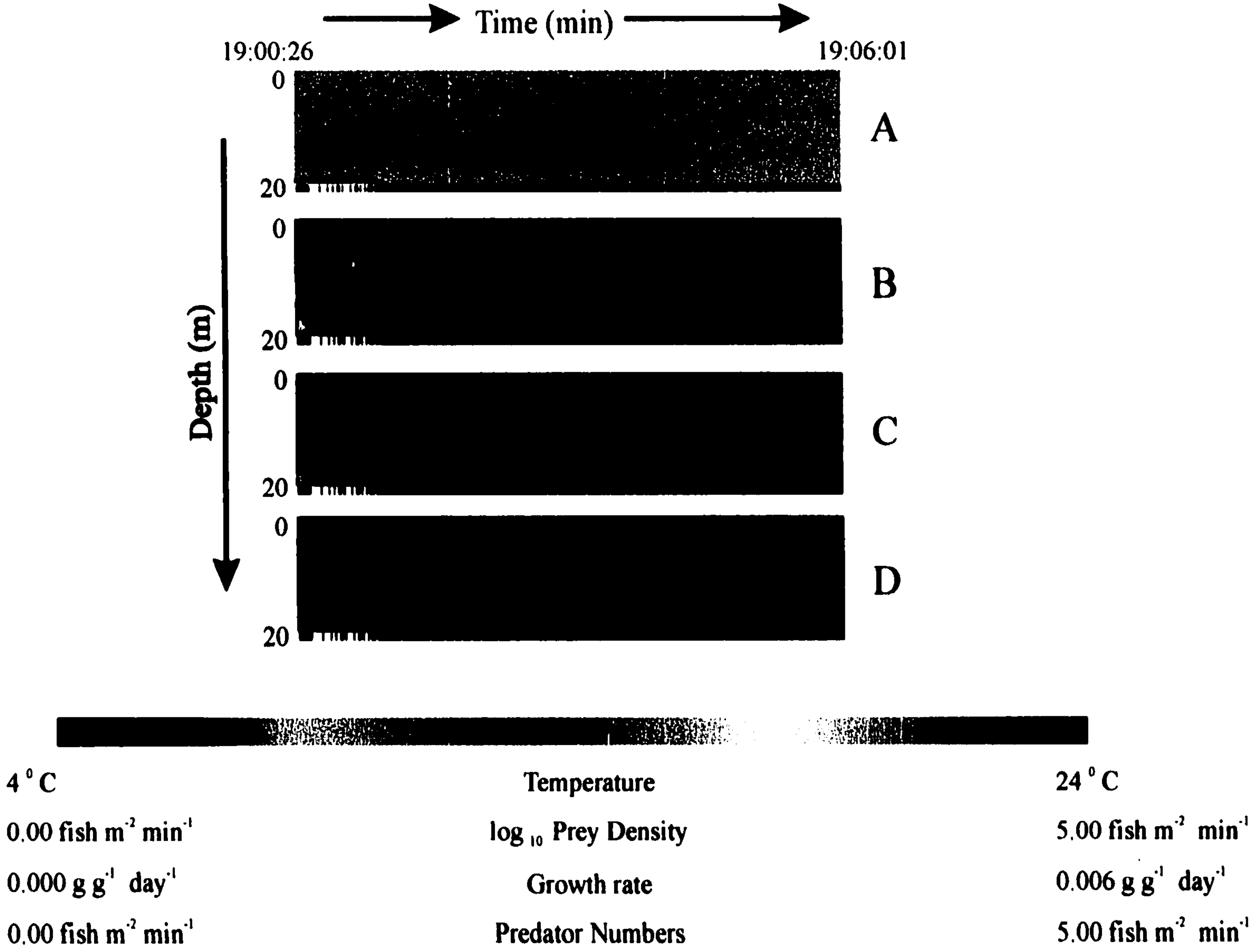
Time (min)
19:00:26
19:06:01
Depth (m)
0
20
0
20
0
20
0
20
A
B
C
D
4 °C
Temperature
24 °C
0.00 fish m-2 min-1
log 10 Prey Density
5.00 fish m-2 min-1
0.000 g g-1 day-1
Growth rate
0.006 g g-1 day-1
0.00 fish m-2 min-1
Predator Numbers
5.00 fish m-2 min-1

Table 3.1 — Pearson correlation coefficient (supported by 10 000 Mantel randomizations) calculated to establish the degree of congruence between monitored environmental conditions and actual Chinook salmon distribution in western Lake Ontario during the May, 1997, 24 hr sampling period.

Time Interval	Environmental Condition	r	Associated p-value	Best Association
	Opt. Temp.	0.043	0.0503	**GRP**
Dawn	Prey Density	0.103	0.0136	Prey Density
	GRP	0.280	0.0001	*Opt. Temp.
	Opt. Temp.	0.020	0.0151	**Prey Density**
Day	Prey Density	0.186	0.0006	GRP
	GRP	0.131	0.0001	Opt. Temp.
	Opt. Temp.	0.000	0.0000	Not Distinguishable
Dusk	Prey Density	0.000	0.0000	
	GRP	0.000	0.0000	
	Opt. Temp.	0.053	0.0001	**Opt. Temp.**
Night	Prey Density	0.013	0.0297	GRP
	GRP	0.045	0.0094	Prey Density

Bold - highest association, Underlined - second highest association, and * not significant at the $\alpha=0.05$ level.

Table 3.2 — Pearson correlation coefficient (supported by 10 000 Mantel randomizations) calculated to establish the degree of congruence between monitored environmental conditions and actual Chinook salmon distribution in western Lake Ontario during the June, 1997, 24 hr sampling period.

Time Interval	Environmental Condition	r	Associated p-value	Best Association
Dawn	Opt. Temp.	0.107	0.0000	**GRP**
	Prey Density	0.112	0.0068	Prey Density
	GRP	0.144	0.0000	Opt. Temp.
Day	Opt. Temp.	0.036	0.0001	**GRP**
	Prey Density	0.129	0.0002	Prey Density
	GRP	0.186	0.0000	Opt. Temp.
Dusk	Opt. Temp.	0.000	0.0000	Not Distinguishable
	Prey Density	0.000	0.0000	
	GRP	0.000	0.0000	
Night	Opt. Temp.	0.053	0.0000	**Opt. Temp.**
	Prey Density	0.008	0.0499	GRP
	GRP	0.049	0.0000	Prey Density

Bold - highest association, Underlined - second highest association, and * not significant at the $\alpha=0.05$ level.

Table 3.3 — Pearson correlation coefficient (supported by 10 000 Mantel randomizations) calculated to establish the degree of congruence between monitored environmental conditions and actual Chinook salmon distribution in western Lake Ontario during the July, 1997, 24 hr sampling period.

Time Interval	Environmental Condition	r	Associated p-value	Best Association
Dawn	Opt. Temp.	0.009	0.2533	**GRP**
	Prey Density	0.068	0.0178	Prey Density
	GRP	0.083	0.0016	*Opt. Temp.
Day	Opt. Temp.	0.192	0.0000	**GRP**
	Prey Density	-0.003	0.5655	Opt. Temp.
	GRP	0.213	0.0000	*Prey Density
Dusk	Opt. Temp.	-0.011	0.6005	**GRP**
	Prey Density	0.037	0.0775	*Prey Density
	GRP	0.071	0.0060	*Opt. Temp.
Night	Opt. Temp.	-0.038	0.9994	**GRP**
	Prey Density	0.068	0.0034	Prey Density
	GRP	0.096	0.0000	*Opt. Temp.

Bold - highest association, Underlined - second highest association, and * not significant at the $\alpha=0.05$ level.

Table 3.4 — Pearson correlation coefficient, supported by Mantel randomizations (10000), calculated to establish the degree of congruence between monitored environmental conditions and actual Chinook salmon distribution in western Lake Ontario during the September, 1997, 24 hr sampling period.

