GROWTH IN FISHES:
SIZE-AT-AGE, TEMPERATURE AND FOOD

by

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Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
December 2007

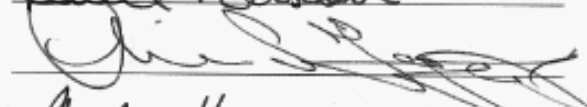DALHOUSIE UNIVERSITY

DEPARTMENT OF OCEANOGRAPHY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "GROWTH IN FISHES: SIZE-AT-AGE, TEMPERATURE AND FOOD" by Anna B. Neuheimer in partial fulfillment of the requirements for the degree of Doctor of Philosophy.
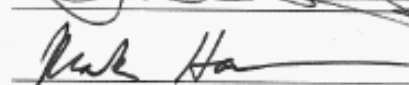
Dated: December 5, 2007

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Examining Committee: _____

_____

Departmental Representative: _____

DALHOUSIE UNIVERSITY

To my parents,

Judith and Ernie,

and their parents,

Beatrice and Roger, Mathilda and Felix,

whose sacrifice, support and love made this possible.

and

To the girl in the bucket.

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Abstract

Variation in fish growth results in variation in size-at-age and directly affects vulnerability to fisheries, predator-prey interactions, as well as reproductive potential of a population. The majority of the variation in growth in fishes can be attributed to variation in the environment, especially temperature and food consumption. My thesis is that I can quantitatively partition the variation in fish size-at-age to that attributable to changes in temperature and that attributable to changes in food consumption. First I explore metrics of temperature and food consumption relevant to fish size-at-age. A measure of the thermal integral, the growing degree-day (GDD), is employed to explain temperature-dependent variation in fish size-at-age. The GDD metric is able to explain between 92 and 99% of variation in fish size-at-age over a range of species among environments, temperature regimes, laboratory and field studies. In addition, the GDD metric is employed to extricate the temperature-dependent variation in Scotian Shelf haddock (*Melanogrammus aeglefinus*) size-at-age by isolating declines in size-at-age among year-classes not explained by temperature variation and most parsimoniously explained by size-selective fishing.

I explore the ability to estimate variation in fish food consumption through an analysis of the accuracy and sensitivity of stomach evacuation models. One such model is then employed using historical stomach content data for southern Gulf of St. Lawrence (sGSL) Atlantic cod (*Gadus morhua*) to obtain temporal variation in food consumption (daily ration, DR, g·day^{-1}) estimates. Finally temperature- (variation in GDD) and food consumption- (variation in DR) dependent variation in sGSL cod size-at-age is extricated and remaining size-at-age variation among year-classes is explored.

My research examines variation in temperature and food consumption in a manner that is physiologically-relevant to the fish, thereby increasing the ability to successfully extricate the many factors influencing size-at-age (i.e. growth) in fishes. Results of my research may be used to formulate more predictive growth models of fish that can be applied to studies on the physiology, ecology and management of fish populations.

List of Abbreviations and Symbols Used

Abbreviation	Definition	Units
GDD	Growing degree-day	ºC·day
LaD	Length-at-day	mm or cm
T	Temperature	ºC
T_{Th}	Threshold temperature	ºC
β	Slope of LaD-at-GDD relation	mm·(°C·day)$^{-1}$
α	Intercept of LaD-at-GDD relation	mm
β'	Slope of LaD-at-Time relation	mm·day^{-1}
α'	Intercept of LaD-at-Time relation	mm
nSFI	Normalized stomach fullness index	
GDH	Growing degree-hour	ºC·hr
θ	Slope of nSFI-at-GDH	(°C·hr)$^{-1}$
ρ	Intercept of nSFI-at-GDH	
M	Instantaneous mortality rate	
A	Annual mortality rate	%·yr^{-1}
W	Fish weight	g
L	Fish length	cm or mm
a	Weight-at-length parameter	g·cm^{-b}
b	Weight-at-length parameter	
K_n	Relative condition	
K_3	Cube-law condition	
$T^{stage}_{area,i}$	Daily temperature in area (in or out) associated with fish stage (immature or mature)	ºC
T^{stage}_{i}	Daily temperature associated with fish stage (immature or mature)	ºC
S	Stomach content weight	g
C	Food consumption rate	g·hr^{-1}
G	Stomach evacuation rate	g·hr^{-1}
p	Rate parameter of evacuation rate function	g^{1-a}·hr^{-1}
a	Shape parameter of evacuation rate function	
μ	Andersen and Riis-Vestergaard function parameter	g^{-v}
v	Andersen and Riis-Vestergaard function parameter	
d	Andersen and Riis-Vestergaard function parameter	ºC^{-1}
P	Prey concentration	mg·m^{-2}
ε	Proportionality constant	m^2·mg^{-1}
D	Half-saturation constant	mg·m^{-2}
H	Maximum stomach contents parameter	

Abbreviation	Definition	Units
S_{max}	Stomach content weight at which ingestion becomes zero	g
p_{wte}	Rate constant as a function of weight, temperature and food energy-density for Andersen 1 evacuation rate function	$g^{1-a-\gamma} \cdot (kJ \cdot g^{-1})^u \cdot hr^{-1}$
E	Food energy-density	kJ·g^{-1}
γ	Predator weight parameter for Andersen 1 and 2 evacuation rate functions	
δ	Temperature parameter for Andersen 1 and 2 evacuation rate functions	ºC^{-1}
μ	Food energy density parameter for Andersen 1 evacuation rate function	
p_{wt}	Rate constant as a function of weight and temperature for Andersen 2 evacuation rate function	$\left(g^{1-a-\gamma} \cdot hr^{-1} \right)$
DR_{model}	Modelled daily ration	g·day^{-1}
DR_P	Daily ration estimated with the Pennington method	g·day^{-1}
DR_P'	Daily ration estimated with the simplified Pennington method	g·day^{-1}
DR_{actual}	Lab-estimated actual daily ration	g·day^{-1}
SFI	Stomach fullness index	g·cm^{-3}
%E	Proportion of stomachs empty	
$DR_P{'}_{L,M,Y,E}$	Mean daily ration at month M, year Y and food energy-density E estimated with the simplified Pennington method	g·day^{-1}
CFC$_E$	Cumulative food consumption using food energy density E	g
DR_{Th}	Threshold daily ration	g·day^{-1}

Acknowledgements

I am grateful for the many people, places and things that have made this a possible and pleasurable journey. In particular:

The People

Dr. C.T. Taggart whose creativity and intelligence is matched only by the patience, encouragement and enthusiasm he gives his students. I have counted myself lucky, honoured and proud every day.

My Committee, Drs. Wendy Gentleman, J. Mark Hanson and Marlon Lewis, who provided valuable comments and guidance. In particular, I am grateful to Dr. Gentleman who taught me that biology and math can and should coexist.

The many others that provided advice and data along the way including Drs. Ken Frank, Barry Ruddick, Alain Vézina, Ken Drinkwater, C.A. Dion and N.F. Hughes as well as the crews of the Opilio (OPL-2003-080), Southern Gulf of St. Lawrence Bottom Trawl Surveys, DFO Cod Stomach Database and Taggart lab (esp. Caroline Chénard).

My parents for unending support of every kind. I hope they know how proud I am, and how lucky I feel, to be their daughter.

My family (proudly O'Leary and Neuheimer because of you) and friends back in Upper Canada who have been my long distance support, especially Laura Simpson, my eternal cheerleader.

My SisterAunt and all my extended family to the West who I think about much more often than I see, who make me feel "sifted" every time I do see them, and who have shown me that the right combination of love and community is strong enough to even get a stranded whale back to the ocean. I am grateful for every one of you.

Kerri (Dr. K) Finlay, Tanya (PST) and Jay (STJ) Bryan, Noreen (Queenie) Kelly, Ramzi (RaRa) Mirshak and the rest of the B-Team$^©$ who have opened up my definition of family and made Halifax a home. MadDog: mark this down as a SVFM.

Janelle (Diamond J) Leblanc, my favourite variable, who turns up the fun all the way to eleven and makes me feel sane just by being the same kind of crazy as me. I met you just in time.

Dan (Wrath) Reed, the Howard to my Vince, who has been a daily source of support, laughter and procrastination (not to mention TOTDs) and whose friendship I count among the most important of my life. Back of the net!

The Money

The Music

My six main chapters were written with the audio motivation of Radiohead's first six studio albums. I recommend the following musical company when reading this thesis:

Chapter 2 – The growing degree-day and fish size-at-age: the overlooked metric:

Pablo Honey
"Here we are with our running and confusion, and I don't see no confusion anywhere"
~ Anyone Can Play Guitar

Chapter 3 – Fishing selection and size-at-age in Scotian shelf haddock (*Melanogrammus aeglefinus*) – application of the growing degree-day metric:

The Bends
"I wish it was the sixties" ~ The Bends

Chapter 4 – Variations in growing degree-day and size-at-age in southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*)

OK Computer
"No alarms and no surprises" ~ No Surprises

Chapter 5 – Estimating food consumption in fish: what really matters?:

Kid A
"You're living in a fantasy world" ~ In Limbo

Chapter 6 – Temporal variation in stomach content and food consumption of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence:

Amnesiac
"Well of course I'd like to stay and chew the fat" ~ Life in a Glass House

Chapter 7 – Variation in Atlantic cod (*Gadus morhua*) size-at-age: disentangling effects of variation in temperature (growing degree-day) and food consumption:

Hail to the Thief
"There's always a siren singing you to shipwreck" ~ There There

"Come with us now on a journey through time and space…"

The Mighty Boosh

Chapter 1

Introduction

1.1 Growth in Fishes

Among fish, variation in growth results in variation in size-at-age which has a direct effect on vulnerability to fisheries, predator-prey interactions, as well as reproductive potential. Francis (1994) summarized this in three ways: 1) individual growth rates determine the time it takes for a fish to reach a given size and affects the individual's vulnerability to predators and its ability to exploit food resources; 2) population mean growth rates affect the productivity of the population as well as the rate at which the population may be sustainably harvested; and 3) growth estimates are therefore essential to population and ecosystem studies, nutrient pathway explorations as well as the assessment of fishing pressure and sustainable management of fisheries.

