Estimating fish production potentials using a temporally explicit model

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Abstract

A temporally explicit model is developed to predict the growth rate potential of fish in response to temporal fluctuations in both prey availability and temperature structure of the water column at both long (seasonal) and short (daily) time scales. The model was tested in a 20 m water column in Lake Ontario using chinook salmon (*Oncorhynchus tshawytcsha*) and alewife (*Alosa pseudoharengus*) as predator and prey species, respectively. Prey availability was assessed using acoustic techniques, while temperature was measured with a temperature–depth profiler. Chinook growth rate potential was significantly greater during June than during other sampled months. The latter months supported little to no chinook growth potential as a result of low overlap in conditions supporting growth. On a diel scale, chinook growth rate potential was typically greater during crepuscular and night periods than during the day. Results reveal that both short and long term variability of prey density and thermal structure impose stringent limits to fish growth potential and production, and that fish grow well only over finite periods. The temporally explicit model provides quantitative predictions of fish production potential as influenced by temporal changes in habitat quality and/or climatic conditions. In light of recent modifications to both local and regional climate conditions, and the localised nature of fish harvesting practices, this model can assist in setting realistic production estimates and future potential harvesting quotas.
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Keywords: Time; Spatially explicit; Bioenergetics; Modelling; Growth rate potential (GRP); Habitat quality; Resource overlap; Alewife; Chinook salmon

Studies suggest that decreased commercial yields and collapse of many global fish stocks have been exacerbated by rapidly changing climatic conditions within environments supporting important fishing harvests (Myers et al., 1997; McFarlane et al., 2000). Yet, there remains a great deal of uncertainty in how global and more localised climate changes influence the production and sustainability of commercially important fish species. Changes in climate patterns can dramatically alter temperature regimes within aquatic systems, and temperature has long been demonstrated to be deterministic of fish growth and production rates (Crowder and Magnuson, 1983; Stewart et al., 1983; Stewart and Ibarra, 1991). To improve forecasting abilities for target species production in light of changing climates, we need to assess and monitor how temperature modulates growth and production within changing aquatic environments (McFarlane et al., 2000).

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Do traditionally productive environments continue to provide adequate conditions for target species growth and production? If so, how persistent or ephemeral are these conditions through time? The answers to these questions become extremely relevant and critical to the future sustainable use of fish stocks throughout the world.

Traditionally, production of target fish stocks has been estimated based on past catch indices from both commercial landings and scientific sampling (McFarlane et al., 2000). These assessments of abundance and production however, are problematic as most protocols involve permanent removal of portions of the target stock and can irreparably damage the environment. This is especially precarious when target stocks are already under substantial anthropogenic and/or natural stress. An alternative to sampling target stocks directly is to determine the quality of the environment as it relates to the target stock production (i.e., habitat quality). More commonly now, production potentials of target species are assumed to be regulated by prey availability within studied systems (e.g., O'Gorman et al., 1987; Stewart and Schaner, 1998). However, prey populations sustaining target stocks can also be under substantial stress, and sampling these former poses the same problem (e.g., anchovy, capelin, and alewife; Lasker, 1978; Frank and Leggett, 1983; Jones et al., 1993).

Associations between environmental conditions and predator–prey interactions have been quantified using a spatially explicit approach (Brandt et al., 1992). These models reveal that spatial complexity within aquatic systems can constrain predator and prey distributions, effectively limiting the amount of prey available to predators in the spatial dimension (e.g., Brandt and Kirsch, 1993; Goyke and Brandt, 1993; Hondorp and Brandt, 1996). Both environmental conditions, such as temperature, and prey availability interact to create a habitat suitable for fish production. If suitable physical conditions and sufficient prey fail to co-occur, the habitat will not support adequate predator growth and production.

An important determinant of both predator and prey distributions within aquatic ecosystems is temperature, wherein species do not necessarily track the same temperature ranges (Crowder and Magnuson, 1983). Spatial models have demonstrated that predators tracking both prey abundances and optimal temperatures

have highest production potentials in areas where these environmental characteristics overlap (Brandt et al., 1992; Brandt, 1993; Luo and Brandt, 1993; Goyke and Brandt, 1993; Hondorp and Brandt, 1996). Spatial modelling, however, is largely limited to 'snapshots' taken over short time periods, and does little to resolve how often these overlapping conditions develop and how long they persist. Although it is thought that temporal variability in the degree of overlap of environmental conditions can influence fish growth rate potential, until now, there has been no method able to quantify the relative importance of this temporal flux.

Thermal regimes of large lakes and oceans are temporally variable as a result of thermal stratification, internal waves, upwellings, and wind events and can be very complicated systems for fish to track (Wetzel, 1975; Crowder and Magnuson, 1983). Both prey and predator populations must track these oscillations in thermal structure, moving up and down through the water column, and/or in and off shore, to remain in thermally preferred regions (Crowder and Magnuson, 1983; O'Gorman et al., 1987, 1997; Olson et al., 1988). There remains a need to determine the suitability of an environment to sustain the production of a target species, and to quantify how this production changes over time, in a non-obtrusive manner.

In this paper, we develop and apply a temporally explicit model of fish growth rate potential to bioenergetically quantify the amount of growth available to a predator within a given water column under prevailing prey distributions and thermal regimes, over time. Such a model emphasises the relative importance of temporal fluctuations of prey densities and water column thermal structure in regulating predator production potentials. The development of a temporally explicit model able to assess and monitor target species potential production is becoming increasingly important considering both global and localised climate change and how these modulate fish production on a temporal basis (Roberts, 1997; Allison et al., 1998; Hall, 1998; Lauck et al., 1998). We develop this modelling approach using chinook salmon (*Oncorhynchus tshawytscha*) and alewife (*Alosa pseudoharengus*) as predator and prey species, respectively, at a near shore station in western Lake Ontario, as an example.

1. Temporally explicit model

1.1. Foraging sub-model

Temporally explicit modelling partitions the time period over which data are collected into cells indexed by time and depth. Environmental conditions within each cell are considered homogenous in terms of prey density and temperature. Within each cell, a species-specific foraging model determines the potential prey available to a particular sized predator occurring in that cell. The foraging model used in this study was originally developed by Tyler (1998), and is based on previous studies by Gerritsen and Strickler (1978), Bailey and Batty (1983), Aksnes and Giske (1993), and Tyler and Rose (1997). The amount of prey available to a predator (PA in $g\,g^{-1}\,d^{-1}$) in each cell is determined by:

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

where, VS is the volume searched by a particular predator (m^3); PD is the biomass density ($g\,m^{-3}$); C_{eff} is the predator capture efficiency (prey consumed/prey encountered); ED_X is the energy density of X, being either that of prey or predator ($cal\,g^{-1}$); and W_{pred} is the wet weight of the predator (g).