Time Interval	Environmental Condition	r	Associated p-value	Best Association
Day	Opt. Temp.	-0.001	0.0013	**GRP**
	Prey Density	-0.003	0.0247	<u>Prey Density</u>
	GRP	0.025	0.0253	Opt. Temp.
Dusk	Opt. Temp.	0.000	0.0000	Not Distinguishable
	Prey Density	0.000	0.0000	
	GRP	0.000	0.0000	
Night	Opt. Temp.	0.046	0.0067	**Opt. Temp.**
	Prey Density	-0.002	0.9986	*<u>Prey Density</u>
	GRP	0.000	0.2038	*GRP

Bold - highest association, <u>Underlined</u> - second highest association, and * not significant at the $\alpha=0.05$ level.

Table 3.5 — Pearson correlation coefficient (supported by 10 000 Mantel randomizations) calculated to establish the degree of congruence between monitored environmental conditions and actual Chinook salmon distribution in western Lake Ontario during the October, 1997, 24 hr sampling period.

Time Interval	Environmental Condition	r	Associated p-value	Best Association
	Opt. Temp.	0.000	0.0000	Not
Dawn	Prey Density	0.000	0.0000	Distinguishable
	GRP	0.000	0.0000	
	Opt. Temp.	0.000	0.0000	Not
Day	Prey Density	0.000	0.0000	Distinguishable
	GRP	0.000	0.0000	
	Opt. Temp.	0.000	0.0010	**GRP**
Dusk	Prey Density	0.032	0.0850	Opt. Temp.
	GRP	0.200	0.0010	*Prey Density
	Opt. Temp.	0.000	0.0000	Not
Night	Prey Density	-0.001	0.8038	Distinguishable
	GRP	0.005	0.0600	

Bold - highest association, Underlined - second highest association, and * not significant at the $\alpha=0.05$ level.

Table 3.6 — Pearson correlation coefficient (supported by 10 000 Mantel randomizations) calculated to establish the degree of congruence between monitored environmental conditions and actual Chinook salmon distribution in western Lake Ontario during the 1997 growing season.

Time Interval	Environmental Condition	r	Associated p-value	Best Association
May	Opt. Temp.	0.001	0.0004	**Prey Density**
	Prey Density	0.101	0.0013	GRP
	GRP	0.100	0.0000	Opt. Temp.
June	Opt. Temp.	0.041	0.0000	**GRP**
	Prey Density	0.080	0.0005	Prey Density
	GRP	0.127	0.0000	Opt. Temp.
July	Opt. Temp.	0.141	0.0000	**Opt. Temp.**
	Prey Density	-0.001	0.3971	GRP
	GRP	0.113	0.0000	*Prey Density
September	Opt. Temp.	-0.001	0.3310	Not Distinguishable
	Prey Density	-0.002	0.2676	
	GRP	-0.002	0.2678	
October	Opt. Temp.	0.000	1.0000	**GRP**
	Prey Density	0.025	0.0101	Prey Density
	GRP	0.148	0.0001	*Opt. Temp.

Bold - highest association, Underlined - second highest association, and * not significant at the $\alpha=0.05$ level.

Discussion

Seasonal habitat preference

Seasonally, no pattern of chinook habitat preference was evident in this study. During each sampling event throughout the growing season (May, June, July, September, and October), a different environmental condition best described chinook salmon distribution at the sampling station, except for June and October which were both best described by chinook growth rate potential (see Table 3.6). These seasonal shifts in chinook distribution can be attributable to two principal causes. The first is that the environment in which chinook are located, changes at the seasonal scale of observation. Boyce et al., (1991), and Simons and Schertzer (1987), both described the seasonal spatial dynamics of water column temperature fluctuations in Lake Ontario. Hondorp (1998), and O'Gorman et al., (1997), also demonstrated seasonal changes in the spatial arrangement of alewife density in this ecosystem. The previous chapter (chapter II), and Goyke and Brandt (1993), meanwhile, demonstrated seasonal variation in the spatial pattern of chinook salmon growth rate potential in this same system. Thus, even if chinook were tracking one particular environmental condition throughout the growing season such as optimal temperature, for example, their distributions would change at this temporal scale of observation simply because the spatial arrangement of water temperature also changes.

The second factor potentially regulating changes in chinook distribution is the relative importance of particular environmental conditions to chinook (Matthews 1990). If, for example, chinook are hungry, food becomes a priority, and their distribution can reflect this need by being highly associated with areas of highest prey densities (optimal foraging theory). When chinook are not hungry, their distribution may be more highly associated with environmental conditions other than prey distributions. Thus, the needs of chinook also change over time causing them to shift their distributions within the environment to fulfill these needs.

Matthews (1990), suggests that these types of shift in environmental conditions and habitat requirements may explain seasonal distribution patterns of many rockfish species (*Sebastes spp*) occurring on different types of reefs along the west coast of North America. Heggenes et al ., (1991) offer similar reasoning to explain shifts in the seasonal distribution of cutthroat trout (*Oncorhynchus clarki*) in small coastal streams.

The absence of consistency in chinook habitat preference in terms of optimal temperature, prey density, and growth rate potential, suggests that chinook were not invariably tracking one of these particular environmental conditions throughout the growing season, and that the relative importance of these particular environmental conditions changes at this temporal scale of observation. Thus measurement of habitat preference, and by proxy the relative importance of monitored environmental conditions made during one particular sampling event within the growing season, is not necessarily representative of the habitat preference occurring over the entire growing season.

Diel habitat preference

On a daily time scale, the pattern of chinook habitat preference was different from that observed on a seasonal scale. Chinook habitat preference was variable within most sampling events except during July when actual chinook distribution was best described by growth rate potential for all time periods (Dawn, Day, Dusk, and Night; Tables 3.1-

3.5). Again, the variability in chinook habitat preference on a daily time scale can be attributed to the same principal causes; changing environmental conditions, and shifts in daily habitat requirements by chinook.

Boyce et al.,(1991) describe how water column temperature structure can change on a daily scale. Janssen and Brandt (1980), and Urban and Brandt (1993), both describe diel changes in alewife vertical distribution in both Lakes Michigan and Ontario respectively. The previous chapter demonstrated diel changes in the spatial distribution of chinook growth rate potential at my sampling station in western Lake Ontario. Thus, the environmental conditions monitored in this study have been known to change on a daily time scale as well as on seasonal time scale.

Previous studies have also demonstrated diel changes in habitat requirements of many fish species including salmonids. For example, Clark and Levy (1988), and Levy (1991; 1990), contend that the diel vertical migration pattern of sockeye and kokanee salmon (*Oncorhynchus nerka*) in several British Columbia lakes can be attributed to trade-offs between predation pressure, food availability and bioenergetics which shift on a daily time frame. Similarly, Bourke et al., (1996), reasoned that shifts in the diel distribution of brook charr (*Salvelinus fontinalis*) in several study lakes in the Mastigouche Reserve in Quebec, Canada is a result of increased food availability during night periods. Brook charr in these lakes migrate and feed nocturnally, returning to digestion and growth conducive temperatures during the day. This shift in diel distribution pattern reflects the changing habitat requirments of these particular salmonids throughout the diel cycle. Thus changes in distribution and in turn habitat preference due to both fluctuating environmental conditions and transient habitat requirements by fish on a diel time scale are not unprecedented.

In this study, chinook growth rate potential was most often the best descriptor of actual chinook distribution at my sampling station over a diel time frame (Tables 3.1-3.5). This suggests that at this time scale of observation chinook most often preferred areas of the water column which were favourable for growth rather than those characterized by optimal temperatures or highest prey densities. This conclusion, however, is by no means absolute as the relative importance of chinook growth rate potential was frequently less than that of the other environmental conditions monitored.

In addition, the relative importance of all 3 monitored environmental conditions was frequently indistinguishable during particular time periods due to the lack of chinook occurring in the water column during these times (for example see Figure 3.21-3.22 and Table 3.5). This could indicate that during these particular time periods, chinook habitat preference may be determined by other environmental conditions not monitored during this study. Alternatively, time periods with no distinguishable chinook habitat preference may be attributable to the limited spatial extent of this study. During these particular periods, chinook may prefer habitat located outside of this study's spatial range.