1.2 Factors Influencing Fish Growth

Growth rate will vary through the life of the fish due to life history events such as maturation where growth slows as energy is diverted from growth to reproduction. In addition, environmental conditions influence growth rate (and subsequently size-at-age) and include temperature, food consumption, size-selective mortality and density-dependent effects (Dutil et al. 1999). These factors vary in time and space and result in variation in size-at-age (Francis 1994). While most studies have focused on examining the effect of variation in one environmental factor on size-at-age variation (Campana et al. 1995, Dutil et al. 1999), "failure to simultaneously consider alternative mechanisms, especially size-selective mortality, can lead to incorrect conclusions about the role of environmental factors in determining growth of fishes" (Sinclair et al. 2002).

1.2.1 Temperature

In most ectotherms (e.g. plants, insects, aquatic invertebrates, and most reptiles, amphibians and fish), many physiological processes that determine growth (e.g. metabolic rate, gas exchange, risks of desiccation in terrestrial animals and oxygen supply in aquatic animals) are directly influenced by temperature and thus time-dependent variations in temperature are reflected in time-dependent variations in size-at-age (Atkinson 1994; van der Have and de Jong 1996; Donker et al. 1998). Within limits, higher temperature will produce higher reaction rates in the enzymatic reactions thought to govern growth (Higley et al. 1986). Diffusion of enzymes or substrates or both increase, resulting in a greater number of enzyme-substrate complexes as well as more energy available to meet the energy requirements of reactions. This relationship is generally linear except at extremes where temperature can cause an inactivation of a control enzyme(s) through conformational change (Sharpe and DeMichele 1977) or the destruction of enzymes or nutrients more rapidly than they are sequestered (Howe 1967). This is true for all ectotherms including plants, insects, aquatic invertebrates and most fish. Indeed, describing the relation between growth and temperature could "help provide a universal biological basis for the production of predictive quantitative models of size-at-[age]." (Atkinson 1994, pp. 43).

1.2.2 Food Consumption

The growth of fish is strongly regulated by the quantity and type of food consumed resulting in a positive relationship between food consumption and growth in many species (e.g. Elliott 1975). As a consequence, there has been a large increase in the scientific literature concerning many aspects of feeding-related fish physiology and ecology. However, clear and reliable relations between environmental influences and stock production, including the relation between food consumption and population structure, are rare (Dutil and Brander 2003). Gerking (1994) made it clear that if "a reasonable estimate of food consumption can be made, [then] several aquatic ecological problems are simplified" (e.g. fish production and growth in different environments).

1.2.3 Size-Selective Fishing

Most fishing gear is size-selective (Sinclair et al. 2002). If a portion of the phenotypic variation in size-at-age is rooted in genetic variation, it is possible that fishing mortality (often exceeding natural mortality by a factor of 2 or 3) may represent a strong force of selection on a population (Engelhard and Heino 2004; Hutchings 2005) resulting in evolutionary changes in growth and maturation (Law 2000; Stokes and Law 2000). Evidence of these changes in growth dynamics often accompanies periods of exploitation and have been shown to have a genetic link for Atlantic cod (Grift et al. 2003, Olsen et al. 2004, Hutchings 2005, Swain et al. 2007). Changes in mean growth dynamics affect population growth and recovery rates through decreased age- and size-at-maturity, fecundity and egg size (Hutchings 2005). Thus, evaluating fishing pressure and its effects on fish size-at-age is instrumental in describing the production capabilities of a population for successful fisheries management.

1.3 Objectives

The goal of my research is the quantitative explanation of the variation in fish growth (size-at-age) due to variation in temperature, food consumption and size-at-age metrics. This requires 1) estimates of variation in temperature and food consumption relevant to fish size-at-age, 2) quantifying the amount of variation in size-at-age that can be explained by variation in these metrics and 3) examination of residual variation in size-at-age with size-selective fishing mortality metrics. The research includes many fish species, marine and freshwater, tropical and temperate and has special emphasis on Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence (sGSL) due to the large decline in size-at-age exhibited by this stock over recent decades (Chouinard et al. 2006). My objectives are 1) the identification and testing of a physiologically-relevant measure of temperature variation in explaining temperature-dependent variation in fish size-at-age, 2) the quantification of the variation in size-at-age of sGSL cod that can be explained by this temperature metric, 3) the estimation of food consumption variation for sGSL cod beginning with an analysis of current food consumption models and associated assumptions and 4) the extrication of variation in sGSL cod size-at-age due to variation in

temperature and food consumption (using the results from Objectives 2 and 3) to quantify residual variation in size-at-age that may be explained by other factors affecting fish growth. My work describes a method of disentangling the many factors affecting size-at-age that may be employed in the more accurate prediction of fish growth and more successful development of management strategies for exploited fish populations.

This document is divided into 8 chapters (including this Introduction). **Chapters 2** through **7** address the above objectives and are designed as manuscripts for primary publication. As such, the reader is forewarned that parts within this Introduction and among the subsequent chapters contain some repetition. **Chapters 2** and **3** explore the ability of the growing degree-day (GDD) metric to explain variation in fish size-at-age. **Chapters 4** through **7** describe the extrication of size-at-age variation in southern Gulf of St. Lawrence (sGSL) Atlantic cod (*Gadus morhua*) due to temperature and food consumption variation. Variation in cod size-at-age with variation in GDD among year-classes is explored in **Chapter 4**. Variation in cod size-at-age with food consumption variation is explored in **Chapters 5** through **7** through an analysis of contemporary food consumption models (**Chapter 5**) and a quantification of the variation in stomach contents and food consumption among sGSL cod (**Chapter 6**). In **Chapter 7** I examine the residual temperature-independent variation in size-at-age from **Chapter 4** with the food consumption estimates made in **Chapter 6** as well as other possible sources of variation. In **Chapter 8** I present the summary conclusions of my research.

Parts of this thesis research have been published, submitted for publication in the primary literature and/or presented at conferences. The majority of **Chapter 2** is published as "The growing degree-day and fish size-at-age: the overlooked metric" (Neuheimer, A.B. and Taggart, C.T. 2007. Can. J. Fish. Aquat. Sci. 64: 375-385). I was responsible for the data analysis, interpretation and implications of results for this manuscript. In addition, as primary author I was responsible for the various drafts and final manuscript. C.T. Taggart provided direction, suggestions and editing. In addition, aspects of **Chapter 2** have been presented at the Canadian Conference for Fisheries Research ("Growing degree-day predicts fish growth", Calgary, Alberta, 2006), Annual Workshop and General Meeting of the Atlantic Canada Coastal and Estuarine Science Society and Canadian Rivers Institute Symposium ("Growth in fishes – a near-universal

metric", Fredericton, New Brunswick, 2006), Northwest Atlantic Fisheries Organization Symposium ("Growth in fishes: a near-universal metric", Dartmouth, Nova Scotia, 2006), and Conference of Dalhousie Oceanography Graduate Students ("Growing degree-day and growth in fishes", Halifax, Nova Scotia, 2006). Aspects of **Chapter 3** have been presented at the 24th Lowell Wakefield Fisheries Symposium ("Growth in fishes: a near-universal metric", Anchorage, Alaska, 2006) and the 2007 Fisheries Oceanography Committee Meeting ("Condition estimates and length-at-age in Scotian Shelf haddock, *Melanogrammus aeglefinus*", Dartmouth, Nova Scotia, 2006) and a portion of **Chapter 3** has been accepted for publication as "Size-at-age in haddock (*Melanogrammus aeglefinus*) - application of the growing degree-day (GDD) metric." (Neuheimer, A.B., Taggart, C.T. and Frank, K.T. Proceedings of the 24th Lowell Wakefield Fisheries Symposium: Resiliency of Gadid Stocks to Fishing and Climate Change Symposium). I was responsible for the data analysis, interpretation and implications of results of this manuscript. In addition, as primary author I was responsible for the various drafts and final manuscript. C.T. Taggart and K. T. Frank provided direction, suggestions and editing. Aspects of **Chapter 5** have been presented at the Conference of Dalhousie Oceanography Graduate Students (2003: "The development of an empirically-based prey consumption model for Atlantic cod of the southern Gulf of St. Lawrence" and 2005: "Estimating food consumption in fish: What really matters?", Halifax, Nova Scotia), Canadian Conference for Fisheries Research ("Estimating daily ration in fish: what really matters?", Windsor, Ontario, 2005) and the Bedford Institute of Oceanography ("Estimating food consumption in fish: What really matters?", Dartmouth, Nova Scotia, 2005).

Chapter 2

The Growing Degree-Day and Fish Size-at-Age: The Overlooked Metric

A portion of this chapter is published in:

Neuheimer, A.B. and Taggart, C.T. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Can. J. Fish. Aquat. Sci. 64: 375-385

2.1 Introduction

The physiological processes that determine growth (e.g. metabolic rate, gas exchange, risk of desiccation in terrestrial organisms and oxygen supply in aquatic animals) are directly influenced by temperature (Atkinson 1994; van der Have and de Jong 1996). Accordingly, time-dependent variations in temperature are reflected in time-dependent variations in ectotherm development and size-at-age where the latter is frequently used to infer growth rate. This appears to be true for most ectotherms including plants, insects, aquatic invertebrates, and most reptiles, amphibians and fish. Within limits, and in general, higher temperatures result in higher enzymatic reaction rates that govern growth (Higley et al. 1986). Diffusion of substrates or enzymes or both increase, resulting in a greater number of enzyme-substrate complexes and more energy to meet reaction demands. This physiological response, greatly simplified in terms of the complex processes involved, is generally linear over a mid-range of temperatures bounded by a lower temperature threshold (T_{Th}) and upper temperature maximum. The physiological response becomes non-linear outside of this temperature range where control enzyme(s) are inactivated by conformational change (Sharpe and DeMichele 1977) or enzymes or substrates are destroyed more rapidly than they are sequestered (Howe 1967).