Volume searched by a particular predator (VS), can be expressed generally as (see Tyler and Rose, 1997; Tyler, 1998):

$$VS = \frac{2\pi \cdot RD^2 \cdot (SS \cdot L) \cdot TF}{10^9} \qquad (2)$$

where RD is the reactive distance of the predator (i.e., detection distance in mm); SS is the swimming speed of the predator (body length s^{-1}); L is the length of the predator (mm per body length); and TF is the time spent foraging (s).

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 a size and species-specific predator within each of the modelled environmental cells (Tyler and Rose, 1997; Tyler, 1998). PA becomes an integral part of the bioenergetics model (described below) as it sets a limit to the consumption rate (C) achievable within a cell, provided conditions within that cell are in-

sufficient for the size and species-specific predator to reach its maximum consumption (Brandt, 1993; Goyke and Brandt, 1993; Tyler, 1998). Foraging model parameters used in the initial chinook salmon size category examined in this study are available in Table 1.

1.2. Bioenergetics sub-model

Bioenergetics models relate environmental conditions to size and species-specific growth rates taking into consideration the inherent non-linear aspects of these relationships (Brandt et al., 1992; Brandt and Kirsch, 1993). Growth rate potential (hereafter GRP) describes the amount of growth achievable by a size and species-specific predator when placed in a predetermined volume of water characterised by a particular suite of environmental conditions. In this study, we make use of the modelling framework originally presented by Kitchell et al. (1977), later modified and implemented to estimate salmonid growth by Stewart et al. (1983), and by Stewart and Ibarra (1991). The synthesis and detailed mechanics of the utilised bioenergetics modelling framework are available in Hewett and Johnson (Fish Bioenergetics Model v. 2.0; 1992), and in references therein. In the following section, we briefly describe modifications to the above model made largely for ease of computation and incorporation of data into software providing graphical presentations of temperature, prey availability and chinook GRP data (GRP Map Maker v. 2.0; Tyler, 1998). In this study, we use the bioenergetics model described below to determine temporal changes in chinook salmon GRP (G, in $g\,g^{-1}\,d^{-1}$) in each environmental cell as follows:

$$G = C - (R + S + F + U) \qquad (3)$$

where C is the consumption ($g\,g^{-1}\,d^{-1}$); R is the respiration and metabolism ($g\,g^{-1}\,d^{-1}$); S is the specific dynamic action; F is the egestion ($g\,g^{-1}\,d^{-1}$); and U is the excretion ($g\,g^{-1}\,d^{-1}$).

1.2.1. Consumption
Consumption (C, in $g\,g^{-1}\,d^{-1}$), is defined by the formula:

$$C = C_{max} \cdot P \qquad (4)$$

Table 1
List of values used in the initial foraging model adapted from Tyler (1998) modelling chinook salmon feeding on alewife in western Lake Ontario

Parameter	Value	Assumptions/sources
Predator length (L)	300 mm	Initial size of chinook for model
Predator weight (W)	512 g	
Target L–W constant (a_i)	4.49×10^{-4}	From formula as follows: $W = a \cdot L^b$, 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)	18,000 s	Estimated time of chinook foraging corresponding to number of crepuscular hours in sampling events, as well as allotting for some daytime foraging. Chinook feed primarily during crepuscular hours and a few hours thereafter (Sagar and Glova, 1998; Kreivi et al., 1999)
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)	1.3 body lengths s^{-1}	Translating to ~39 cm s^{-1} and within the range reported by Stewart and Ibarra (1991)
Prey energy density (ED$_{prey}$)	4987 J g^{-1} May	For Lake Ontario alewives, taken from Rand et al. (1994). J g^{-1} converted to cal g^{-1} for entry into model
	5326 J g^{-1} June	
	5347 J g^{-1} July	
	5100 J g^{-1} September	
	6318 J g^{-1} October	
Predator energy density (ED$_{pred}$)	6268 J g^{-1}	Initial value and formula taken form Stewart and Ibarra (1991) (varies with size of chinook). J g^{-1} converted to cal g^{-1} for entry into model

Once the model was developed, parameters were adjusted to model foraging for chinook sizes from 300 to 700 mm in length (incrementing salmon size by 25 mm).

where C_{max} is the maximum consumption rate for a particular sized predator at a given temperature, and is defined as:

$$C_{max} = aW^b \cdot f(T) \qquad (5)$$

where a is the intercept for weight-dependent maximum consumption achieved at optimal temperature (g g^{-1} d^{-1}; Stewart et al., 1983); W is the wet weight of the predator fish (g); b is the coefficient for a predator's weight-dependent consumption (a fish of a certain size can consume only a finite amount of prey); $f(T)$ is the exponential function using ambient temperature as a coefficient modifier, defined by Thornton and Lessem (1978), and used to model chinook salmon temperature dependence of maximum consumption as per Stewart and Ibarra (1991).

P, in Eq. (4), is defined as the proportion or ration (ranging from 0 to 1) of maximum consumption (C_{max}) possible for a given species at a given temperature and prey availability (PA), where:

$$P = \frac{PA}{C_{max}} \qquad (6)$$

Prey availability (PA from Eq. (1)) contributes to consumption only until P in the consumption equation (Eq. (4)) reaches 1. When PA $\geq C_{max}$, P is set to 1, as further increases in prey availability cannot be used or eaten by the predator due to physiological constraints such as gut fullness, and digestion rate (see Brandt et al., 1992; Brandt, 1993; Tyler, 1998). When PA $< C_{max}$, consumption (C) becomes a proportion (P) of maximum consumption (C_{max}).

1.2.2. Respiration

Respiration (R, in g g^{-1} d^{-1}) is modelled as a function of predator weight, ambient temperature and activity according to the following (from Stewart et al., 1983; Stewart and Ibarra, 1991; Hewett and Johnson, 1992):

$$R = \alpha W^{\beta} \cdot f(T) \cdot ACTIVITY \qquad (7)$$

where α is the intercept of standard specific metabolism taking into account the influence of temperature, weight, and predator swimming speed. This parameter is estimated for a 1 g fish at 0 °C, with a swimming speed of 0, and is updated daily for the relative energy density of the predator and its prey (in $g\,O_2\,g^{-1}\,d^{-1}$; see Stewart and Ibarra, 1991; Hewett and Johnson, 1992; Brandt, 1993; Tyler, 1998). β is the exponent relating weight-dependent respiration; W is the wet weight of the predator (g); $f(T)$ represents an exponential function using ambient temperature as a coefficient modifier. This function modulates respiration as described in both Stewart et al. (1983), and Hewett and Johnson (1992), and has been previously used for chinook salmon by Stewart and Ibarra (1991), and Brandt (1993).