Thus, although chinook growth rate potential best described actual chinook distributions more often than other monitored environmental conditions, variability in the relative importance of these particular conditions brings into question their predictive power in determining chinook habitat preference on a diel scale of observation. This leads to the conclusion that the quatification of the relative importance of the monitored environmental conditions to, and thus habitat preference of, chinook salmon at my sampling station in western Lake Ontario, over a short time period within 24 hours is not necessarily representative of that occurring over the entire 24 hour period.

Scaling

Another important consideration is the confounding effect of the chosen temporal scale on the observed pattern of chinook habitat preference. In this study, chinook habitat preference observed at the seasonal scale did not correspond to that observed at the shorter diel scale. For example, chinook habitat preference considered on a diel scale in July is best described by chinook growth rate potential during all time periods (dawn, day, dusk, and night), indicating a preference for areas supporting positive chinook growth. Meanwhile, on a seasonal scale which considers the entire July sampling event as a whole, chinook habitat preference was best described by optimal temperatures (see Tables 3.3 & 3.6). The disparity in chinook habitat preference occurring at the seasonal and diel time scales supports the hypothesis that different habitat requirements may be operating to regulate species distribution at different spatio-temporal scales of observation (Goyke and Brandt 1993). Many studies have shown that patterns in ecology are intimately linked to the spatio-temporal scale of observation (Hondorp 1998; Sale 1998; Pearson et al., 1995; Holling 1992; Levin 1992; Lawton 1987; Legendre and Demers 1984; Harris 1980; Stommel 1963).

For example, Thomas (1991) found that yearly estimates of variation among butterfly (*Plebejus argus*) sub-populations fluctuated synchronously. Such synchronous patterns were not observed, however, when the same estimates were made at 3-year intervals. Similarly, Pearson et al., (1995) showed that at the small spatial scale of grazing area, winter foraging patterns of bison (*Bison bison*) in Yellowstone National Park appeared to be random. When the spatial scale of observation was extended to include many such grazing areas, bison foraging became highly associated with recently burned (2-3 years previous) grass fields. Further expansions of the spatial resolution to include 7 500 ha indicated that bison grazing typically occurred on southern-facing slopes of large hills, where snow accumulation and density is less (Pearson et al., 1995). Both studies mentioned above demonstrate that the perception of patterns in ecology is scale-dependent.

Thus, caution should be exercised when attempting to characterize ecological patterns, so as to explicitly state the spatio-temporal scale at which these patterns are observed. More often than not, patterns observed, and conclusions derived at one scale cannot be easily applied, or extrapolated to others.

Limitations

Perhaps the largest handicap of this study is its lack of spatial coverage or extent. Many studies have demonstrated the inherent variability of aquatic environments through space (Hondorp 1998; Brandt 1993; Brandt et al., 1992; Nero et al., 1990; Mc Eadie and Keast 1984; Lasker 1978). Yet, this study bases its conclusions on the results obtained from a single sampling location in the south-western region of the Lake Ontario system. Prevailing environmental conditions at the chosen sampling site may be radically different from conditions at other sites within this system. Similarly, the patterns observed and the derived conclusions of this study describe chinook habitat preference only at the chosen spatial scale, yet, it is very likely that different chinook habitat preference rules operate at different spatial scales of observation.

Another limiting factor is the relatively small number of environmental parameters considered to influence chinook distribution. Several studies have shown that fish distributions can also be influenced by a myriad of other environmental factors such as turbulence, dissolved oxygen, in stream vegetation concentration, depth, and others (Hondorp 1998; Gadomski and Barfoot 1998; Levin et al., 1997; Eklöv and Presson 1996; Gregory and Levings 1996; Burke 1995; Levin 1994; Mason and Patrick 1993; Levy 1991; 1990; Clark and Levy 1988; Crowder and Magnuson 1983; Janssen and Brandt 1980; Brett 1971;1952; Wells 1968). The inclusion of more environmental parameters in this type of habitat preference study could enhance the predictability of species-specific habitat preferences, and could lead to a better understanding of the importance of these factors in regulating fish distributions over time.

The use of temporally explicit models of fish growth rates (see chapter II) also limits the applicability of this study. Temporally explicit models of fish growth rates are parameter intense, at times including up to 30 different parameters each with its own associated error (see chapter II). When these parameters are used in concert, the variability associated with each parameter adds to the overall error term of the model. This accumulated error can be very large consequently limiting the predictive power of the model, and bringing into question its overall usefulness (Hansen et al., 1993; Ney 1993; Ney 1990).

Implications

Chinook habitat preference in this study demonstrates that at both the seasonal and diel scales of observation, actual chinook distribution was seldomely best described by areas of highest prey densities. This has major implications in terms of the trophic cascade theory and the use of biomanipulation as a management tool. The trophic cascade theory describes how changes in the abundance of top predators within an aquatic ecosystem can be reverberated through the food web to influence the production at lower trophic levels, ultimately causing variability in Chlorophyll concentrations, primary productions, and water quality (Carpenter 1989; Carpenter and Kitchell 1988; Carpenter et al., 1985). Biomanipulation typically bases management strategies of aquatic systems based on the trophic cascade theory. Several studies provide variable evidence for the existence of such trophic cascades in many different types of aquatic ecosystems (for review see McQueen et al ., 1989; McQueen 1990; and DeMelo et al., 1992).

A major tenet of the trophic cascade theory and its biomanipulation counter-part, however, is the tight linkage between adjacent trophic levels, especially at the top piscivore-planktivore level (Carpenter et al., 1985; McQueen 1990). Indeed, much of community and population ecological theory relies on the principle of tight coupling between predator-prey populations within ecosystems (Carpenter and Kitchell 1988; Holt 1977; Gilpin 1972; Rosenzweig and MacArthur 1963; Volterra 1926; Lotka 1925).

The results presented in this study, however, suggest that even at the top of the trophic cascade, predator-prey dynamics may not be so tightly linked as previously thought. At both time scales of observation, I demonstrate that chinook do not always prefer regions of the water column containing the densest aggregations of prey. If any pattern is evident, it is at the short, diel scale where chinook distribution is more readily described by growth rate potential. This indicates that factors other than prey density alone contribute in dictating chinook distribution at this time scale, and that top piscivores, such as chinook, are not simply selecting their habitat based on a need to find prey. Even in a relatively straight forward system like Lake Ontario with a well established salmonid predator base and alewife prey supply, predator-prey interactions are much more complex than that predicted by the trophic cascade hypothesis. Both Goyke and Brandt (1993), and Hondorp and Brandt (1996), argue that the amount of prey available to predators in an aquatic system is not merely reliant on the abundance of prey within this system, but rather on the degree of overlapping habitat range between the predator and its prey. Other habitat requirements such as temperature, and dissolved oxygen, effectively restrict the amount of prey available to predators. Thus, predator-prey interactions are not only dependent on the abundance of both within an ecosystem, but on a plethora of external conditions both biotic and abiotic in nature, which limit the extent to which predators can control and impact their prey populations.

The lack of tight coupling between adjacent trophic levels brings in question the predictive power of the trophic cascade theory and the use of biomanipulation as a management tool. This lack of predictive power prevents the quantification of impacts derived from biomanipulative management options. For example, what does a two-fold increase in piscivorus top predators relate to in terms of planktivore populations, zooplankton assemblages, phytoplankton and eventually primary production? The quantitative aspects of these relationship continue to elude this type of management practice (DeMelo et al., 1992; McQueen 1990).