In fish, variation in size influences predator-prey interactions, maturation, reproduction and recruitment potential and vulnerability to size-selective fishing. Thus, explaining or predicting growth variation through size-at-age is often essential to

population and ecosystem studies and nutrient/energy pathway explorations (food webs) as well as in determining fishing pressures suitable for sustainable fisheries. The greatest impediment to most fish-growth models, including the pervasive von Bertalanffy Growth Function (VBGF, von Bertalanffy 1938), is their dependence on calendar time to explain length variation (i.e. length-at-age). Calendar time may be appropriate for growth of endotherms that experience relatively constant temperatures (e.g. humans, for which the VBGF was originally formed, von Bertalanffy 1938). However, use of a calendar time growth model such as the VBGF for ectotherms explicitly ignores time-dependent and physiologically-meaningful variables such as temperature. Some growth models do attempt to incorporate temperature; usually instantaneous measures of temperature (Francis 1994; Mallet et al. 1999; Dion and Hughes 2004). However, instantaneous local temperature estimates (e.g. daily mean) do not necessarily reflect the phenotypic expression of the growth integral (i.e. length-at-age) in an equally instantaneous manner. For over 270 years in agriculture and for at least 45 years in entomology, the time-based integral of the heat available for growth – heat transferred from the environment to the ectotherm – has been employed with remarkable success in explaining and predicting growth and development (e.g. Seamster 1950; Atkinson 1994; Bonhomme 2000). The most prevalent approximation of the heat integral is the growing degree-day (GDD, ºC·day); the time integral of the daily temperature measured above some temperature threshold (T_{Th}, ºC). The GDD method allows growth and development to be correctly scaled to the physiology that drives ectotherm growth and development. Simply stated, growth and development are proportional to the time spent at temperature (thermal time, Trudgill et al. 2005) within the range where metabolic reaction rates are near-linear functions of temperature. The thermal-integral concept should be applicable to most fish studies simply because fish are ectotherms; their metabolic rate is largely determined by the heat transferred from the environment during the period of growth and development (e.g. Leggett et al. 1984; Hamel et al. 1997; Kjellman et al. 2001). However, relative to agriculture and entomology, my examination of the primary literature (Fig. 2.1) demonstrates only a handful (4.6%) of studies that address temperature and growth in fishes refer to the GDD metric (e.g. Mills 1988; Mills et al. 1989; Kjellman et al. 2001). Though several fish studies address the combination of time and temperature (e.g. Iwama

and Tautz 1981, Brander 1995), none appear to follow through on the implications of the thermal integral or explore its generality. To paraphrase Reaumur (1735, in Bonhomme 2000): "*The same* [fish] *are harvested in very different climates; it would be interesting to compare the sums of heat degrees over the months during which the* [fish] *does most of its growing and reaches complete maturity in hot countries, like Spain or Africa… in temperate countries like France and in the colder countries of the North.*".

In this chapter, I examine the utility of the GDD metric in explaining variation in fish length-at-day (LaD), in most cases prior to maturation, within and among published datasets drawn from marine and freshwater environments, temperate and tropical climes, constant and variable temperature regimes, and laboratory and field studies. In addition, I examine the ability of GDD variation to explain variation in fish-egg development-time and in aquatic invertebrate (crab) size-at-age.
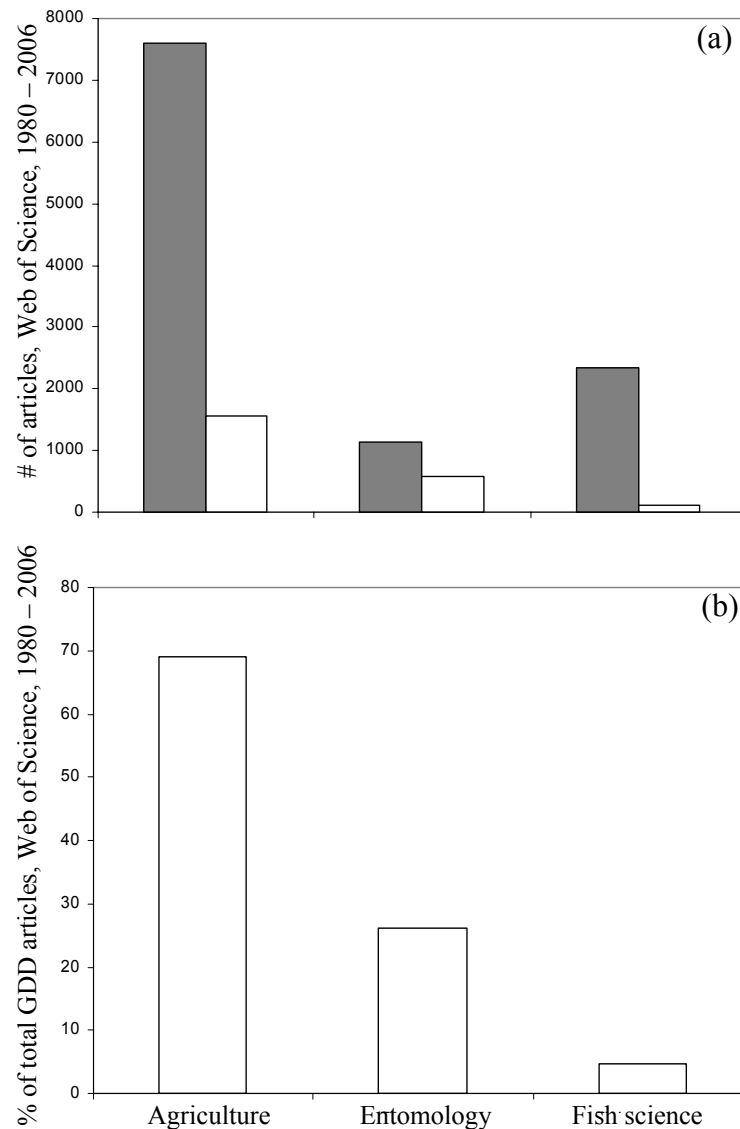
Figure 2.1: Histograms of (a) the number of articles listed by Web of Science® for the period 1980 through 2006 referring in title, keywords or abstracts to temperature and growth, gray bars, key words: "temperature" AND ("development" OR "growth"); or GDD, open bars, key words: "degree day*" OR "thermal sum" OR "day degree*" OR "growing degree day*" OR "thermal time"; in agriculture, entomology and fish science, and (b) the per cent total number of articles listed by the Web of Science® for the period 1980 through 2006 referring in title, keywords or abstracts to GDD (key words: "degree day*" OR "thermal sum" OR "day degree*" OR "growing degree day*" OR "thermal time") in agriculture, entomology and fish science.

2.2 Methods

Temperature, length-at-day, and development-time data were extracted from data tables and/or by digitizing figures retrieved from the published literature (Table 2.1). It is important to measure the length of the fish in studies where the intent is to use a thermal integral. Although weight, as a function of length, should, in general, be explained by GDD, seasonal variations in weight-at-age compromise the size measure in contrast to length-at-age that is relatively invariant on a seasonal basis. In all, 58 datasets were collected representing 9 fish species and different life-history stages (most prior to maturation), among sub-tropical, temperate, freshwater and marine environments, including control experiments with constant and variable temperature and field studies. The Atlantic cod data (Brander 1995, Imsland et al. 2007) were an exception where the stock-specific weight-at-age estimates were converted to stock-specific length-at-age estimates by using literature-based stock-specific weight-at-length regressions (Kohler et al. 1970; Daan 1974; O'Brien and Monroe 2001; Lilly et al. 2003; Marshall et al. 2004). The latter regressions revealed one general (model) relation for the 19 cod stocks across their North Atlantic range (Fig. 2.2). The validity of this strong relation was tested by examining the mean annual length- and weight-at-age estimates for northern cod (North Atlantic Fisheries Organization, statistical Division 2J3KL) over the period 1977 to 1992 inclusive (n=551); data in hand. This examination showed that the observed 2J3KL data fit within one standard deviation of the general model (Fig. 2.2).

Table 2.1: Summary of published data used to examine the GDD method.

Species Study	Location (field/lab; environment; location)	Source, length (mm), data secured	GDD provided? (Threshold temperature, T_{Th})	Calculation of GDD	
				Temperature (°C) obtained in source from:	daily mean temperature
herring (*Clupea harengus*) Folkvord et al. 2004	lab; marine; Norway	Figure 2a (digitized)	no	Figure 1	digitized
houting (*Coregonus oxyrhynchus*) Malzahn et al. 2003	lab; marine; North Sea	Figure 3 (digitized)	Figure 3 (digitized) [+]	n/a	
Atlantic cod *(Gadus morhua)* Imsland et al. 2007	lab; marine; Norway	Figure 2 (digitized)	no	text, constant	
Arctic grayling (*Thymallus thymallus*) Dion and Hughes 2004	field; freshwater; Alaska	Figure 1e-h (digitized)	no	daily temperature provided by originating authors	
minnow (*Phoxinus phoxinus*) Mills 1988	field; freshwater; Finland	Table 2	Table 2 (T_{Th}=5°C)	n/a	
spider crab (*Mithraculus forceps*) Penha-Lopes et al. 2006	lab ; marine; Florida	Table 1	no	Table 1	

Table 2.1 cont.

Species Study	Location (field/lab; environment; location)	Source, length (mm), data secured	GDD provided? (Threshold temperature, T_{Th})	Calculation of GDD	
				Temperature (°C) obtained in source from:	daily mean temperature
red king crab (*Paralithodes camtschatics*) Stevens 1990	field; marine; Alaska	Figure 3 (digitized)	Figure 3 (digitized)[+]	n/a	
European grayling (*Thymalluis thymallus*) Mallet et al. 1999	field; freshwater; France	Figure 4ab (digitized)	no	Figure 4ab	digitized and interpolated
snapper (*Pagrus auratus*) Francis 1994	field; marine: New Zealand	Figure 8 (digitized)	no	Figure 4	digitized and interpolated
Atlantic salmon (*Salmo salar*) Jones et al. 2002	field; anadromous; Scotland	Figure 1a (digitized)	no	Figure 1c	digitized and interpolated
threespine stickleback (*Gasterosteus aculeatus*) Wright et al. 2004	lab; freshwater; Scotland	Figure 2a (digitized)	no	text, constant	
Atlantic cod (*Gadus morhua*) Brander 1995	field, marine, North Atlantic	Table 1	no	Table 1	interpolated

Table 2.1 cont.