ACTIVITY in Eq. (7), is an exponential function with temperature-dependent coefficients relating activity and respiration to swimming speed, water temperature, and specific weight of a predator according to the following (Stewart et al., 1983; Hewett and Johnson, 1992);

$$\text{ACTIVITY} = e^{[(T_o - (T_m \cdot T)) \cdot \text{VEL}]} \tag{8}$$

where T_o is the coefficient for swimming speed dependence of metabolism; T_m is the coefficient for temperature dependence of metabolism; T is the ambient temperature (°C) and,

$$\text{VEL} = K1 \cdot W^{K4}, \quad \text{if } T > T_L \tag{9}$$

$$\text{VEL} = \text{ACT} \cdot e^{(\text{BACT} \cdot T)} \cdot W^{K4}, \quad \text{if } T \leq T_L \tag{10}$$

Swimming speed VEL ($\text{cm}\,\text{s}^{-1}$), estimated differently than that in the foraging model, uses the following parameters: $K1$ is the intercept for weight dependence of swimming speed ($\text{cm}\,\text{s}^{-1}$); $K4$ is the coefficient for weight dependence of swimming speed; ACT is the intercept of swimming speed versus water temperature at temperatures below T_L ($\text{cm}\,\text{s}^{-1}$, for a 1 g fish at 0 °C); T_L is the threshold temperature for respiration (°C); and BACT is the coefficient for temperature dependence of swimming speed for temperatures below T_L.

1.2.3. Specific dynamic action

Energy, accounted for by specific dynamic action (S), can be calculated as:

$$S = \text{SDA} \cdot (C - F) \tag{11}$$

where SDA is the proportion of energy lost related to the cost of digestion, absorption, and assimilation of consumed energy (see Stewart et al., 1983; Hewett and Johnson, 1992; Brandt, 1993; Tyler, 1998); C is the consumption term estimated from Eq. (4) ($g\,g^{-1}\,d^{-1}$); and F is the egestion term of the growth equation (see egestion below; $g\,g^{-1}\,d^{-1}$).

1.2.4. Egestion/excretion

While several expressions are available to model fish growth as a function of egestion and excretion, we chose the formulation described originally by Elliott (1976), and presented in Hewett and Johnson (1992), which is as follows:

$$F = \alpha_F \cdot T^{\beta_F} \cdot e^{(\gamma_F \cdot P)} \cdot C \tag{12}$$

where α_F is the intercept for temperature and ration dependence of egestion ($g\,g^{-1}\,d^{-1}$); β_F is the coefficient for temperature dependence of egestion; γ_F is the coefficient for feeding level dependence of egestion; P is the proportion of maximum consumption defined in Eq. (6); and C is the consumption rate determined in Eq. (4) above.

Similarly, excretion is expressed as:

$$U = \alpha_U \cdot T^{\beta_U} T \cdot e^{(\gamma_U \cdot P)} \cdot (C - F) \tag{13}$$

where α_U is the intercept for temperature-dependent excretion ($g\,g^{-1}\,d^{-1}$); β_U is the coefficient for temperature dependence of excretion; and γ_U is the coefficient for feeding level dependence of excretion.

Proportion of maximum consumption (P), and consumption (C, in $g\,g^{-1}\,d^{-1}$) are the same as those calculated for the egestion equation (Eq. (12)), while egestion (F, in $g\,g^{-1}\,d^{-1}$) is calculated in Eq. (12). This formulation of egestion/excretion models a chinook salmon diet composed exclusively of fish, and although a more complex egestion/excretion formulation is available (Stewart and Ibarra, 1991), the simplified diet is more appropriate for our test site in Lake Ontario where alewife have been identified as the primary prey item of chinook (Brandt, 1986).

This modelling framework considers both environmental conditions and predator abilities in terms of foraging and growth to predict species-specific GRP within a predetermined volume of water. Applied in a temporally explicit manner, this model describes and quantifies changes in predator GRP over a set time interval. The above model was used to predict chinook

salmon GRP in individual volumes of water defined by our sampling device. Individual volumes were defined as cones of increasing diameter with depths (h) of 1 m and whose volumes can be estimated using the following formula:

$$V_{Cell} = \frac{\pi h}{12} \cdot (d_{bot}^2 + d_{bot} \cdot d_{top}^2 + d_{top}) \tag{14}$$

where d_{bot} is the bottom diameter of the cone (m); and d_{top} is the top diameter of the cone (m).

Chinook GRP was estimated through the entire water column by integrating 1 m depth volumes until the bottom depth was reached. The water column was then sampled every minute separating the sampled environment into unitary cells indexed by minutes and cubic metres. Summation of the GRP estimated in all cells within a water column and from a predetermined time interval quantifies the amount of growth achievable within a water column during a specified time frame (Fig. 1). This modelling framework estimates potential growth rate rather than realised growth rates, and therefore predicts fish production potentials of a water column as it relates to species-specific habitat quality over time.

2. Methods

2.1. Field application

The western end of Lake Ontario is a temporally dynamic system (Boyce et al., 1991) with well established fish species assemblages (O'Gorman et al., 1987). Lake Ontario is stocked with salmonids, such as chinook salmon, which use alewife as their principle prey (Brandt, 1986; O'Gorman et al., 1997; Stewart et al., 1998). Salmonids have limited natural reproduction in this system and their populations are maintained by annual stocking (Goyke and Brandt, 1993; Stewart et al., 1998).

Chinook salmon was selected as the model predator in this study because it accounts for upwards of 40% of the salmonids stocked into Lake Ontario (Goyke and Brandt, 1993). We initially modelled the GRP of a 512 g, 300 mm chinook in western Lake Ontario (Table 1). We chose this particular sized salmon as a starting point because it represents the smallest acoustic target that can safely be considered to be a
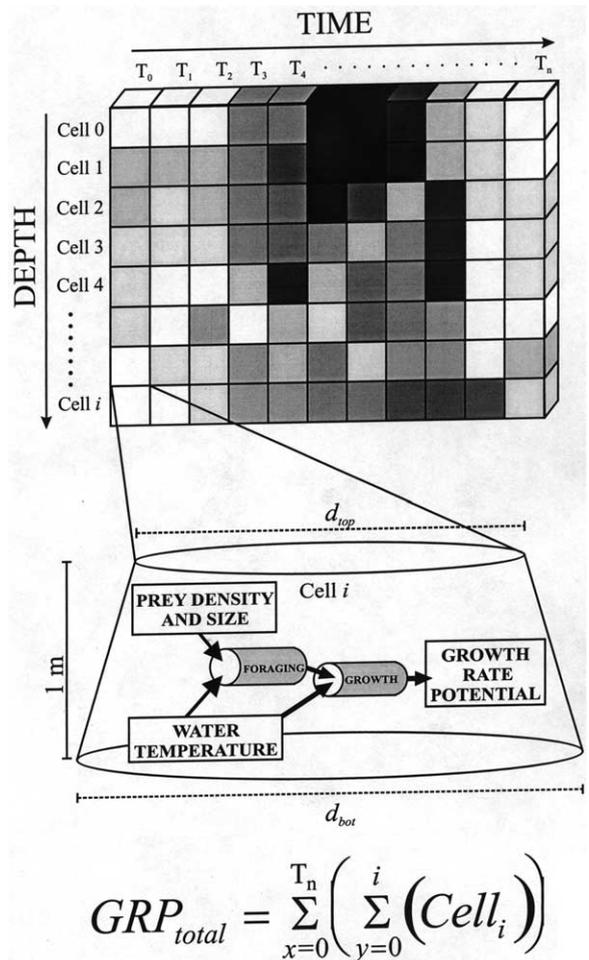