In a review of many biomanipulation studies, McQueen et al., (1989), revealed that in several circumstances, shifts in top-predator abundances show only limited impacts on lower trophic levels. In certain instances, there was no evidence of interaction beyond the level of the top, piscivorus predators and their planktivorus prey. Other studies showed evidence of a reversed trophic cascade where the physico-chemical inputs into an aquatic ecosystem can influence production at all trophic levels starting from the most basic primary production, extending all the way to top predators (for review see McQueen et al., 1986). Again, however, McQueen et al., (1989) argued that the influence of these bottom-up forces on trophic cascades were also limited and could, at times, be restricted to only the very basic nutrient-phytoplankton levels. These authors contended that the extent to which both top-down, bottom-up forces exert their influence on the trophic cascade depends on the unique trophic status of the system (McQueen et al., 1986; McQueen et al., 1989).

Scheffer (1991), pushes this 'unique status' argument even further by stating that two systems, exactly alike in terms of trophic cascades, containing the same species assemblages, and with all environmental influences removed, will not exhibit similar trophic interactions among trophic levels. Scheffer (ibid), argues that each system is unique in terms of its starting points at all trophic levels and the inherent chaotic fluctuations between each adjacent level will result in a system specific trophic network which cannot be easily be classified or categorized. Thus although there is evidence which supports the existence of trophic cascades within aquatic systems, system wide manipulations based on this theory should also consider the genuine aspects of each system and the degree to which trophic cascades can account for the variability of the trophic levels within it.

Conclusion

Fish distribution within aquatic systems can be highly variable, and the sources of these variations are diverse. However, it is important to realize that these variations are not only attributable to transient environmental conditions, but also to the way fish respond to these transient conditions at different times. Fish distributions, therefore, not only depend on the prevailing environmental conditions at a particular time, but also on what the fish needs. This study emphasizes the need to consider both changing conditions and their relative importance when assessing fish habitat preferences. This study also provides a framework that allows the quantification of the relative importance of environmental conditions as they relate to fish distribution in a dynamic environment and at a variety of time scales.

References

Bodwitch, N. 1982. American Practical Navigator. Vol 2. An Epitome of Navigation. Defense Mapping Agency, Hydrographic/Topographic Center, Washington, D.C.

Bourke. P., P. Magnan, and M. Rodriguez. 1996. Diel locomotor activity of brook charr, as determined by radiotelemetry. *Journal of Fish Biology*. 49:1174-85.

Boyce, F., W. Schertzer, P. Hamblin, and C. Murthy. 1991. Physical behaviour of Lake Ontario with reference to contaminant pathways and climate change. *Can. J. Fish. Aquat. Sci.* 48:1517-28.

Brandt, S. 1996. Acoustic assessment of fish abundance and distribution. Chapter 13 in Fisheries Technologies. 2nd ed. B. Murphy, and D. Willis eds. American Fisheries Society publication. Bethesda. Maryland.

Brandt, S. 1993. Effect of thermal fronts on fish growth:a bioenergetics evaluation of food and temperature. *Estuaries*. 16(1):142-59.

Brandt, S., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Trans. Amer. Fish. Soc.* 122:845-69.

Brandt, S., D. Mason, and E. Patrick. 1992. Spatially-explicit models of fish growth rate. *Fisheries*. 17(2):23-35.

Brandt, S., and six co-authors. 1991 .Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 48:894-908.

Brett, J. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zoologist*. 11:99-113.

Brett, J. 1952. Temperature tolerance in young pacific salmon, genus *Oncorhynchus*. *J. Fish. Res. Bd. Can.* 9(6):265-309.

Burke, J. 1995. Role of feeding and prey distribution of summer and southern flounder in selection of estuarine nursery habitats. *Journal of Fish Biology*. 47:355-66.

Carpenter, S. 1989. Replication and treatment strength in whole-lake experiments. *Ecology*. 70(2):453-63.

Carpenter, S., and J. Kitchell. 1988. Consumer control of lake productivity. *BioScience*. 38(11):764-69.

Carpenter, S., J. Kitchell, and J. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience*. 35(10):634-39.

Clark, C., and D. Levy. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. *Am. Nat.* 131(2):271-90.

Clay, C., amd J. Horne. 1994. Acoustic models of fish: the Atlantic cod (Gadus morhua). *J. Acoust. Soc. Am.* 75:1077-83.

Combreau, O., and T. Smith. 1997. Summer habitat selection by houbara bustards introduced in central Saudi Arabia. *Journal of Arid Environments*. 36:149-60.

Crowder, L., and J. Magnuson. 1983. Cost-benefit analysis of temperature and food resource use: A synthesis with examples from the fishes. In Behavioral Energetics: The cost of survival in vertebrates. W. Aspey, and S. Lustick eds. Ohio State University Press. Columbus.

DeMelo, R., R. France, and D. McQueen. Biomanipulation: Hit or myth? *Limnol. Oceanogr.* 37(1):192-207.

Eklöv, P., and L. Presson. 1996. The response of prey to the risk of predation: proximate cues for refuging juvenile fish. *Anim. Behav.* 51:105-15.

Gilpin, M. 1972. Enriched predator-prey systems: Theoretical stability. *Science*. 177:902-4.

Godomski, D., and C. Barfoot. 1998. Diel and distributional abundance patterns of fish embryos and larvae in the lower Columbia and Deschutes rivers. *Enverionmental Biology of Fishes*. 51:353-68.

Goyke, A., and S. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. *Trans. Am. Fish. Soc.* 122:870-83.

Gregory, R., and C. Levings. 1996. The effects of turbidity and vegetation on the risk of juvenile salmonids, *Oncorhynchus* spp., to predation by adult cutthroat trout, *O. clarkii. Environmental Biology of Fishes*. 47:279-88.

Haila, Y., A. Nicholls, I. Hanski, and S. Raivio. 1996. Stochasticity in bird habitat selection: year-to-year changes and territory location in a boreal forest bird assemblage. *Oikos*. 76:536-52.

Hansen, M., and six co-authors. 1993. Applications of bioenergetics models to fish ecology and management: Where do we go from here? *Trans. Am. Fish. Soc.* 122:1019-30.

Harris, G. 1980. Temporal and spatial scales in phytoplankton ecology, mechanisms, methods, and management. *Can. J. Fish. Aquat. Sci.* 37:877-900.

Hastings, A. 1998. Transients in spatial ecological models. *In* J. Bascompte, and R. Solé. Eds. Modeling spatiotemporal dynamics in ecology. Springer-Verlag. Berlin.

Heggenes, J., T. Northcote, and A. Peter. 1991. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. *Can. J. Fish. Aquat. Sci.* 48:1364-70.

Holling, C. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* 62(4):447-502.

Holt, R. 1997. From Metapopulation dynamics to community structure: Some consequences of spatial heterogeneity. In Metapopulation Biology, Ecology, Genetics, and Evolution. I. Hanski, and M. Gilpin eds. Academic Press. San Diego.

Hondorp, D. 1998. Spatial distributions of planktivorous fish and zooplankton in western Lake Ontario: Implications for fish thermal ecology, fish bioenergetics modeling and trophic interactions. M. Sc. thesis State Univ. New York Coll. Buff. New York. 126 p.

Hondorp, D., and S. Brandt. 1996. Spatially-explicit models of fish growth rate: Tools for assessing habitat quality. *Great. Lak. Res. Rev.* 2(2):11-19.

Horne, J., and C. Clay. 1998. Sonar systems and aquatic organisms: matching equipment and model parameters. *Can. J. Fish. Aquat. Sci.* 55:1296-1306.

Jackson, D., and K. Somers. 1989. Are probability estimates form the permutation model of Mantel's test stable? *Can. J. Zool.* 67:766-69.

Janssen, J., and S. Brandt. 1996. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 37:177-84.

Jech, J., and J. Luo. 1998. Digitial Echo Visualization and Information System (DEVIS) for processing spatially-explicit fisheries acoustic data. Submitted manuscript, *Fisheries Oceanography.*

Jones, M., and E. Boulding. 1999. State-dependent habitat selection by an intertidal snail: the cost of selecting a physically stressful microhabitat. *Mar. Ecol. Prog. Ser.* In press.