Species / Study	Location (field/lab; environment; location)	Source, length (mm), data secured	GDD provided? (Threshold temperature, T_{Th})	Calculation of GDD	
				Temperature (ºC) obtained in source from:	daily mean temperature
burbot (*Lota lota*) Kjellman and Eloranta 2002	field; freshwater; Finland	Figure 1b (digitized)	Figure 1b (digitized)[+]		n/a
chinook salmon (*Onchorhynchus tshawytscha*) Alderdice and Velsen 1978	lab; anadromous; Pacific	Table 1*	no	Table 1: Incubation temperatures 1.7 to 18.1ºC	
trout (*Salmo fario*) Gray 1928	lab; freshwater; unknown	Table 1*	no	Table 1: Incubation temperatures 2.8 to 12.2ºC	
Atlantic cod (*Gadus morhua*) Pepin et al. 1997	lab; marine; Newfoundland	Figure 1*	no	Figure 1: Incubation temperatures 1 to 7ºC	
yellowtail flounder (*Pleuronectes ferrugineus*) Benoit and Pepin 1999	lab; marine; Northwest Atlantic	Figure 4*	no	Figure 1: Incubation temperatures 5 to 13ºC	

*days to hatching
[+]T_{Th} = 0 assumed
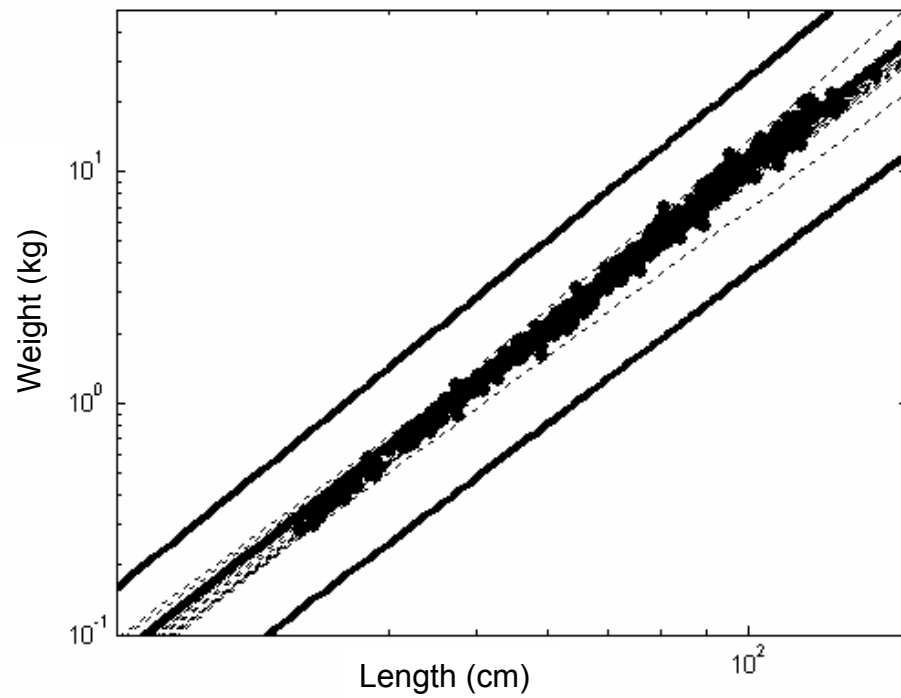
Figure 2.2: Weight-at-length relation used to convert weight-at-age (kg) to length-at-age (cm) for Atlantic cod data. Thin dotted lines denote length-weight relations for 17 cod stocks across the North Atlantic (Kohler et al. 1970; Daan 1974; O'Brien and Monroe 2001; Lilly et al. 2003; Marshall et al. 2004). Thick solid lines denote mean length-at-weight parameters ± standard deviation ($W = 8.9 \times 10^{-6} \cdot L^{3.03}$). Filled circles are mean annual length- and weight-at-age estimates for northern cod (North Atlantic Fisheries Organization, statistical Division 2J3KL) over the period 1977 to 1992 inclusive (n=551); data on hand.

Where average daily temperature estimates were not provided, they were estimated using linear interpolation of the weekly, monthly, annual etc. estimates. The GDD estimate at day n (°C·day) was calculated as:

$$GDD(n) = \sum_{i=1}^{n} \left(T_i - T_{Th}\right) \cdot \Delta d, \quad T_i \geq T_{Th} \; , \tag{1}$$

where T_i is the mean daily temperature at day i, T_{Th} is the predetermined threshold temperature and Δd is a set time step (sampling frequency, i.e. 1 day). As the Celsius scale is an arbitrary one (McLaren 1995), any growth model including temperature as °C must include an estimate of the threshold temperature (T_{Th}). When a growth model uses a mean temperature there is an implicit assumption that $T_{Th} = 0$°C. This may be avoided by using an absolute temperature scale based on heat energy (i.e. Kelvin, the S.I. unit for thermodynamic temperature). However, integration of Kelvin temperature results in smoothing (due to the relatively large values each datum in the series will have; e.g. 10°C = 283.15°K) of fluctuations in the GDD series (°C) that parallel those of the LaD series. Thus, it is more physiologically-relevant to choose a temperature scale and threshold that correspond to the minimum limit of the organism and its environment; e.g. perhaps near -2°C for marine fish. Initially, T_{Th} was set at 0°C. I tested the incorporation of various threshold temperatures (T_{Th}; °C) in the GDD metric (relative to the 0°C default) by examining the change in the coefficient of determination (r^2) in the LaD-at-GDD relation when varying T_{Th} between -20 and 20°C in 1°C increments. This range more than captured the variation in temperature in the published literature. Only those data offering a variation in temperature and accompanied by time were included (20 datasets). While the location of the maximum r^2 varied greatly among datasets, each described a characteristic and rapid decay in the r^2 at some positive T_{Th} (Fig. 2.3). The location of this rapid decay was defined as the maximum useable threshold arbitrarily, but conservatively, determined at the point of a 10% decrease in explained variation relative to the maximum r^2 (i.e. maximum explained variation in LaD by GDD); here termed the "$10\%T_{Th}$". While there is considerable variation in the value of the $10\%T_{Th}$ among datasets, two interesting patterns were revealed (Fig. 2.4). First, warm-water snapper (*Pagrus auratus*) exhibited a higher (Wilcoxon Rank Sum, n = 20, P = 0.0076) geometric

mean $10\%T_{Th}$ = 19.3°C than did cold-water fish (grayling *Thymallus thymallus*, Atlantic salmon *Salmo salar*, herring *Clupea harengus*) with geometric mean $10\%T_{Th}$ = 12.2°C; possibly the result of life-history adaptation to their temperature environments. Second, the $10\%T_{Th}$ does not fall below 4°C. Interestingly, and perhaps meaningfully, this is the average temperature below the thermocline in temperate marine waters (Dando and Burchett 1996) and is the temperature of maximum density in freshwater. Changing the 10% criterion to some lower value (i.e. < 10%) results in a similar pattern at lower T_{Th}.

All GDD and LaD time series were validated for normality using a Shapiro-Wilk test (significance level = 0.05). Variation in size (LaD) and variation in physiological time, GDD, were compared and quantified through linear regression for each dataset, producing a relation of the form:

$$LaD = \beta \cdot GDD + \alpha , \qquad (2)$$

where β is the slope, mm·(°C·day)$^{-1}$, and α is the intercept, mm, of the LaD at GDD relation. The above methods were applied in a similar manner to resolve LaD as a function of calendar time. All statistical analyses were performed using Matlab (Version 6.5, MathWorks Inc.). Statistical significance was generally evaluated at significance level = 0.05.
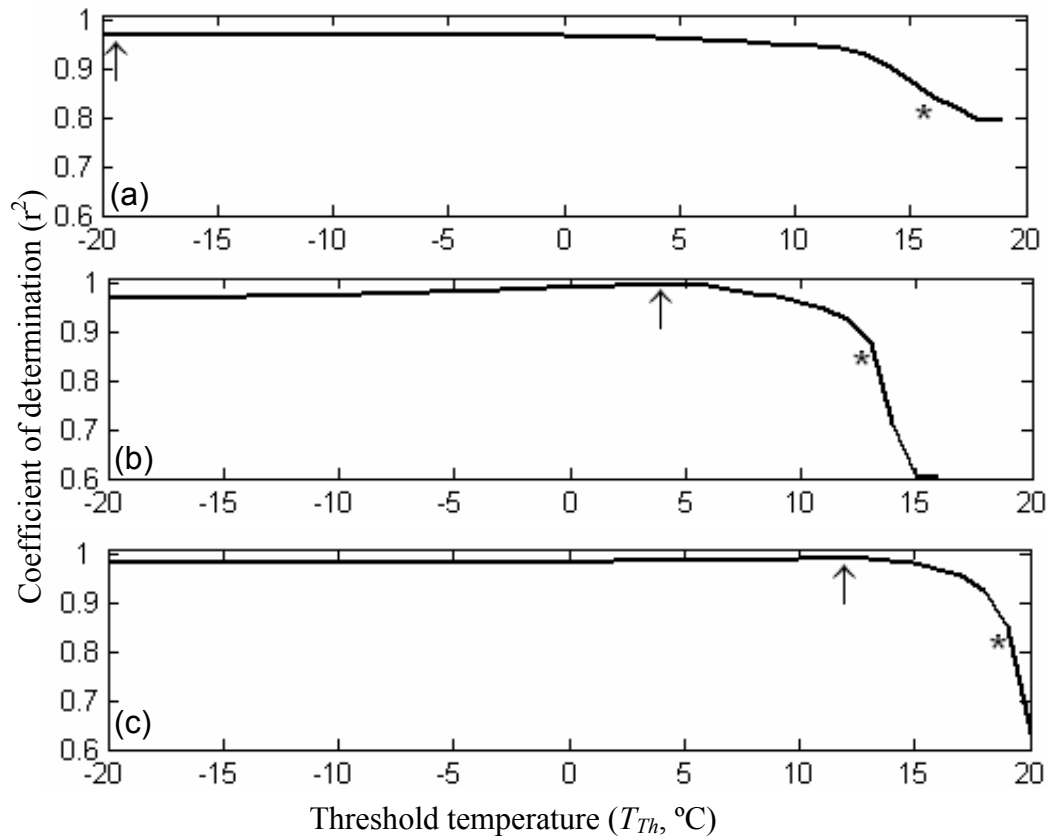
Figure 2.3: Variation in the coefficients of determination (r^2) in the LaD at GDD relation due to changing the threshold temperature (T_{Th}) between -20ºC and 20ºC for three example datasets covering the full range in the position of the maximum r^2 (arrow): a) Arctic Grayling (Alaska, Dion and Hughes 2004), b) European grayling (France, Mallet et al. 1999), c) snapper (New Zealand, Francis 1994). * indicates position of *10%T_{Th}*; i.e. a 0.10 decrease in r^2 relative to the maximum.
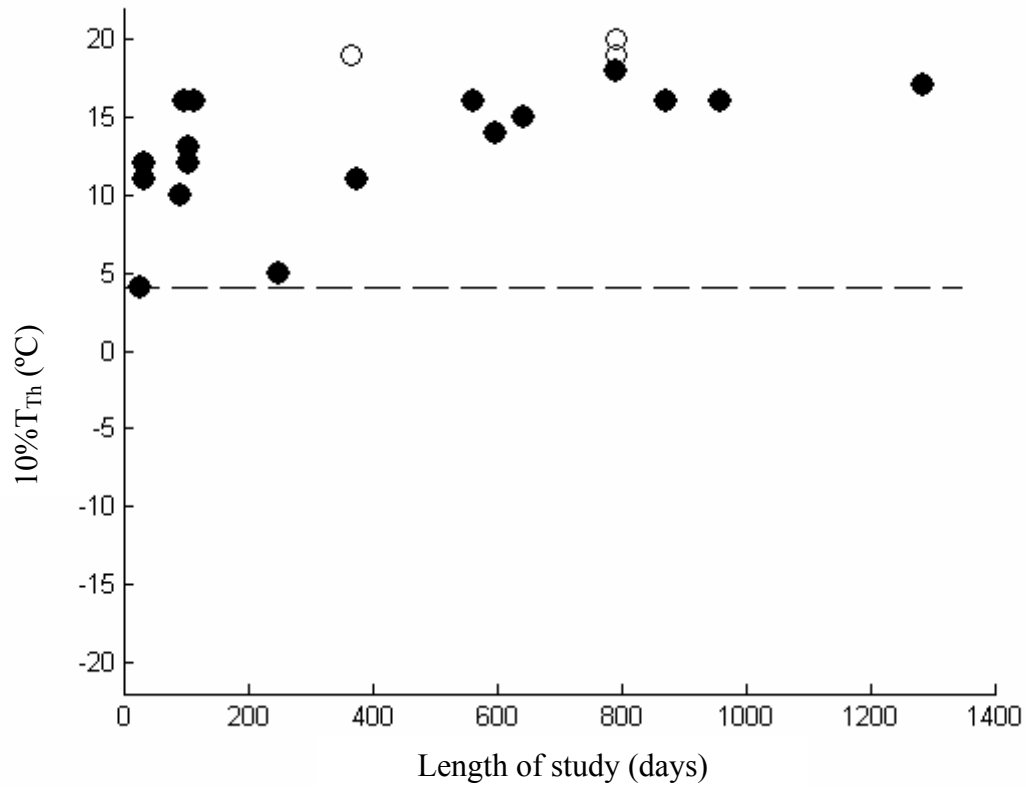
Figure 2.4: Position of the *10%T$_{Th}$* within -20°C and 20°C test range for cold-water (filled circles; *n* = 17) and warm-water (open circles; *n* = 3) fish where cold-water fish are those inhabiting a mean temperature of 10 ± 3°C and warm-water fish are New Zealand snapper inhabiting 17 ± 2°C. Dashed line indicates *10%T$_{Th}$* = 4°C.