Fig. 1. Conceptualisation of the temporally explicit modelling framework, dividing the sampled environment into volumetric cells indexed by time and depth. Each cell (Cell$_i$) is characterised by a particular suite of environmental conditions which are entered into the foraging, and bioenergetics sub-models determining species, and size-specific fish production potential. Each cell has the shape of a cone and is re-sampled every minute (T_n) and provides a temporal assessment of potential production within that cell. Production potential integrated through each depth cell (G all Cell$_i$s) and summed over all times ($\sum T_n$) demonstrates and quantifies the production potential of the sampled environment over a specified time interval (adapted from Brandt and Kirsch, 1993).

predator. Foraging and bioenergetics parameters were then adjusted to model GRPs for chinook in a size range of 300–700 mm using 25 mm increments. Chinook GRPs from all sizes were then integrated together to determine overall GRP of chinook ranging in sizes 300–700 mm, occurring at our sampling sta-

Table 2
Parameter values used for modelling chinook salmon bioenergetics

Symbol	Symbol in Hewett and Johnson (1992)	Parameter description	Value used
Consumption (C)			
a	CA	Intercept: C and C_{max} (g g^{-1} d^{-1})	0.303
b	CB	Coefficient: C and C_{max} vs. weight	−0.275
f(T) in chinook salmon, temperature modulations to consumption are modelled by the Thornton and Lessem (1978) algorithm which has two components; K1 (increasing) and K4 (decreasing)			
	CQ	Water temperature for low K1 (°C)	5
	CTO	Water temperature for high K1 (°C)	15
	CTM	Water temperature for high K4 (°C)	18
	CTL	Water temperature for low K4 (°C)	24
	CK1	Proportion of C_{max} at CQ	0.36
	CK4	Proportion of C_{max} at CTL	0.01
Respiration (R)			
α	RA	Intercept: R (g O$_2$ g^{-1} d^{-1})	0.00264
β	RB	Coefficient: R vs. weight	−0.217
f(T) temperature modulates respiration as an exponential function which is described in Stewart et al. (1983) and in Hewett and Johnson (1992)			
	RQ	Coefficient: R vs. temperature	0.06818
T_O	RTO	Coefficient: R vs. swimming speed (VEL)	0.0234
T_M	RTM	Coefficient: R vs. metabolism	0
T_L	RTL	Temperature threshold for R (°C)	25
K1	RK1	Intercept: VEL vs. weight (cm s^{-1})	1
K4	RK4	Coefficient: VEL vs. weight	0.13
ACT	ACT	Activity multiplier	9.7
BACT	BACT	Coefficient: VEL vs. temperature	0.0405
SDA	SDA	Specific dynamic action	0.172
Egestion (F)/excretion (U)			
$α_F$	FA	Intercept: proportion egested vs. temperature and ration (g g^{-1} d^{-1})	0.212
$β_F$	FB	Coefficient: F vs. temperature	−0.222
$γ_F$	FG	Coefficient: F vs. feeding level	0.631
$α_U$	UA	Intercept: proportion excreted vs. temperature and ration (g g^{-1} d^{-1})	0.0314
$β_U$	UB	Coefficient: U vs. temperature	0.58
$γ_U$	UG	Coefficient: U vs. feeding level	−0.299

Parameter symbols are presented both in the notation used in this study and their corresponding values in Hewett and Johnson (1992).

tion. Values used for the specific bioenergetics parameters described above, and in formulae described by Hewett and Johnson (1992), were previously derived for chinook salmon by Stewart and Ibarra (1991) and are available in Table 2.

2.2. Estimating prey abundance and distribution

Prey abundance and distribution was estimated using hydroacoustic technology which allowed for nearly continuous sampling of the environment in a non-obtrusive manner (MacLennan and Simmonds, 1992; Brandt, 1996). Acoustic data were collected continuously for 24-h periods on May 27–28, June 19–20, July 30–31, September 5–6, and October 18–19. Sampling was done at a station 43°13.28′N, 079°18.00′W, 2 km offshore in 20 m of water in the south western portion of Lake Ontario (Fig. 2).

The sampling station was selected based on logistics of the sampling strategy. Each sampling event was designed to last 24 h. However, sampling was interrupted in September and October due to adverse weather conditions.

Acoustic data of fish abundance and distribution were collected using a 120 kHz, EY500 Simrad© echo-sounder equipped with a split-beam transducer and specified by a 7.1° half beamwidth. The transducer was mounted to a free floating stable plat-
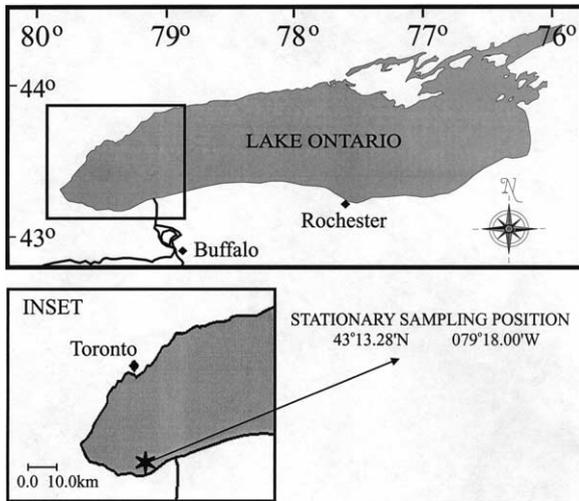
Fig. 2. Sampling location in western Lake Ontario.

form which kept it in a vertical position within the water column tethered away from the vessel. The acoustic signal was characterised with a pulse length of 0.3 ms, and a pulse repetition rate of $2\,\text{pulses s}^{-1}$. Acoustic signals were corrected for spreading and absorption in the water by applying a $40\log_{10} R$ time varied gain (where R is distance), and recorded to magneto-optical disk. The acoustic signal was also calibrated by suspending a standard tungsten carbide reference sphere of known target strength ($-40.4\,\text{dB}$) under the transducer at varied depths.

Once collected, acoustic data were processed using Digital Echo Visualisation and Integration System (DEVIS; Jech and Luo, 2000). Echo-integration converts echoes of targets within the acoustic beam to estimates of relative fish density. The speed of sound in water ($\sim 1500\,\text{m s}^{-1}$) allows for each target to be measured repeatedly. Absolute fish numerical density (m^{-3}) is then derived by dividing relative densities by the mean target strength (as discussed by MacLennan and Simmonds, 1992; Jech and Luo, 2000). Absolute fish density data were $\log_{10}$ transformed and resolved into each environmental cell. A GIS-type program was written in Interactive Data Language (IDL, Research systems, 1998) produced a 2-dimensional representation of the prey density within the water column using time and depth as indices.