Krebs, J., and A. Kacelnik. 1993. Decision-making. *In* J. Krebs, and N. Davies. Eds. Behavioural Ecology: An evolutionary approach. 3rd edition. Blackwell Scientific Publications. Oxford.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. *Rapp. P. -v. Réun. Cons. int. Explor. Mer.* 173:212-30.

Lawton, J. 1987. Problems of scale in ecology. *Nature.* 325:206.

Legendre, L., and S. Demers. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.* 41:2-19.

Levin, P., R. Petrik, and J. Malone. 1997. Interactive effects of habitat selection, food supply, and predation on recruitment of an estuarine fish. *Oecologia.* 112:55-63.

Levin, P. 1994. Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Environmental Biology of Fishes.* 40:271-81.

Levin, S. 1992. The problem of patterns and scale in ecology. *Ecology.* 73(6):1943-67.

Levy, D. 1991. Acoustic analysis of diel vertical migration behavior of *Mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. *Can. J. Fish. Aquat. Sci.* 48:67-72.

Levy, D. 1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia Lakes. *Can. J. Fish. Aquat. Sci.* 47 1755-64.

Lotka, R. 1925. Elements of physical biology. Williams & Wilkins, Baltimore.

MacLennan, D., and J. Simmonds. 1992. Fisheries Acoustics. Chapman Hall. London.

Mäki-Petäys, A., T. Muotka, A. Huusko, P. Tikkanen, and P. Kreivi. 1997. Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. *Can. J. Fish. Aquat. Sci.* 54:520-30.

Mason, D., and S. Brandt. 1996. Effects of spatial scale and foraging efficiency on the predictions made by spatially explicit models of fish growth rate potential. *Environmental Biology of Fishes.* 45:283-98.

Mason, D., and E. Patrick. 1993. A model for the space-time dependence of feeding for pelagic fish populations. *Trans. Amer. Fish. Soc.* 122:884-901.

Matthews, K. 1990. Environmental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (*Sebastes* spp.). *Environmental Biology of Fishes*. 29:161-78.

Mc Eadie, J., and A. Keast. 1984. Resource heterogeneity and fish species diversity in lakes. *Can. J. Zool.* 62:1689-95.

McQueen, D. 1990. Manipulating lake community structure: where do we go from here. *Freshwater Biology*. 23:613-20.

McQueen, D., M. Johannes, J. Post, T. Stewart, and D. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.* 59(3):289-309.

McQueen, D., J. Post, and E. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43:1571-81.

Mixter, G. 1966. Primers of Navigation. 6th edition. Van Nostrand, Reinhold.

Nero, R., J. Magnuson, S. Brandt, T. Stanton, and J. Jech. 1990 . Finescale biological patchiness of 70 kHz acoustic scattering at the edge of the Gulf Stream—EchoFront 85. *Deep-Sea Research*. 37(6):999-1016.

Ney, J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Trans. Amer. Fish. Soc.* 122:736-48.

Ney, J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences*. 2:55-81.

Nisikawa, U., and S. Nakano. 1998. Temporal variation in foraging group structure of a size-structured stream fish community. *Environmental Biology of Fishes*. 52:357-70.

O'Gorman, R., O. Johannsson, and C. Schneider.1997. Age and growth of alewives in the changing pelagia of lake Ontario, 1978-1992. *Trans. Am. Fish. Soc.* 126:112-26.

O'Gorman, R., R. Bergstedt, and T. Eckert. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978-84. *Can. J. Fish. Aquat. Sci.* 44(Suppl.2):390-403.

Pearson, S., M. Turner, L. Wallace, and W. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecological Applications*. 5(3):744-55.

Post, J., L. Rudstam, and D. Schael. 1995. Temporal and spatial distribution of age 0 fish in Lake Mandota. *Trans. Amer. Fish. Soc.* 124:84-93.

Rosenzweig, M., and R. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *Amer. Nat.* 97:209-223.

Sale, P. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Australian Journal of Ecology.* 23:202-08.

Scheffer, M., 1991. Should we expect strange attractors behind plankton dynamics—and if so, should we bother? *Journal of Plankton Research.*13(6):1291-1305.

Schneider, C., and T. Schaner. 1994. The status of pelagic prey stocks in Lake Ontario in 1993. *In* Lake Ontario Fisheries Unit 1994 Annual Report. New York State Department of Environmental Conservation.

Simons, T., and W. Schertzer. 1987. Stratification, currents, upwelling in Lake Ontario, summer 1982. *Can. J. Fish. Aquat. Sci.* 44:2047-58.

Sokal, R., and F. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Company, New York, NY.

Stewart, D., and M. Iberra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. *Can J. Fish. Aquat. Sci.* 48:909-22.

Stewart, D., J. Kitchell, and L. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Amer. Fish. Soc.* 110:751-63.

Stewart, T., M. Rawson, and J. Bowlby. 1998. Managing the chinook fishery. *Great Lakes Res. Rev.* 3(2):32-34.

Stommel, H. 1963. Varieties of oceanographic experience. *Science* 139:572-76.

Svensson, B. 1999. Environmental hetrogeneity in space and time: patch use, recruitment and dynamics of a rock pool population of a gyrinid beetle. *Oikos.* 84:227-38.

Thomas, C. 1991. Spatial and temporal variability in a butterfly population. *Oecologia* 87:577-80.

Turner, A. 1997. Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources. *Behavioural Ecology.* 8(2):120-25.

Urban, T., and S. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. *Environmental Biology of Fishes*. 36:359-72.

Volterra, V. 1926. Fluctuations in the abundance of species considered mathematically. *Nature*. 118:558-60.

Wallis de Vries, M., and P. Schippers. 1994. Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia*. 100:107-17.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. *Fish. Bull.* 67(1):1-15.

Zar, J. 1984. Biostatistical Analysis 2nd edition. Prentice Hall, Engelwood Cliffs, NJ.

Chapter IV

General Conclusions:

Lake Ontario

The extirpation of the endemic populations of top predators from the Lake Ontario system, including Atlantic salmon (*Salmo salar*), Lake trout (*Salvelinus namaycush*), and the burbot (*Lota lota*) has been attributed to large scale exploitation of these populations from commercial fishing, sea lamprey (*Petromyzon marinus*) predation, and the anthropogenic destruction of natural habitat (Krueger et al., 1995; Steedman et al., 1995; Ferreri et al., 1995).

Early management efforts of this system were geared toward bringing the lake back to pre-settlement conditions (Noakes and Curry 1995). This strategy involved restoring self-sustained populations of the once abundant indigenous top predators in order to recreate a predator community. To this end, fishing moratoria were called preventing further commercial harvests, millions of dollars were spent establishing an elaborate lamprey control network, and natural habitat restoration projects recreated ample natural habitat sites (Krueger et al., 1995; McAughey and Gunn 1995; Noakes and Curry 1995; Edsall and Kennedy 1995). Although these restoration efforts achieved some degree of success, for a brief period the Lake Ontario system was left essentially without a top predator community. This allowed the exotic alewife (*Alosa pseudoharengus*) population to flourish (Stewart and Schaner 1998; Jones et al., 1993).

Introduced to the Great Lakes in the late 1860s, the exotic alewife colonized the lower Great Lakes with relative ease. This colonization was exacerbated by the development of commercial waterways which interconnected the Great Lakes system (O'Gorman and Schneider 1986). The alewife is a highly competitive species capable of displacing other natural forage species (Stewart et al., 1998; Brandt et al., 1987). For example, Brandt et al., (1987), suggest that Lake Ontario alewives not only prey on larval yellow perch (*Perca flavescens*) but also disrupt spawning attempts, and out-compete juveniles for zooplankton prey.

Although the alewife first established itself in Lake Ontario during the 1920s, the lack of top predatory control on the alewives imposed by the extirpation of the top predator community in the early 1960s allowed the alewife to become dominant in the pelagic environment of this system (Stewart and Schaner 1998; Rand et al., 1994; Jones et al., 1993). The alewife population, in the absence of predatory control bloomed and began experiencing density-dependant effects (O'Gorman et al., 1997; Rand et al., 1994). During periods of high density, individual alewife condition decreases making them more susceptible to stress (O'Gorman et al., 1997; Trippel 1995). Indeed, enormous alewife populations are subject to massive die-offs during unusually cold winters (Stewart et al., 1998; O'Gorman et al., 1997; Rand et al., 1994; Jones et al., 1993; Stewart and Iberra 1991).