2.3 Results

Across all the data, variation in length-at-day (LaD; mm) is a strong linear function ($r^2 \geq 0.92$, P < 0.05) of the variation in GDD (Table 2.2). Further GDD is frequently able to explain variation in LaD within <u>and</u> among datasets – something that calendar time cannot do in environments where there are temporal variations in temperature within or among trials or field studies.

Table 2.2: A comparison of the relation between calendar time (days) and physiological time (GDD, ºC·day) to size-at-age and egg development among the datasets examined. Shaded values indicate statistical similarity among trials of a given study. Arrow indicates common linear relation among trials of a given study when possible.

Species and relevant figures	Descriptors	Data (n)	Calendar time (d) Linear regression: $LaD=\beta' \cdot Time + \alpha'$				Comparison	Physiological time (GDD; ºC·day) Linear regression: $LaD=\beta \cdot GDD + \alpha$				Comparison
			Slope (β') mm·d^{-1}	Intercept (α') mm	r^2	P (α=0.05)		Slope (β) x 10^{-2} mm· (ºC·day)$^{-1}$	Intercept (α) mm	r^2	P (α=0.05)	
herring (*Clupea harengus*) Folkvord et al. 2004 Fig. 2.5abcdef	constant 4ºC	5	0.12	10.6	0.95	0.005	ANCOVA Different slopes P<0.0001	3.0	10.5	0.93	0.0074	ANCOVA Similar slopes P=0.91 Similar intercepts P=0.19
	constant 12ºC	6	0.38	10.7	0.98	0.0002		3.2	10.8	0.98	0.0012	
	variable 4ºC,8ºC,4ºC	6	0.18	10.0	0.94	0.0016		3.1	10.2	0.96	0.0004	
	variable 12ºC,8ºC,12ºC	6	0.33	11.0	0.97	0.0003		3.3	10.6	0.98	0.0001	
	Combined Trials	23			n/a			3.4	10.3	0.98	<0.0001	
Atlantic cod (*Gadus morhua*) Imsland et al. 2007 Fig. 2.6	7ºC + LDN	5	0.54	94.6	0.99	0.0001	ANCOVA Different slopes P<0.0001	7.8	94.6	0.99	0.0001	ANCOVA Similar slopes P=0.17 Similar intercepts P=0.32
	7ºC + LD24:0	5	0.53	95.0	0.99	0.0003		7.6	95.0	0.99	0.0003	
	10ºC + LDN	5	0.72	97.4	0.99	<0.0001		7.2	97.4	0.99	<0.0001	
	10ºC + LD24:0	5	0.78	95.6	0.99	<0.0001		7.8	95.6	0.99	<0.0001	
	Combined Trials				n/a			7.6	95.5	0.99	<0.0001	
	13ºC + LDN	5	0.78	97.9	0.99	<0.0001		6.0	97.9	0.99	<0.0001	ANCOVA Different slopes P=0.0008
	13ºC + LD24:0	5	0.87	98.3	0.99	<0.0001		6.7	98.3	0.99	<0.0001	

Table 2.2 cont.

Species and relevant figures	Descriptors	Data (n)	Calendar time (d) Linear regression: $LaD=\beta'\cdot Time + \alpha'$				Comparison	Physiological time (GDD; ºC·day) Linear regression: $LaD=\beta\cdot GDD + \alpha$				Comparison
			Slope (β') mm·d^{-1}	Intercept (α') mm	r^2	P (α=0.05)		Slope (β) x 10^{-2} mm· (ºC·day)$^{-1}$	Intercept (α) mm	r^2	P (α=0.05)	
houting (*Coregonus oxyrhynchus*) Malzahn et al. 2003 Fig. 2.5gh	17.5ºC, fed	5	0.41	9.82	0.97	0.0018	ANCOVA Different slopes P=0.0001	2.3	9.8	0.97	0.0017	ANCOVA Similar slopes P=0.10 Different intercepts P=0.0009
	17.5ºC, starved	5				0.13					0.13	
	8.4ºC, fed	9	0.22	10.2	0.99	<0.0001		2.7	10.2	0.99	<0.0001	
	8.4ºC, starved	9				0.11					0.11	
Arctic grayling (*Thymallus thymallus*) Dion and Hughes 2004 Fig. 2.5ij, 2.6, 2.7	Nordale 2000	16	0.71	-89.9	0.94	<0.0001	ANCOVA Marginal slopes P=0.032	6.5	15.6	0.99	<0.0001	ANCOVA Similar slopes P=0.44 Different intercepts P=0.0088
	Nordale 2001	14	0.84	-110.5	0.98	<0.0001		6.2	14.7	0.98	<0.0001	
	Bona 2000	13	0.57	-72.7	0.97	<0.0001	ANCOVA Different slopes P=0.0003	5.0	13.5	0.97	<0.0001	ANCOVA Marginal slopes P=0.026
	Bona 2001	14	0.80	-111.3	0.96	<0.0001		6.1	8.7	0.95	<0.0001	
minnow (*Phoxinus phoxinus*) Mills 1988 Fig. 2.5kl	1978 year-class	7	0.017	14.3	0.99	<0.0001	ANCOVA Similar slopes P=0.85 Different intercepts P=0.0014	1.1	7.4	0.99	<0.0001	ANCOVA Similar slopes P=0.19 Marginal intercepts P=0.032
	1979 year-class	6	0.017	15.7	0.99	<0.0001		1.1	7.6	0.99	<0.0001	
	1980 year-class	5	0.017	14.1	0.99	0.0003		1.1	7.1	0.99	<0.0001	
	1981 year-class	4	0.018	11.9	0.99	0.0022		1.1	7.0	0.99	0.0003	

Table 2.2 cont.

Species and relevant figures	Descriptors	Data (n)	Calendar time (d)				Comparison	Physiological time (GDD; ºC·day)				Comparison
			Linear regression: LaD= β' ·Time + α'					Linear regression: LaD= β ·GDD + α				
			Slope (β') mm·d^{-1}	Intercept (α') mm	r^2	P (α=0.05)		Slope (β) x 10^{-2} mm· (ºC·day)$^{-1}$	Intercept (α) mm	r^2	P (α=0.05)	
spider crab (*Mithraculus forceps*) Penha-Lopes et al. 2006 Fig.2.5mn	25ºC	4	0.079	0.58	0.98	0.0077	ANCOVA Similar slopes P=0.41 Different intercepts P=0.01	0.11	0.97	0.99	0.001	ANCOVA Similar slopes P=0.86 Marginal intercepts P=0.031
	28ºC	4	0.086	0.70	0.99	0.0015		0.11	1.0	0.99	0.001	
red king crab (*Paralithodes camtschatics*) Stevens 1990 Fig. 2.8		11			n/a			1.1	-10.6	0.92	<0.001	n/a
European grayling (*Thymallus thymallus*) Mallet et al. 1999	1977 year-class	10	0.28	107.5	0.95	<0.0001	ANCOVA Different slopes P<0.0001	2.7	98.4	0.96	<0.0001	ANCOVA Different slopes P<0.0001
	1978 year-class	9	0.30	-22.4	0.97	<0.0001		2.8	84.5	0.98	<0.0001	
	1979 year-class	10	0.27	-90.5	0.95	<0.0001		2.6	96.4	0.95	<0.0001	
	1980 year-class	7	0.33	-295.96	0.96	0.0001		3.2	56.6	0.98	<0.0001	
	1981 year-class	6	0.20	-185.6	0.94	0.0014		1.9	110.9	0.94	0.0014	
	1993 year-class	9	0.21	46.3	0.93	<0.0001		1.8	116.2	0.93	<0.0001	
	1994 year-class	10	0.31	-157.3	0.97	<0.0001		2.6	47.8	0.97	<0.0001	
	1995 year-class	6	0.38	-361.8	0.97	0.0003		3.4	18.3	0.98	0.001	

Table 2.2 cont.