Individual acoustic target strengths were converted to fish lengths using a target strength—fish length re-

lationship derived for Lake Ontario species (Schneider and Schaner, 1994). Fish densities were separated by size to distinguish prey fish from predators. Because echoes scattered by targets of different species are not readily identifiable (MacLennan and Simmonds, 1992; Brandt, 1996), all prey targets were considered alewife. This assumption is supported by the fact that alewives are the dominant planktivore in Lake Ontario, comprising almost 67% of the system's forage base (O'Gorman et al., 1987, 1997). Trawls conducted routinely from 1991 to 1997, by the New York Department of Environmental Conservation (NYDEC), revealed maximum alewife fork lengths consistently below 180 mm (Lantry and Schaner, 1997). Thus, a conservative threshold was set at 180 mm below which all targets were considered to be alewife. Targets above this set threshold were excluded from further analysis (Fig. 3).

2.3. Time period formation

Because fish, and certainly alewife distributions, are known to respond to light intensity shifts, acoustic data were split into four time periods based on the diel light intensity cycle namely; dawn, day, dusk, and night (Janssen and Brandt, 1980; Appenzeller and Leggett, 1995). The length of each period was based on sunrise
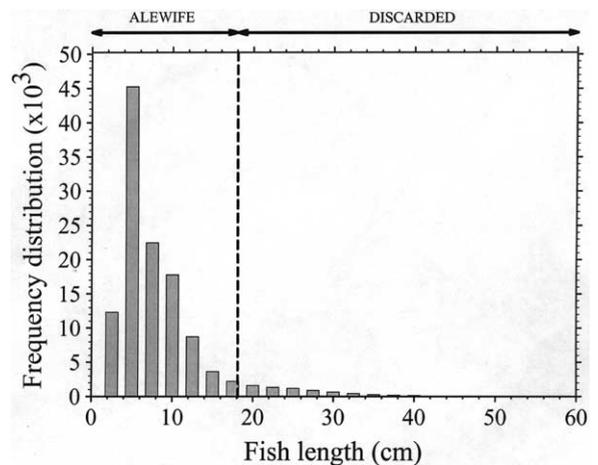

Fig. 3. Frequency distribution of fish lengths (mm) converted from acoustic targets collected during 1997 in western Lake Ontario. Fish lengths to the left of the hatched line ($\leq 180\,\text{mm}$) were considered alewife, while those to the right ($>180\,\text{mm}$) were excluded from further analysis.

and sunset times collected from the United States Astrological and Naval Time Department, and the National Weather Service (NWS). The sunrise–sunset times were taken for the topographical latitude and longitude corresponding to Buffalo, New York, USA (eastern standard time), approximately 40 km away from our sampling site. One hour was added to sunset times to form the dusk period, while the same was subtracted from sunrise to create the dawn period. This correction 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). All daylight hours not included within dawn or dusk periods formed the day periods, while all dark hours after dusk and leading to dawn periods were considered night.

2.4. Temperature

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 lowering the CTD to near bottom depth and setting the device to measure water temperature every 0.5 s as it was retrieved. The retrieval rate of the CTD was approximately $0.5\,\text{m s}^{-1}$, and the thermistor response time was 0.5 s (Baumann, 2000, Seabird Electronics, Inc., personal communication). The water column was then divided into 1 m depth cells characterised by the median of the temperature values collected within each cell.

For each study period, a temperature profile was taken immediately upon arrival on station, and repeated every hour thereafter. Fluctuations in the thermal regime of the water column at temporal scales less than 1 h are generally small (Boyce et al., 1991). Water temperature within each depth cell was resolved per minute using linear interpolation between temperature casts. Temperature data were then resolved into each environmental cell similar to the fish data. Again, the same GIS-type program (see above) was used to produce a 2-dimensional thermal structure of the water column indexed by time and depth similar to that of the prey density data. Once collected, temperature data were split into the four time delimited periods as per the acoustic data (described above).

Both the temperature and prey density data with corresponding cells were incorporated into the foraging and bioenergetics models described above, allowing estimation of chinook GRP in every environmental cell (see Fig. 1). The same GIS-type program was then used to generate a 2-dimensional representation of chinook salmon GRP over the same time intervals as that produced for both the prey density, and temperature date.

Kolmogorov–Smirnov analyses were performed to determine if there were significant differences in chinook salmon GRP between specific time periods within the sampling season (May, June, July, September, and October), and between specific time periods within one sampling event (dawn, day, dusk, and night). Kolmogorov–Smirnov (D) test statistics were evaluated against a critical (D_α) values adjusted for multiple comparisons (see Sokal and Rohlf, 1995). Unplanned comparisons were selected to evaluate D statistics because D_α values adjusted for multiple comparisons are generally more conservative (i.e., larger) reducing the risk of type II errors (Sokal and Rohlf, 1995). All statistical tests were evaluated at the $\alpha = 0.05$ level of confidence.

3. Results

3.1. Temperature structure

Average water column temperature gradually increased from 6.4 °C in May, to a maximum of 19.6 °C in July and then decreased during September and October to 13.6 °C (Fig. 4A). During May, June, and July, the water column had a distinct thermocline structure (Fig. 4A, see also Fig. 5A). During September and October, however, the water column was nearly isothermal (Fig. 4A, see also Fig. 6A).

3.2. Prey density

Alewife were most abundant during June, July, and September, but were relatively rare during May and October (Fig. 4B). The seasonal pattern of alewife abundance at our nearshore station is a function of annual inshore and offshore migrations of alewife in Lake Ontario (O'Gorman et al., 1987). Alewife were less frequently observed during the day, forming dense
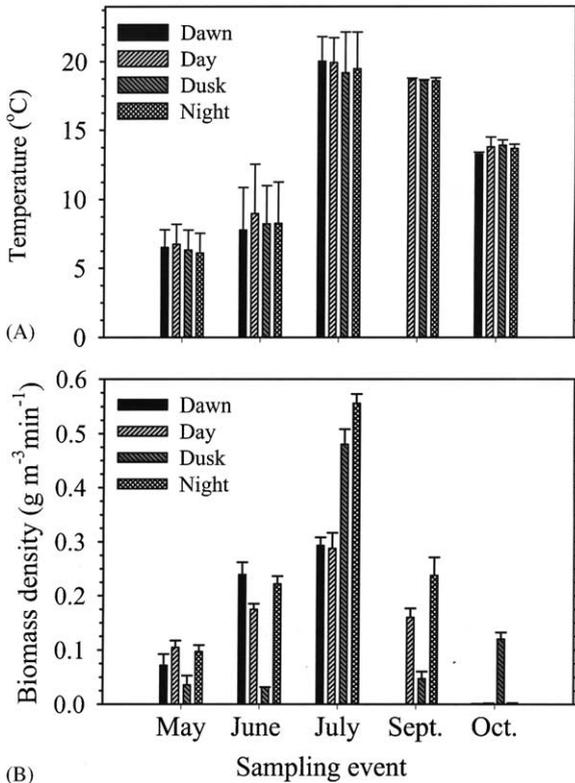
Fig. 4. (A) Mean temperature of the water column (±2 S.D.), and (B) mean alewife biomass (±2 S.D.) collected at a sampling location in western Lake Ontario during 1997.

isolated clusters which did not persist over long time intervals. During night, and crepuscular periods however, alewife tended to be more frequent and occurred more consistently throughout the time periods. This diurnal pattern in alewife density and distribution was observed in May, June, July and September (Fig. 5B; Roy, 1999).