Such an event occurred in 1976-77, when the winter temperatures were unusually low (Rudstam et al., 1996; Jones 1993; Stewart and Iberra 1991; O'Gorman and Schneider 1986). This massive alewife mortality littered beaches and water front properties, clogged essential water intakes systems, and fouled the water with dead alewife carcasses (Stewart and Schaner 1998). Large die-offs such as this, however, cause intraspecific competition within the alewife population to decrease allowing individual alewife condition to ameliorate. This amelioration of individual alewife health and fitness gives this fish a keen ability to rebound from such massive population reductions (Stewart and Schaner 1998; Stewart and Iberra 1991; O'Gorman and Schneider 1986). In the absence of predation pressure, the alewife population could potentially cycle between good alewife years and periodic overwintering mortality.

In the early 1970s, Lake Ontario managers began stocking pacific salmon, the natural predator of the alewife, into this system. This was done primarily to re-establish predatory control over the abundant alewife population, and to create a substantial recreational fishery for these large fast-growing, predatory fish (Stewart and Schaner 1998; O'Gorman and Schneider 1986). Chinook (*Oncorhynchus tschawytscha*), and coho (*O. Kisutch*) were chosen based on their natural affinity for selecting alewife as prey, and on their natural temperature range matching that of the Lake Ontario annual cycle. Both these factors however, proved only marginally successful in establishing self-sustained pacific salmon populations in this system. Pacific salmon have very limited natural reproduction and recruitment success in the Great Lakes ecosystem. As such, their populations are maintained artificially by annual multi-governmental stocking practices (Stewart and Schaner 1998; Stewart et al., 1998; Rudstam et al., 1996; Goyke and Brandt 1993; Jones et al., 1993).

The creation of this salmonid based recreational fishery brought considerable economical benefit and stability to the Great Lakes region. Over several years, the lucrative nature of this fishery motivated increases in the salmonid stocking rate which reached a pinnacle in 1986 (Elrod and O'Gorman 1991). Stocking rates remained near 1986 levels through the early 1990s, during which research conducted by multi-national agencies indicated substantial declines in alewife abundance estimates (Stewart and Schaner 1998; Elrod and O'Gorman 1991). There is mounting concern that the stocked salmonid predatory demand on alewife in Lake Ontario is too high and cannot be supported by the dwindling alewife population.

This is reminiscent of events occurring earlier this century in Lake Michigan which, until recently, had a similar species assemblage as Lake Ontario (Rudstam et al., 1996; Mason et al., 1995; Rand et al., 1994). In the early 1980s, the Lake Michigan alewife population collapsed rendering the abundant stocked pacific salmonids in a state with very little food. This food shortage manifested itself with decreased abundances, higher incidence of dead and moribund fish, and a higher rate of stress related diseases such as bacterial kidney disease (Stewart et al., 1998; Rudstam et al., 1996; Stewart and Ibarra 1991).

The 1980s alewife collapse significantly altered the Lake Michigan species assemblage. Continual declines in abundance coupled with existing high salmonid demand relaxed the alewife's ability to displace other forage species in this system (Jude et al., 1987; Eck and Wells 1987; Jude and Tesar 1985). Native coregonids such as the bloater (*Coregonus hoyi*) have since replaced the alewife as the dominant prey items in Lake Michigan (Goyke and Brandt 1993; Jude and Tesar 1985). Because salmonids and bloaters typically share substantially less overlapping habitats than do salmonids and alewives, less prey is thought to be available to support salmonid growth (Stewart and

Iberra 1991). This translates to a considerable reduction in potential revenues associated with the salmonid fishery in Lake Michigan.

The recent declines in alewife abundance in Lake Ontario caused considerable concern among Lake Ontario stakeholders who feared a repeat of the Lake Michigan alewife crash. Since 1993, the Lake Ontario management strategy has been to considerably reduce the predatory demand for alewife by curbing salmonid stocking rates. In 1994, estimated alewife annual abundance reached an all time minimum and has remained relatively low since, which prompted further considerations of stocking cuts (Lantry and Schaner 1998; GLFC Lake Ontario meeting 1998, Niagara Falls Ontario; GLFC Lake Ontario meeting 1997, Kingston Ontario).

This has anglers and financial stakeholders of the recreational fishery pitted against managers and scientists who contest that the continuation of large scale stocking efforts without consideration for the forage species abundance will cause a complete collapse of the Lake Ontario sport fishery for salmonids, not unlike the one recently experienced by Lake Michigan. This conjectural issue creates a need to further understand the Lake Ontario environment, and the ability of the stocked fish to make use of it.

Synopsis (Chapter II)

Previous studies have attempted to quantify the suitability of Lake Ontario to support salmonid predators (Rand and Stewart 1998; Rand et al., 1995; Rand et al., 1994; Jones et al., 1993). Most of these studies however, make such assessments by relating the amount of prey produced to the predator demands estimated on a system-wide, annual basis — ignoring the inherent spatio-temporal complexities driving the system (Hondorp 1998; Mason et al., 1995).

More recent studies demonstrate that the ability of large systems like Lake Ontario to support large populations of predators, relies on more than just prey supply, but on a multitude of environmental parameters which have both spatial and temporal dimensions (Hondorp 1998; Horne et al., 1996; Mason et al., 1995; Goyke and Brandt 1993; Brandt et al., 1992). For example, Hondorp (1998), illustrates how the lack of consideration for the spatial heterogeneity of the environment and the response of alewife and zooplankton to this spatially complex system can grossly misrepresent alewife predatory demand and zooplankton supply in western Lake Ontario. Still, even these latter, more refined studies focus more on the spatial aspects of the environment and admit to inadequate temporal coverage (Hondorp 1998; Horne et al., 1996; Mason et al., 1995; Goyke and Brandt 1993).

In the second chapter of this thesis, I developed a hydroacoustic based, temporally explicit modelling framework similar to the spatial framework previously developed by Brandt et al., (1992) to characterize the temporal complexity of Lake Ontario's ability to support chinook salmon (Chapter II). Temporally explicit modelling uses species specific bioenergetically derived measures of growth rate potential as a proxy of species specific habitat quality within a given system (Hondorp and Brandt 1996; Mason and Brandt 1996; Mason et al., 1995; Goyke and Brandt 1993; Brandt and Kirsch 1993; Brandt 1993; Brandt et al., 1992). Growth rate potential is a more appropriate index of habitat quality because it integrates both physical (temperature), and biological (prey abundance) features of the environment as they relate to the physiological demands and constraints of a specific species (Horne et al., 1996; Mason and Brandt 1996; Mason et al., 1995). In the temporally explicit modelling framework, species specific growth rate potential measurements are indexed through time, rather than space, to describe the evolution of species specific habitat quality over a specified time interval (Chapter II). This modelling framework takes into consideration the inherent transient nature of the environment to quantify changes in the species specific habitat suitability through time.

In chapter II, I applied the temporally explicit modelling approach to evaluate the habitat quality of chinook salmon in western Lake Ontario at two time scales of observation. This study demonstrated temporal fluctuations of both water column temperature structure, and alewife abundance and distribution at my sampling station at both the seasonal and diel scales. Because chinook growth rate potential measurements made in this study rely on outputs from foraging and bioenergetic sub-models which incorporate both temperature and prey abundances, it is not astonishing that the derived chinook habitat quality estimates also fluctuated at these time scales.