Species and relevant figures	Descriptors	Data (n)	Calendar time (d) Linear regression: LaD= β'·Time + α'				Comparison	Physiological time (GDD; ºC·day) Linear regression: LaD= β·GDD + α				Comparison
			Slope (β') mm·d^{-1}	Intercept (α') mm	r^2	P (α=0.05)		Slope (β) x 10^{-2} mm·(ºC·day)$^{-1}$	Intercept (α) mm	r^2	P (α=0.05)	
snapper (*Pagrus auratus*) Francis 1994	1987 year-class	14	0.18	50.2	0.98	<0.0001	ANCOVA Similar slopes P=0.38 Similar intercepts P=0.23 ←	1.1	51.7	0.98	<0.0001	ANCOVA Similar slopes P=0.26 Similar intercepts P=0.78
	1988 year-class	17	0.18	53.6	0.97	<0.0001		1.1	55.5	0.97	<0.0001	
	1989 year-class	7	0.21	47.8	0.95	0.0002		1.2	70.8	0.97	0.0001	
	Combined Trials	38	0.18	52.6	0.97	<0.0001		1.1	50.6	0.98	<0.0001	←
Atlantic salmon (*Salmo salar*) Jones et al. 2002 Fig. 2.10	mean, front	15	0.10	84.9	0.84	<0.0001	n/a	1.9	83.6	0.97	<0.0001	n/a
threespine stickleback (*Gasterosteus aculeatus*) Wright et al. 2004	Frongoch, front	13	0.36	5.3	0.99	<0.0001	ANCOVA Different slopes P<0.0001	2.0	5.3	0.99	<0.0001	ANCOVA Different slopes P<0.0001
	Ayrs Burn, front	13	0.43	4.8	0.99	<0.0001		2.4	4.8	0.99	<0.0001	
	Endrick, front	14	0.34	5.2	0.99	<0.0001		1.9	5.2	0.99	<0.0001	
	Hogganfield, front	12	0.38	4.9	0.99	<0.0001		2.1	4.9	0.99	<0.0001	
	Kelvin, front	12	0.41	5.6	0.99	<0.0001		2.2	5.6	0.99	<0.0001	

Table 2.2 cont.

Species and relevant figures	Descriptors	Data (n)	Calendar time (d) Linear regression: LaD= β'·Time + α'				Comparison	Physiological time (GDD; ºC·day) Linear regression: LaD= β·GDD + α				Comparison
			Slope (β') mm·d^{-1}	Intercept (α') mm	r^2	P (α=0.05)		Slope (β) x 10^{-2} mm· (ºC·day)$^{-1}$	Intercept (α) mm	r^2	P (α=0.05)	
Atlantic cod (*Gadus morhua*) Brander 1995 Fig. 2.2, 2.11	1	2				n/a	Linear Regression P=0.10				n/a	Linear Regression P<0.0001; r^2=0.93
	2	1				n/a					n/a	
	3	2				n/a					n/a	
	4	3				0.16					0.16	
	5	3	0.37	230.5	0.99	0.028		3.7	230.5	0.99	0.028	
	6	3	0.35	192.9	0.99	0.014		4.0	192.9	0.99	0.014	
	7	3	0.45	238.4	0.99	0.043		4.1	238.4	0.99	0.043	
	8	3	0.33	317.8	0.99	0.05		3.3	317.8	0.99	0.05	
	9	2				n/a					n/a	
	10	2				n/a					n/a	
	11	2				n/a					n/a	
	12	2				n/a					n/a	
	13	2				n/a					n/a	
	14	2				n/a					n/a	
	15	3				0.19					0.19	
	16	3	0.19	300.1	0.99	0.010		3.2	300.1	0.99	0.010	
	17	3				0.11					0.11	
	Combined Trials				n/a			3.4	280	0.93	<0.0001	
burbot (*Lota lota*) Kjellman and Eloranta 2002	1978 year-class	14						3.7	10.5	0.98	<0.0001	ANCOVA Similar slopes P=0.06 Marginal intercepts P=0.04
	1979 year-class	6			n/a			4.8	2.9	0.99	<0.0001	

Table 2.2 cont.

Species and relevant figures	Descriptors	Data (n)	Calendar time (d) Linear regression: LaD= β' ·Time + α'				Comparison	Physiological time (GDD; ºC·day) Linear regression: LaD= β ·GDD + α				Comparison
			Slope (β') mm·d^{-1}	Intercept (α') mm	r^2	P (α=0.05)		Slope (β) x 10^{-2} mm· (ºC·day)$^{-1}$	Intercept (α) mm	r^2	P (α=0.05)	
chinook salmon eggs (*Onchorhynchus tshawytscha*) Alderdice and Velsen 1978 Fig. 2.9ab	Mean time to hatching	57	64.7 ± 41.9 d (±65%)					516 ± 40ºC·day (±7.8%)				
trout eggs (*Salmo fario*) Gray 1928 Fig. 2.9ab	Mean time to hatching	14	86.4 ± 38.2 d (±44%)					493 ± 48ºC·day (±9.7%)				
Atlantic cod eggs (*Gadus morhua*) Pepin et al. 1997 Fig. 2.9cd	Mean time to hatching	11	20.0 ± 5.01 d (±25.1%)					65.6 ± 29.1ºC·day (±44.4%)				
yellowtail flounder eggs (*Pleuronectes ferrugineus*) Benoit and Pepin 1999 Fig. 2.9cd	Mean time to hatching	57	6.38 ± 2.05 d (±32%)					52.2 ± 3.33ºC·day (±6.4%)				

2.3.1 GDD in the Laboratory

Among constant-temperature growth-trials (Folkvord et al. 2004) with Atlantic herring (*Clupea harengus*), calendar time explains most of the variation in LaD within a given trial (Fig. 2.5a), but each trial requires a different parameterisation (ANCOVA, different slopes P = 0.0003). In contrast, the thermal integral (i.e. GDD) explains the LaD variation within <u>and</u> among trials (Fig. 2.5b) using a single parameterisation (ANCOVA, similar slopes P=0.74, similar intercepts P=0.59; LaD=0.033·GDD+10.4; r^2=0.99; P<0.0001). Other growth-trials with herring (Folkvord et al. 2004), now employing a time-varying temperature, show that although calendar time again explains much of the LaD variation within a given trial (Fig. 2.5c), the explanatory power is less than under constant temperature (Fig. 2.5a). Further, and more importantly, each trial requires a different parameterisation (ANCOVA, different slopes P=0.0032). In contrast, GDD explains a greater degree of variation in LaD within <u>and</u> among trials (Fig.2.5d) and a single parameterisation is sufficient (ANCOVA, similar slopes P=0.55, similar intercepts P=0.064; LaD=0.035·GDD+10.1; r^2=0.98; P<0.0001). The strength of the GDD metric becomes readily apparent when one recognizes that there are no differences among the above parameterisations of LaD as a function of GDD in the constant-temperature (Fig. 2.5b) <u>and</u> in the time-varying temperature (Fig. 2.5d) growth trials (Fig. 2.5f; ANCOVA, similar slopes P=0.91, similar intercepts P=0.19; LaD=0.034·GDD+10.3; r^2=0.98; P<0.0001). In summary, a single parameterisation of LaD as a function of physiological time is sufficient to explain size-at-age variation, with considerable accuracy, among any of the above temperature growth-trials that require four different parameterisations when LaD is expressed as a function of calendar time.