3.3. Growth rate potential

In May and June, chinook GRP closely tracked alewife distributions through both depth and time. During these months, chinook GRP was higher in the warmer, upper regions of the water column (Fig. 5). This pattern differed during July and September when part or all of the water column was characterised by temperatures well above chinook salmon's thermal optima (12–16 °C; Stewart and Ibarra, 1991). During

these periods, the nearshore water column did not support chinook growth despite the availability of prey (Fig. 6). Chinook GRP in July was confined to the coolest available water occurring at the deepest depths (Roy, 1999). The warm, well-mixed nature of the water column in September inhibited positive GRP, regardless of prey availability (Fig. 6). Although alewives were plentiful throughout the water column in September, chinook salmon GRP was negligible because the 20 °C water column did not provide adequate thermal conditions for positive chinook growth to occur.

Fig. 7A summarises the percentage of cells supporting positive chinook growth rates as predicted by the prevailing temperature structure and prey availability during a particular time interval. Statistical differences in GRPs observed between sampling events are summarised in Table 3. Highest positive growth rate potentials occurred in June, and corresponded to times when prey were abundant and water column temperatures were such that chinook salmon could use this prey resource for growth. The water column supported relatively little to no positive chinook GRPs during the other months sampled.

Fig. 7B–F summarises diel changes in chinook GRP observed at our sampling station based on ambient water column temperatures and prey availabilities. Table 4 compares estimates of chinook GRP observed for dawn, day, dusk, and night during each monthly

Table 3

Kolmogorov–Smirnov statistic (D) calculated to assess significant differences among growth rate potential of chinook salmon during different sampling periods within the 1997 growing season

Comparison	D	D_α
May vs. June	0.208[a]	0.031
May vs. July	0.920[a]	0.031
May vs. September	0.981[a]	0.038
May vs. October	0.991[a]	0.031
June vs. July	0.757[a]	0.031
June vs. September	0.968[a]	0.038
June vs. October	0.820[a]	0.031
July vs. September	0.449[a]	0.038
July vs. October	0.756[a]	0.031
September vs. October	0.971[a]	0.038

D statistics are evaluated against a critical D_α for unplanned comparisons.

[a] D values $> D_\alpha$ indicate significant differences at the $\alpha = 0.05$ level (Sokal and Rohlf, 1995).
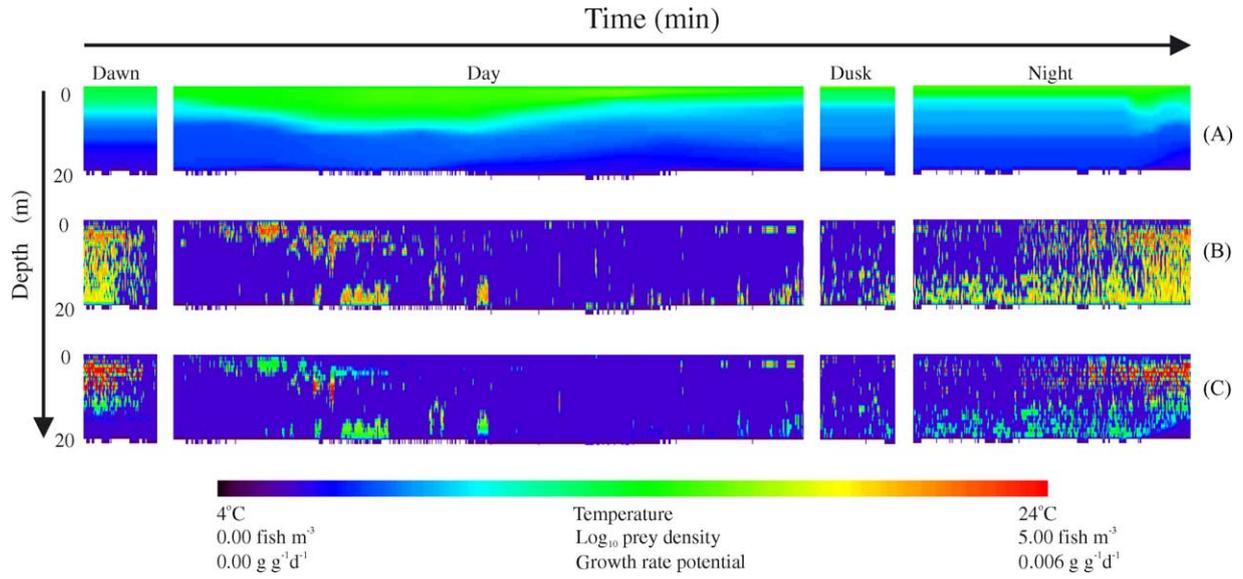
Fig. 5. The development of (A) temperature, (B) acoustically derived alewife density, and (C) chinook salmon growth rate potential at our sampling site in western Lake Ontario during 19–20 June 1997.
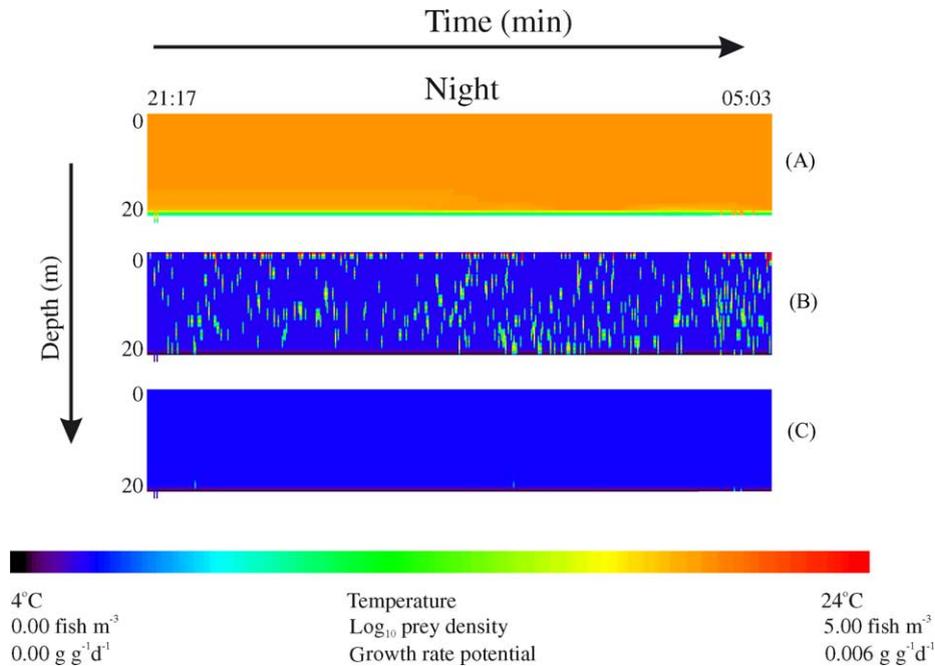
Fig. 6. The development of (A) temperature, (B) acoustically derived alewife density, and (C) chinook salmon growth rate potential at our sampling site in western Lake Ontario during the night of 5–6 September 1997.