Overall, I found that chinook habitat quality was best in areas of the water column where chinook optimal temperatures and alewife density overlapped (see results chapter II). This makes sense, as these areas give chinook access to alewife prey, and provide thermal conditions which maximize the transformation of ingested prey into growth. Seasonally, such habitat conditions occurred more frequently during the June and July sampling events. In May, September, and October, however, the ability of the sampled environment to support positive chinook growth was much more sporadic or even absent, indicating that environmental conditions during these sampling periods did not provide good chinook habitat. These results differed from those of Goyke and Brandt (1993) who found chinook growth rate potential and thus habitat quality along a Lake Ontario, cross-lake transect to be maximized during the fall period (October 31-November1) . Goyke and Brandt (ibid), however, used a spatially explicit modelling framework to estimate chinook habitat quality, and as a consequence had better spatial coverage and captured more of the spatial complexity within the Lake Ontario environment than was presented here (chapter II).

Nevertheless, results from both Goyke and Brandt (1993) and my study demonstrate the variability in chinook habitat quality throughout the growing season. This emphasizes the notion that habitat quality assessments made at one time during the growing season may not adequately represent seasonal or annual habitat quality, and thus should not be extrapolated to make annual habitat quality estimates.

Similarly, this study also demonstrated variability in chinook habitat quality at the diel scale. Typically, chinook habitat quality was better and more consistent during the night and crepuscular hours than during the day (chapter II results). This was thought to be related to the diel vertical migration exhibited by the alewife prey. Alewife have been shown to spend daylight hours at near bottom depth, night hours in the mid water region, and, migrate to and fro during crepuscular periods (Urban and Brandt 1993; Janssen and Brandt 1980). Daily fluctuations in the ability of the environment to support positive chinook growth reflected daily changes in alewife distribution and showed that the chinook habitat quality changed significantly at this temporal scale (see results chapter II).

Thus habitat quality estimates based on one specific period during the diel cycle and extrapolated to daily, or longer, time scales may grossly misrepresent the actual ability of a habitat to sustain chinook growth.

In a general sense, I found that the temperature structure of the water column exerted its influence on chinook habitat quality predominantly on a seasonal level, but that alewife abundance and distribution was influential at both seasonal and diel time scales (Chapter II). Thus, chinook habitat quality measured in this study reflected temporal differences in the spatial arrangement of alewives and thermal structure of the sampled environment.

Although this study has a long list of limitations (see Chapter II—discussion) it does provide an initial modelling framework which incorporates transient environmental conditions while quantifying species-specific habitat quality dynamics over time. The temporally explicit modelling framework developed here has many potential applications (see Chapter II—discussion) but has been applied in this study to demonstrate the seasonal and diel variations in Lake Ontario's capacity to support chinook salmon growth.

Synopsis (Chapter III)

In the third chapter, I used the chinook habitat quality (chinook growth rate potential) measurements obtained in the previous chapter (Chapter II), along with other monitored environmental variables, such as temperature and alewife distribution, to assess chinook habitat preference at my sampling station in western Lake Ontario at two time scales. The primary purpose was to determine chinook habitat preference by quantifying the relative importance of the monitored environmental conditions to chinook. This was done by determining which working hypothesis, namely; behavioural thermoregulation, optimal foraging or prey taxis, or behavioural bioenergetics, best described actual chinook distribution over a specified time interval (Chapter I; Chapter III). This study was based on the implicit assumption that actual chinook distribution was indicative of habitat preference at my sampling station (Chapter III).

On a seasonal scale, I demonstrated that chinook distribution and thus habitat preference was variable with no observable pattern. For each sampling event within the growing season, chinook habitat preference was more highly associated with a different environmental condition, except for June and October in which were both best described by chinook growth rate potential (Chapter III — results). The lack of consistency in terms of chinook habitat preference over the growing season was indicative of, chinook salmon at this sampling station not always tracking the same environmental parameter, and the changing relative importance of these environmental conditions to chinook at this temporal scale (Chapter III — discussion). Therefore, I contend that habitat preference, and the relative importance of different environmental conditions to chinook, determined during one sampling event during the growing season is not necessarily reflective of that occurring during other sampling events, or of that occurring throughout the growing season.

At the diel scale of observation, the pattern of chinook habitat preference and the relative importance of monitored environmental conditions was quite different. Within most 24 hour periods, chinook habitat preference was variable except during July when chinook growth rate potential best described actual chinook distribution during all time periods (dawn, day, dusk, and night) (Chapter III — results). Again, this was attributed to both the changing environmental conditions and the changing relative importance of these conditions to chinook at my sampling station. Over all time periods within 24 hours, however, chinook growth rate potential was most often the best descriptor of chinook habitat preference, indicating that chinook most often preferred areas of the water column where growth was maximized at this temporal scale (Chapter III). This conclusion, however, is by no means absolute as the relative importance of other environmental conditions were frequently higher than those of chinook growth rate potential.

Furthermore, on several occasions, the relative importance of all three monitored environmental conditions were indistinguishable due to an absence of chinook within the water column. During these particular periods, chinook distribution may have been determined by other factors not monitored in this study and/or by factors acting outside this study's spatial range. Thus, although chinook growth rate potential was most often the best descriptor of chinook habitat preference, the variability in this parameter, at this scale, remained high inhibiting my ability to draw predictions from it (Chapter III — discussion). Therefore, habitat preference of, and the relative importance of environmental conditions to chinook at one time during a typical 24 hours, is not necessarily representative of that occurring at other times within, or for the entirety of, the 24 hour period (Chapter III).

In this study I also demonstrated confounding patterns observed at different temporal scales of observation. Chinook habitat preference perceived at the seasonal scales was often dramatically different from that observed at the diel scale (see Chapter III — discussion). The notion of the confounding effects of spatio-temporal scales on observed patterns is a well documented concept in the literature (Hondorp 1998; Sale 1998; Pearson et al., 1995; Holling 1992; Levin 1992; Lawton 1987; Legendre and Demers 1984; Harris 1980; Lasker 1978). As such, caution should be exercised in any study attempting to describe ecological patterns so as to explicitly state the spatio-temporal scale of the observed patterns. Patterns observed at one scale frequently cannot be easily applied to larger or smaller scales.

This study provides an initial framework allowing both the assessment of species specific habitat preferences, and the quantification of the relative importance of monitored environmental conditions to a chosen species. However, it is not without several caveats which can potentially limit its application (see Chapter III — discussion).

The overall results presented in this chapter, demonstrate that chinook habitat preference not only depends on temporally dynamic environmental conditions within an ecosystem but also on its predominant habitat requirements. When chinook are too warm, they find cooler water. This state dependent habitat preference, or selection, imposes constraints on the ability of chinook to consistently forage for their prey. This has major implications in terms of predator-prey dynamics within large ecosystems. Predator-prey dynamics may not be as tightly linked as previously thought. This study shows that at both seasonal and diel scales, chinook are very rarely distributed in such a way so as to maximize food intake. Rather, their distributions are highly variable indicating that these predators respond to other environmental stimuli exerting their influence at these temporal scales. This study suggests that predator-prey dynamics are controlled by a multitude of environmental stimuli acting at a variety of temporal scales which can effectively limit the predators capacity to eradicate its prey.

This is a significant find especially for a large highly managed ecosystem like Lake Ontario, where stakeholders fear that high salmonid predatory demand may collapse its principal alewife prey population. In this thesis, I showed in a very rudimentary fashion, that Lake Ontario continues to support salmonid (chinook) habitat, but that this habitat is highly variable over time. I also demonstrated that, although the environment exerts a considerable influence on the distribution of fish, the relative importance of these conditions, and ultimately the habitat requirements of the fish can also limit its ability to use resources. Thus, because of the plurality of environmental conditions acting to constrain salmonid distribution in Lake Ontario, it is in my opinion that moderate and conservatively set, stocking rates will not cause the eradication of alewife from this system.