Figure 2.5: Length-at-day (mm) as a function of calendar time (day, left panels) and as a function of GDD (ºC·day, right panels) for: herring (Folkvord et al. 2004; a,b,e,f, for 4ºC constant trial, filled circles and 12ºC constant trial, crosses; c,d,e,f, for 4,8,4 ºC variable trial, open circles; c,d,e,f, for 12,8,12 ºC variable trial, squares); houting (Malzahn et al. 2003; g,h, for 8.4°C constant and fed, open circles and 17.5°C constant and fed, filled circles and 8.4°C constant and starved, squares and 17.5°C constant and starved, crosses); Arctic grayling (Dion and Hughes 2004; i,j, for 2000 year-class, filled circles and 2001 year-class, open circles); minnows (Mills 1988; k,l, for 1978 year-class, filled circles and 1979 year-class, open circles and 1980 year-class, crosses and 1981 year-class, squares). Also shown is carapace width (mm) in spider crab (Penha-Lopes et al. 2006; m,n, for 25ºC constant, filled circles and 28ºC constant, open circles). The linear regression (solid line) and 95% prediction intervals (dashed lines) are provided for each relation (see Table 2.2 for details) except where not significant.
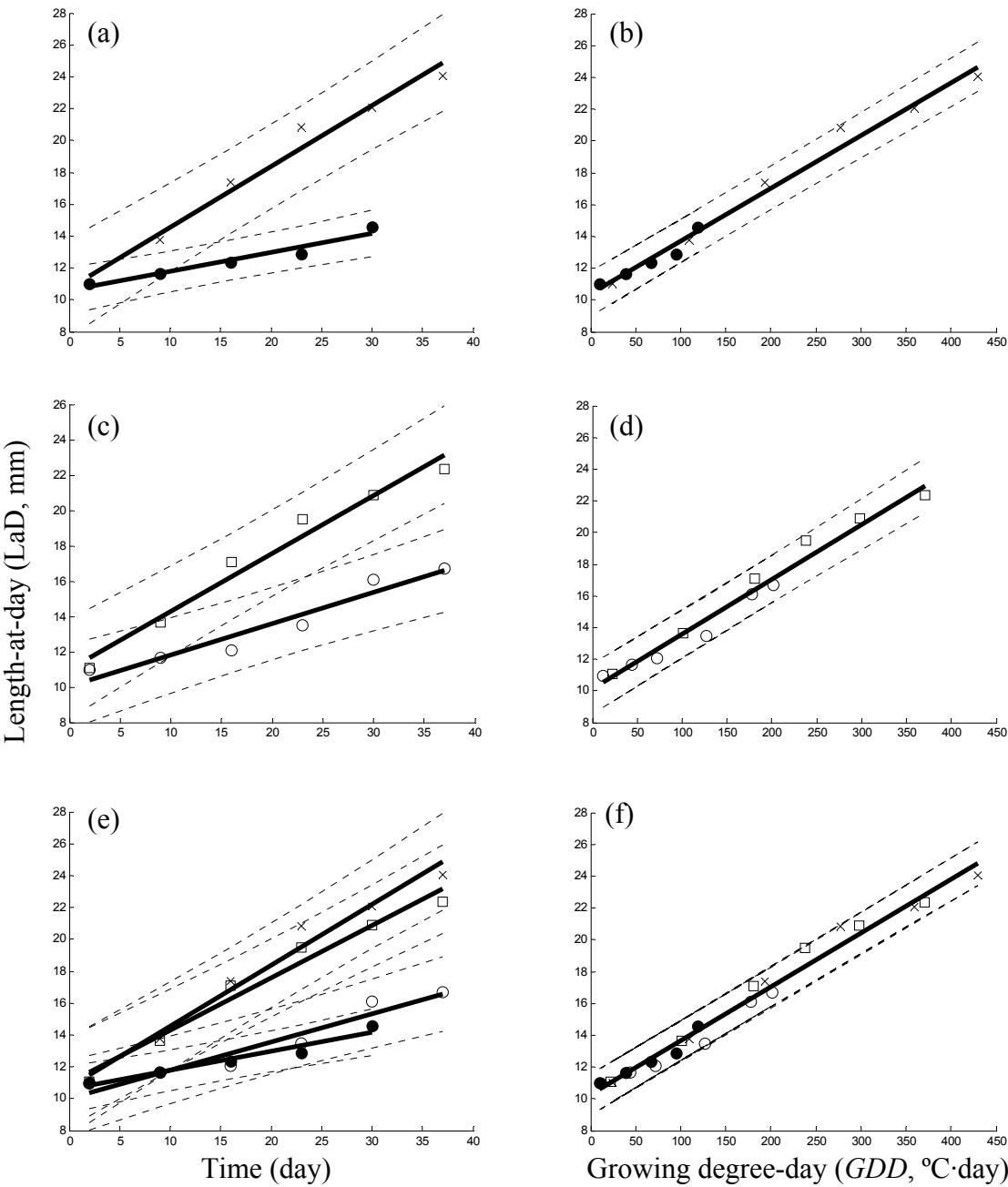
Figure 2.5
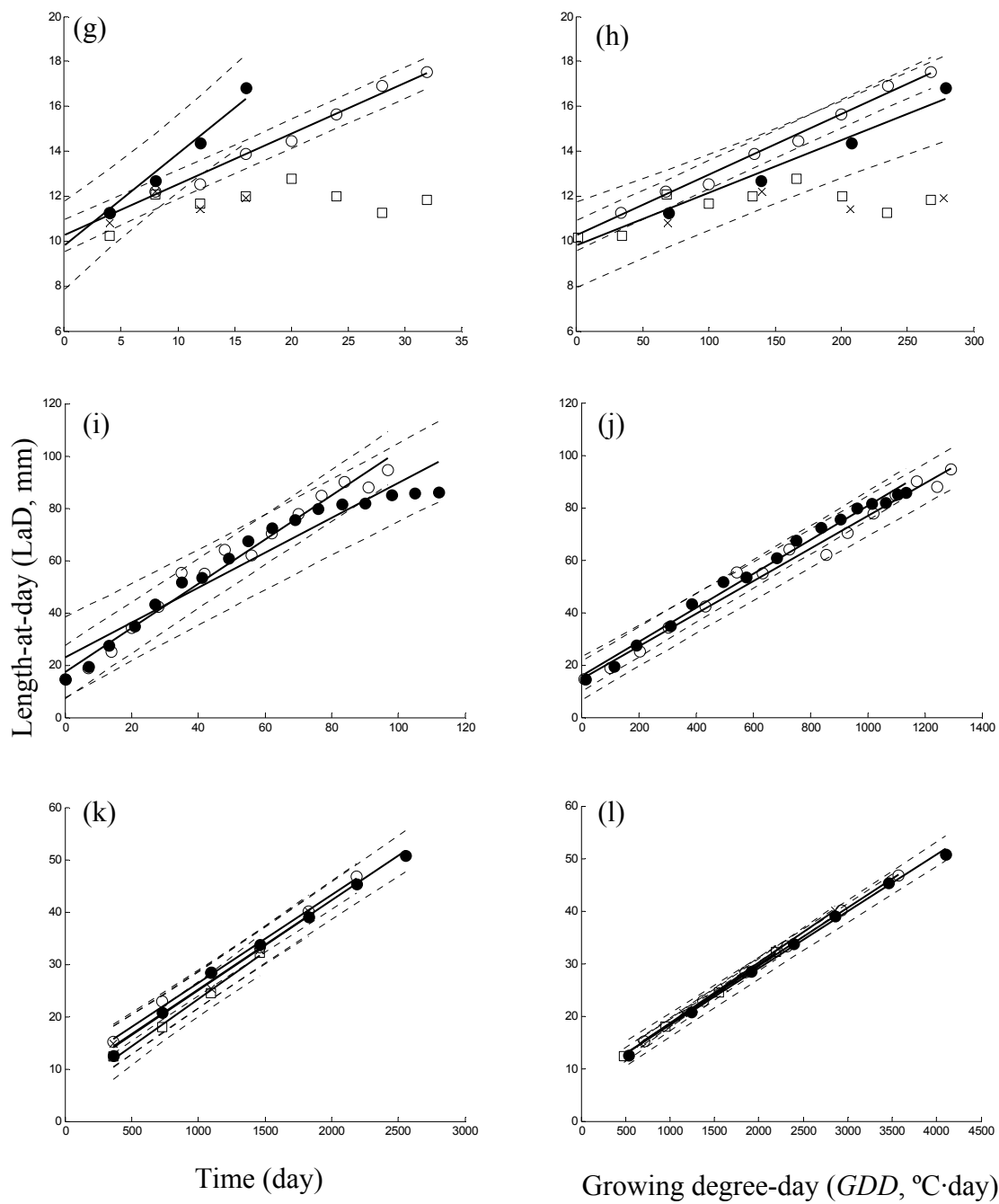
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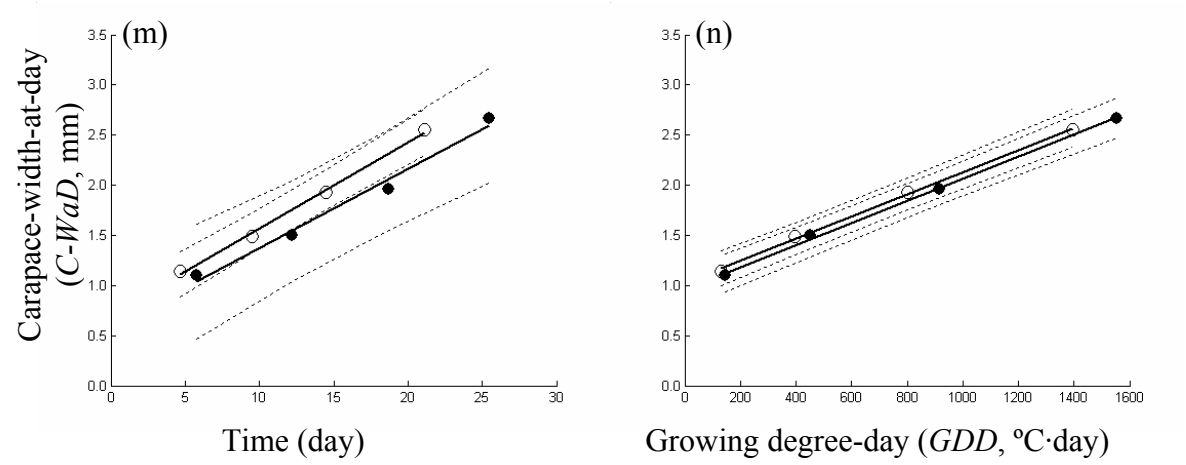
Figure 2.5

A further example of the strength of the GDD metric in assessing fish size-at-age can be demonstrated using the Malzahn et al. (2003) lab-rearing of larval houting (*Coregonus oxyrhynchus*). Here, two different parameterisations of LaD as a function of calendar time are required for each trial (Fig. 2.5g, ANCOVA, different slopes P=0.0001) though they, like the herring above, collapse to a simpler parameterisation when GDD is used (Fig. 2.5h, ANCOVA, similar slopes P=0.10; different intercepts, P<0.0001).

When GDD is unable to explain the variation in LaD among trials it is an indication that other factors (e.g. food availability, genetic composition) are contributing to the size-at-age variation (or the thermal record is incorrect, see below). How much of that size-at-age variation is due to temperature vs. other factors can only be teased apart once the trials are compared on the same physiological timescale; i.e. with GDD. When size-at-age is assessed in the same larval houting as above (Malzahn et al. 2003) but now under food limitation, there is no relation (i.e. no growth) between LaD and either calendar time or GDD (Fig 2.5gh; linear regression; $0.11 \leq P \leq 0.13$). However, when calendar time is used as the predictor, it is not clear how much of the variation in LaD is a function of temperature and how much is a function of food.