sampling period. Chinook GRPs were typically highest during crepuscular and night periods. These times corresponded to periods when prey distributions and growth-conductive temperatures for chinook salmon overlapped the most. Results support the conclusion that chinook GRP is restricted in time by the amount of overlap occurring between adequate prey availability and preferred temperatures at both short and long temporal scales.

4. Discussion

Fluctuations in chinook salmon GRP estimated in this study revealed significant variations in the ability of the water column to support chinook salmon growth on both short and long time scales. The relatively low chinook GRP in May was caused by water temperatures being below chinook thermal optimum (12–16 °C), and to the relatively low densities

Table 4

Kolmogorov–Smirnov statistic (D) calculated to assess significant differences among growth rate potential of chinook salmon during different times within each sampling period during the 1997 growing season

Comparison	May		June		July		September		October	
	D	D_α	D	D_α	D	D_α	D	D_α	D	D_α
Dawn vs. day	0.149[a]	0.069	0.351[a]	0.070	0.370[a]	0.066	–	–	0.631[a]	0.066
Dawn vs. dusk	0.248[a]	0.092	0.549[a]	0.093	0.404[a]	0.090	–	–	0.352[a]	0.087
Dawn vs. night	0.510[a]	0.074	0.182[a]	0.075	0.452[a]	0.070	–	–	0.371[a]	0.070
Day vs. dusk	0.254[a]	0.069	0.198[a]	0.069	0.420[a]	0.069	0.291[a]	0.064	0.459[a]	0.066
Day vs. night	0.517[a]	0.040	0.216[a]	0.041	0.477[a]	0.039	0.330[a]	0.048	0.404[a]	0.040
Dusk vs. night	0.263[a]	0.074	0.367[a]	0.074	0.081[a]	0.073	0.349[a]	0.052	0.317[a]	0.070

D statistics are evaluated against a critical D_α for unplanned comparisons.

[a] D values > D_α indicate significant differences at the $\alpha = 0.05$ level (Sokal and Rohlf, 1995).
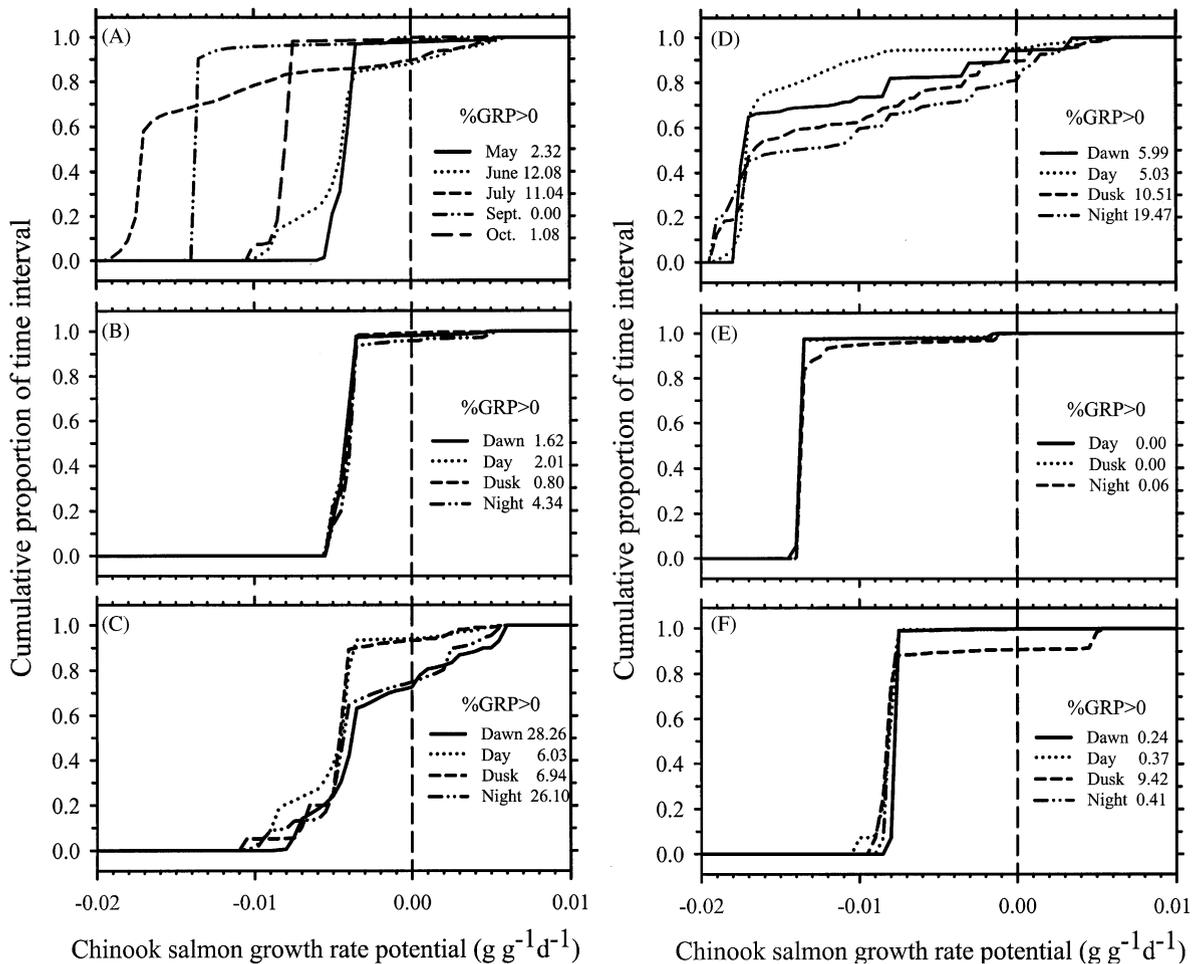
Fig. 7. Cumulative frequency distributions of, and the proportion of (A) each sampling event during 1997 (May, June, July, September, and October), (B) each time period (dawn, day, dusk, and night) during May, (C) June, (D) July, (E) September, and (F) October, supporting positive chinook salmon growth rate potential at our sampling location in western Lake Ontario.

of alewife in the sampling area. Substantial increases in the chinook GRP in June were a function of an increasing proportion of the water column where both chinook thermal optima and high prey densities overlapped.