Future Research

Future research of this topic could be centred on the refinements of the temporally explicit modelling framework. In its current state, there are a variety of simplifying assumptions on which the model is based that seriously limit its potential application (Chapter II and III). Further research could also focus on the refinement of hydroacoustics as a sampling tool for fish within aquatic systems. As previously mentioned, hydroacoustics provide a non-obtrusive, effective means of sampling the aquatic environment, but cannot discriminate between sources of acoustic backscatter

(Horne and Clay 1998; Brandt 1996; Clay and Horne 1994; MacLennan and Simmonds 1992). Refinements of the hydroacoustic technology to allow acoustic target discrimination would not only further enhance the modelling framework presented here, but elevate the usefulness of hydroacoustics to an unfathomable level. Future work could also concentrate on the inclusion of more environmental conditions within the temporally explicit framework. Although this would add complexity to the model, it could be useful in two ways. First, an increased number of environmental conditions could be used to more accurately delimit the amount of potential habitat available to a particular species. Secondly, determining the relative importance of a greater number of environmental conditions could lend to a greater understanding of species specific behaviour. Finally, other research could focus on the coupling of both the temporally and spatially explicit modelling frameworks so as to derive a more complete spatio-temporal representation of the environment and the ability of a particular species to make use of it.

Whoever said ..."Time is of the essence (*Anon*)..." had no idea how real this is!

References

Brandt, S. 1996. Acoustic assessment of fish abundance and distribution. Chapter 13 in Fisheries Technologies. 2nd ed. B. Murphy, and D. Willis eds. American Fisheries Society publication. Bethesda. Maryland.

Brandt, S. 1993. The effects of thermal fronts on fish growth: A bioenergetics evaluation of food and temperature. *Estuaries* (1):142-59.

Brandt, S., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Trans. Am. Fish. Soc.* 122:845-69.

Brandt, S., D. Mason, and V. Patrick. 1992. Spatially-explicit models of fish growth rate. *Fisheries.* 17(2):23-33.

Brandt, S., D. Mason, D. MacNeill, T. Coates, and J. Gannon. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. *Trans. Amer. Fish. Soc.* 116:641-45.

Clay, C., amd J. Horne. 1994. Acoustic models of fish: the Atlantic cod (Gadus morhua). *J. Acoust. Soc. Am.* 75:1077-83.

Eck, G., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa Pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 44(Suppl. 2):53-60.

Edsall, T., and G. Kennedy. 1995. Availability of lake trout reproductive habitat in the Great Lakes. *J. Great Lakes. Res.* 21(Suppl. 1):290-301.

Elrod, J., and R. O'Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979-1987. *Trans. Amer. Fish. Soc.* 120:290-302.

Ferreri, C., W. Taylor, and J. Koonce. 1995. Effects of improved water quality and stream treatment rotation on sea lamprey abundance: implications for lake trout rehabilitation in the Great Lakes. *J. Great Lakes Res.* 21(Suppl. 1):176-84.

Goyke, A., and S. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. *Trans. Am. Fish. Soc.* 122:870-83.

Harris, G. 1980. Temporal and spatial scales in phytoplankton ecology, mechanisms, methods, and management. *Can. J. Fish. Aquat. Sci.* 37:877-900.

Holling, C. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr*. 62(4):447-502.

Hondorp, D. 1998. Spatial distributions of planktivorous fish and zooplankton in western Lake Ontario: Implications for fish thermal ecology, fish bioenergetics modeling and trophic interactions. M. Sc. Thesis. State University of New York, College at Buffalo, Buffalo, New York.

Hondorp, D., and S. Brandt. 1996. Spatially-explicit models of fish growth rate: Tools for assessing habitat quality. *Great. Lak. Res. Rev.* 2(2):11-19.

Horne, J., and C. Clay. 1998. Sonar systems and aquatic organisms: matching equipment and model parameters. *Can. J. Fish. Aquat. Sci.* 55:1296-1306.

Horne, J., J. Jech, and S. Brandt. 1996. Spatial modeling of aquatic habitat from a fish's perspective. http://www.ncgia.ucsb.edu/conf/SANTA_FE_CD-ROM/sf_papers/horne_john/hornpap.html.

Janssen, J., and S. Brandt. 1996. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 37:177-84.

Jones, M., J. Koonce, and R. O'Gorman. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. *Trans. Amer. Fish. Soc.* 122:1002-18.

Jude, D., F. Tesar, S, Deboe, and T. Millar. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973-1982. *Trans. Amer. Fish. Soc.* 116:677-91.

Jude, D., and F. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. *Can. J. Fish. Aquat. Sci.* 42:1154-57.

Krueger, C., M. Jones, and W. Taylor. 1995. Restoration of lake trout in the Great Lakes: Challenges and strategies for future management. *J. Great Lakes Res.* 21:(Suppl. 1):547-58.

Lantry, B., and T. Schaner. 1998. The status of the pelagic preyfish in Lake Ontario, 1997. *In* Lake Ontario Fisheries Unit 1998 Annual Report Section 6. NewYork State Department of Environmental Conservation.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. *Rapp. P. -v. Réun. Cons. int. Explor. Mer.* 173:212-30.

Lawton, J. 1987. Problems of scale in ecology. *Nature*. 325:206.

Legendre, P., and S. Demers. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.* 41:2-19.

Levin, S. 1992. The problem of pattern and scale in ecology. *Ecology*. 73(6):1943-67.

MacLennan, D., and J. Simmonds. 1992. Fisheries Acoustics. Chapman Hall. London.

Mason, D., and S. Brandt. 1996. Effects of spatial scale and foraging efficiency on the predictions made by spatially explicit models of fish growth rate potential. *Environmental Biology of Fishes.* 45:283-98.

Mason, D., A. Goyke, and S. Brandt 1995. A spatially explicit bioenergetics measure of habitat quality for adult salmonines: Comparison between Lakes Michigan and Ontario. *Can. J. Fish. Aquat. Sci.* 52:1572-83.

McAughey, S., and J. Gunn. 1995. The behavioral response of lake trout to a loss of traditional spawning sites. *J. Great Lakes Res.* 21(Suppl. 1):375-83.

Noakes, D., and R. Curry. 1995. Lessons to be learned from attempts to restore *Salvelinus* species other than *S. namaycush*: A review of reproductive behavior. *J. Great Lakes Res.* 21(Suppl. 1):54-64.

O'Gorman, R., O. Johannsson, C. Schneider.1997 a. Age and growth of alewives in the changing pelagia of lake Ontario, 1978-1992. *Trans. Am. Fish. Soc.* 126:112-26.

O'Gorman, R., and C. Schneider. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. *Trans. Amer. Fish. Soc.* 115:1-14.

Pearson, S., M. Turner, L. Wallace, and W. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecological Applications*. 5(3):744-55.

Rand, P., and D. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: A test of a bioenergetics model prediction. *Can. J. Fish. Aquat. Sci.* 55:307-17.

Rand, P., and eight other authors. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. *Can. J. Fish. Aquat. Sci.* 52:1546-63.

Rand, P., B. Lantry, R. O'Gorman, R. Owens, and D. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978-1990: Implications of salmonine energetics. *Trans. Am. Fish. Soc.* 123:519-34.

Rudstam, L., and eleven other authors. 1996. A review of the current status of Lake Ontario's pelagic fish community. Report of 1996 Lake Ontario technical panel. *Great Lakes Res. Rev.* 2(2):4-10.

Sale, P. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Australian Journal of Ecology*. 23:202-08.

Steedman, R., and seven other authors. 1995. Use of historical information for conservation and restoration of Great Lakes aquatic habitat. *Can. J. Fish. Aquat. Sci.* 53(Suppl. 1):415-23.

Stewart, D., and M. Iberra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. *Can J. Fish. Aquat. Sci.* 48:909-22.

Stewart, T., M. Rawson, and J. Bowlby. 1998. Managing the chinook fishery. *Great Lakes Res. Rev.* 3(2):32-34.

Stewart, T., and T. Schaner. 1998. Alewife and their role in structuring the Lake Ontario fish community. *Great. Lak. Res. Rev.* 3(2):28-31.

Trippel, E. 1995. Age at maturity as stress indicator in fisheries. *BioScience*. 45(11):759-70.

Urban, T., and S. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. *Environmental Biology of Fishes*. 36:359-72.

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