In July, chinook GRP decreased, despite abundant prey, largely as a result of the water column becoming too warm to support positive growth. Lower estimates of chinook GRP in July, and its absence in September, support the conclusion that thermal structure can play a critical role in regulating GRP of species such as chinook salmon. In September, the water column was uniformly warm and well above chinook thermal optimum. Although prey were available, the use of this prey by chinook would not result in positive growth rates. The negative GRPs estimated during these warm periods predict that chinook would lose rather than gain weight despite the occurrence of abundant prey (e.g., Figs. 6C and 7E). Mason et al. (1995) obtained similar results for chinook GRP estimated in waters exceeding 20 °C in Lake Ontario during the late summer of 1987.

Higher estimates of chinook GRP in October were associated with the return of better thermal conditions (13.6 °C). Improved thermal condition were concurrent, however, with decreasing alewife

abundances resulting from their annual offshore migration (O'Gorman et al., 1987). Although better thermal conditions return during late autumn, chinook GRP was limited by prey availability rather than temperature. Hence, a seasonal pattern in chinook GRP based on both water column thermal structure and alewife density was evident at the nearshore station in western Lake Ontario.

Seasonal fluctuations of GRP, as observed in this study, have been reported elsewhere (Mason et al., 1995; Brandt and Kirsch, 1993; Goyke and Brandt, 1993; Luo and Brandt, 1993). Using a spatially explicit approach, Goyke and Brandt (1993) demonstrated seasonal fluctuations in chinook GRP measured along a cross-lake transect of Lake Ontario during 1991–1992. In their study, however, Goyke and Brandt (1993) reported maximum chinook GRP in autumn rather than in early summer as reported here. The discrepancy between these studies implies that GRP estimates made in the nearshore zone do not necessarily represent the lake as a whole but are representative of a more localised area. Predator GRP estimated at one specific location in the lake may be radically different form that measured at another based on the prevailing structure of both biotic (prey density) and abiotic (temperature) conditions at each site. Therefore, the spatial extent of areas where both prey distributions and optimal thermal regimes overlap needs to be known before this model can be applied to whole lake estimates of predator GRP (Mason and Patrick, 1993; Goyke and Brandt, 1993; Mason et al., 1995). A combined spatio-temporally explicit model would better describe system wide predator production potentials within large aquatic systems.

Significant fluctuations in chinook GRP were also observed during short time periods and current spatial models of whole lake GRP do not account for short term fluctuations. Positive chinook GRP occurred more often, and more consistently during crepuscular and night hours than during the day. This difference in GRP is associated with higher densities of alewife occurring within 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 changes in distribution. Alewife tended to form tight aggregations during day periods, but dispersed throughout the water column at night (Fig. 5, see also Janssen and Brandt, 1980; Ross et al., 1993). When dispersed throughout the water column at night and during crepuscular periods, the probability of alewife intersecting thermal regions conducive to chinook growth increases. Essentially, alewife contribution to chinook growth is more plausible during migration and/or midwater residency.

This study demonstrated a time 'window' occurring at both the seasonal and diel scales (June; crepusculars and night hours) when environmental conditions (thermal structure and prey availability) overlapped sufficiently for positive chinook growth to occur. These results suggest that chinook GRP is limited at both the seasonal and diel scales to critical, punctuated, growth events, which are a function of both adequate thermal conditions and prey availability co-occurring in both space and time. Failure in the realisation of these growth events due to subtle changes in the temporal dynamics of environmental conditions can have important consequences in terms of overall chinook production, especially if these changes are persistent, and occur over large areas. Punctuated growth events have been demonstrated in other aquatic ecosystems, and have proven to be deterministic of community structure (e.g., Lasker, 1978; Harris, 1980; Frank and Leggett, 1981, 1983; Fortier and Leggett, 1984; Legendre and Demers, 1984).

4.1. Application

Climate change, whether anthropogenically induced, or due to natural fluctuations, is occurring at an alarming rate (McFarlane et al., 2000). As demonstrated here, temperature plays a deterministic role in both the formation of thermal structure and in the distribution of prey within the water column. Consequently, the ability of the water column to support important fish stock production is also temperature dependent. Currently, the ability to predict the impacts of climate change on important fish stock production is limited by our ability to quantify the dynamics of the overlap in fundamental resources determining habitat quality in critical environments.

This study has demonstrated that fish GRP, and by proxy, habitat quality, is determined by transient blends of environmental conditions. Independent measurements of environmental conditions such as temperature or prey abundances are of limited value

without the knowledge of how these variables relate to each other both spatially and temporally to provide suitable habitats for growth. The modelling framework presented here, provides a mechanism for quantifying the relative importance and interconnectedness of environmental conditions with respect to target species habitat quality over time. As such, the temporally explicit modelling framework can assess how a water column changes in its ability to promote, sustain, or restrict fish production in response to changes in climate patterns.

Adaptation of this model to important species such as alewife or capelin (*Mallotus villosus*) can be used in critical spawning or nursery grounds to monitor the habitat available for the production and recruitment of new year classes supporting commercially valuable top predators such as cod (*Gadus morhua*) and various salmonids. Applying this model to such key areas will be useful in evaluating the effects of changes (e.g., habitat and/or density-dependent fluctuations) in the prey base on the production of target species threatened by over-exploitation.

Recent studies suggest that the establishment of protected areas in both marine and freshwater environments can provide a buffer against over-exploitation, habitat and community degradation, and high degrees of uncertainty associated with current management practices (Allison et al., 1998; Hall, 1998; Lauck et al., 1998). A fundamental obstacle to the ubiquitous adoption and use of protected areas in aquatic systems management is the inherent inability to systematically assess where these areas ought to be established (Allison et al., 1998). Which areas would provide the best sanctuaries, breeding grounds, or areas of target species production?

Once established, monitoring of these areas must be initiated in order to understand how these areas contribute to the conservation of both target and ecologically related species (Roberts, 1997; Allison et al., 1998; Lauck et al., 1998). Moreover, and especially in light of both global and localised changes in climate pattern, it becomes essential to understand how these protected areas are also changing and whether or not they continue to provide their intended protection.

The temporally explicit modelling framework developed here will be valuable in the establishment and monitoring of marine protected areas (MPA) and their freshwater counterparts. Applying a temporally explicit model to these critical areas will help determine the size and status (i.e., sink or source) of protected areas by demonstrating their production potential over time. For example, when these areas provide suitable conditions for target species, how often do these conditions arise, and how long do they last? In short, the temporally explicit model demonstrates the inherent temporal fluctuations and ephemeral nature of environmental conditions supporting growth of a specific species of fish, and provides a method to assess these changes on a variety of temporal scales.

Acknowledgements

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