The GDD metric may also be used to disentangle the temperature and light effects in a laboratory study on Atlantic cod (Imsland et al. 2007) where I find that 98% of the variation in LaD over all trials is explained by GDD (P<0.0001, Fig. 2.6). Here, I preserved the linearity of the size-at-GDD relation by converting the cod weight-at-day to length-at-day according to the general weight-at-length relation as addressed above (Fig.2.2), although similar results are shown in a non-linear manner using weight (Fig. 2.6cd). Variation in LaD among four of the six trials is explained by one parameterisation of GDD (ANCOVA, similar slopes P=0.17, similar intercepts P=0.32). The remaining two trials, 13ºC + Natural light (LDN) and 13ºC and Constant light (LD24:0), demonstrate different parameterisations (ANCOVA, different slopes, P=0.0008) that could be explored through variation in other factors (e.g. feeding rate via light levels) now unencumbered by using physiological time. While there was no significant variation in length-at-day (i.e. no difference in LaD-at-GDD relations) among light trials with fish held at 7ºC and 10ºC, it should be noted that these lower temperature

trials did not extend over the same physiological period as the 13ºC trials. Although the study period was 96 days for all trials, the 13ºC trials are 1.3 fold longer than the 10ºC trials and 1.8 fold longer than the 7ºC trials when physiological time is used; 1248, 960 and 672 ºC·day respectively. It would be interesting to explore how much size variation due to variation in the light regime would become apparent in the 7ºC and 10ºC trials if they were extended for the same physiological period as the 13ºC trials (i.e. to 1248 ºC·day). This is left to future work.
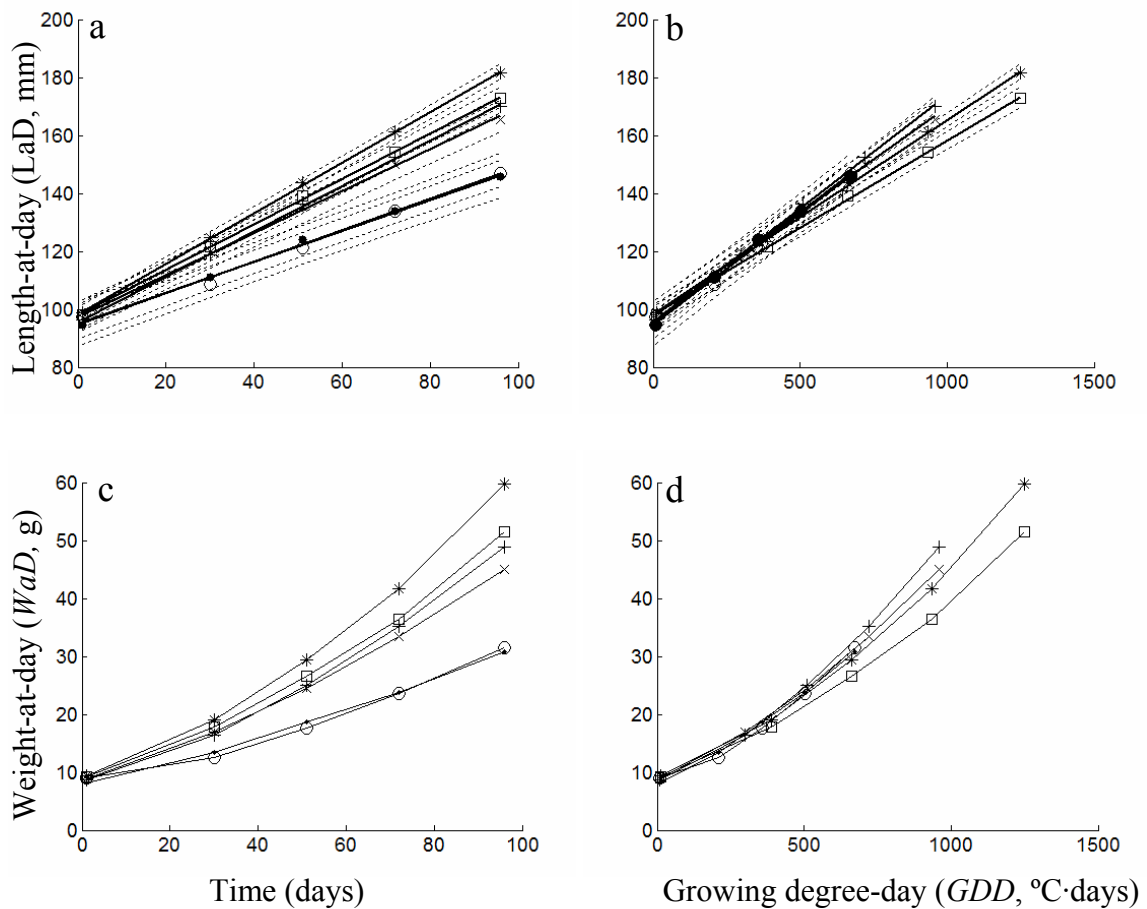
Figure 2.6: Length-at-day (mm) as a function of a, calendar time (days), and as a function of b, GDD (ºC·day) and weight-at-day (g) as a function of c, calendar time (days), and as a function of d, GDD (ºC·day) for Atlantic cod (Imsland et al. 2007) held at constant temperatures (7ºC, 10ºC, or 13ºC) under natural light (LDN, for Bergen at 60º25'N) or constant light (LD24:0) with 7ºC and LDN, filled circles, 7ºC and LD24:0, open circles, 10ºC and LDN, crosses, 10ºC and LD24:0, +, 13ºC and LDN, squares, 13ºC and LD24:0, *. The linear regression (solid line) and 95% prediction intervals (dashed lines) are provided for each length-at-day trial (ab, P<0.0001, Table 2.2).

The GDD appears to explain the variation in size-at-age due to variation in thermal histories of fish in controlled conditions and thus can be used to identify the remaining size-at-age variation that can be explored (e.g. other factors). This is explored further in **Chapters 3**, **4**, and **7**. In addition, laboratory growth-studies need not control for temperature (within limits) if GDD is employed in the analyses because the GDD can account for the temperature variation through integration as illustrated above (Fig. 2.5e,f, 2.6) and below (Fig. 2.5i,j).

2.3.2 GDD in the Field

The strength of the GDD is also demonstrated among field studies (Dion and Hughes 2004), where, for example, the non-linear evolution in GDD is able to explain the non-linear evolution of LaD in two different year-classes of age-0+ Arctic grayling (*Thymallus thymallus*) in consecutive years in the same habitat (Fig. 2.7), and does so in a linear manner (Fig. 2.5ij). The original study (Dion and Hughes 2004) used the growth model of Mallet et al. (1999) that was developed for grayling to incorporate seasonal size-at-age variation in the VBGF through a "coefficient of temperature"; a coefficient requiring estimates of the minimum, maximum and optimum growth temperatures for grayling based on "expert opinion". A comparison of the residuals resulting from the GDD metric applied to the grayling and those obtained using the modified VBGF (Dion and Hughes 2004), reveals that the residuals (Fig. 2.8) from the former are smaller, more uniform and trend-free relative to the modified VBGF (although both are autocorrelated – as are most variables of this nature). Thus, consistent with all above, the GDD method provides a simpler metric with greater explanatory power and obviates the five parameters required by the modified VBGF (Dion and Hughes 2004) and by its analogues used elsewhere that incorporate asymptotic length, growth coefficient, optimum temperatures, seasonal amplitudes and phases etc.
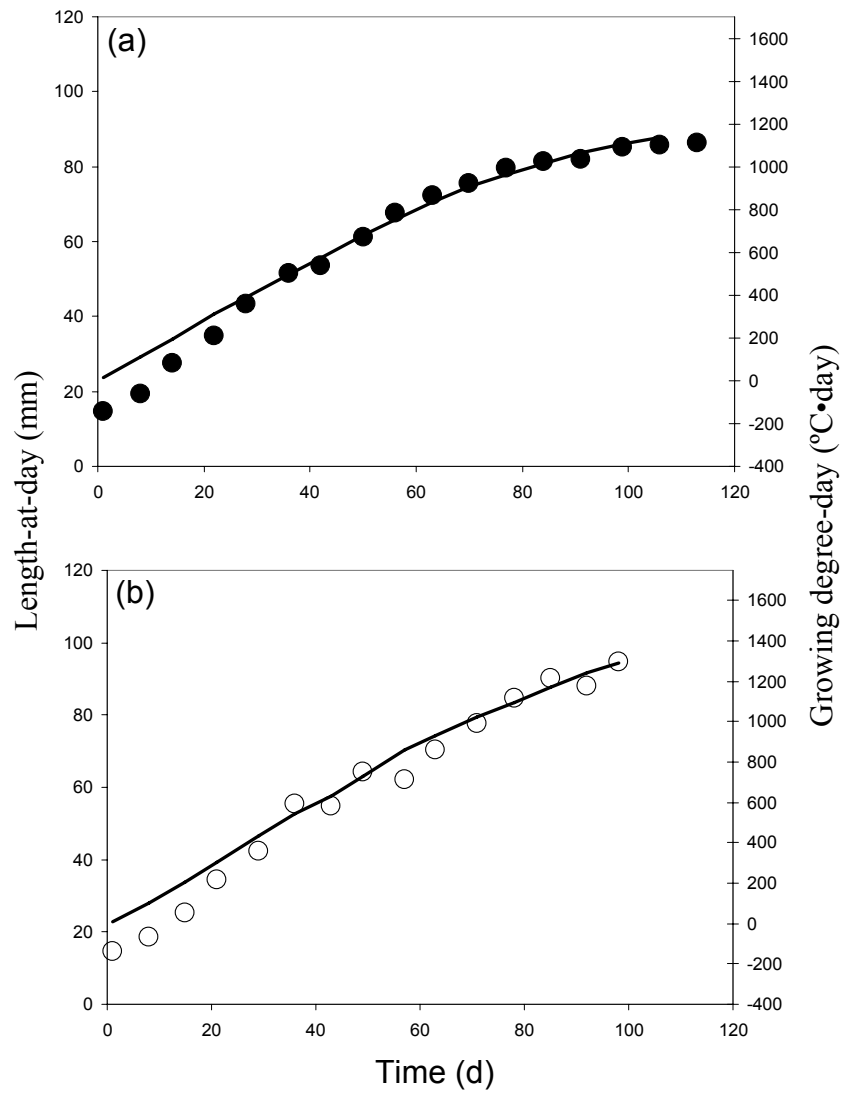
Figure 2.7: Non-linear evolution of length-at-day (mm) for: a, 2000-year-class, solid circles; b, 2001-year-class, open circles, of age 0+ Arctic grayling (Dion and Hughes 2004) and the parallel and non-linear evolution of GDD (°C·day; solid line) in time for each year and year-class.
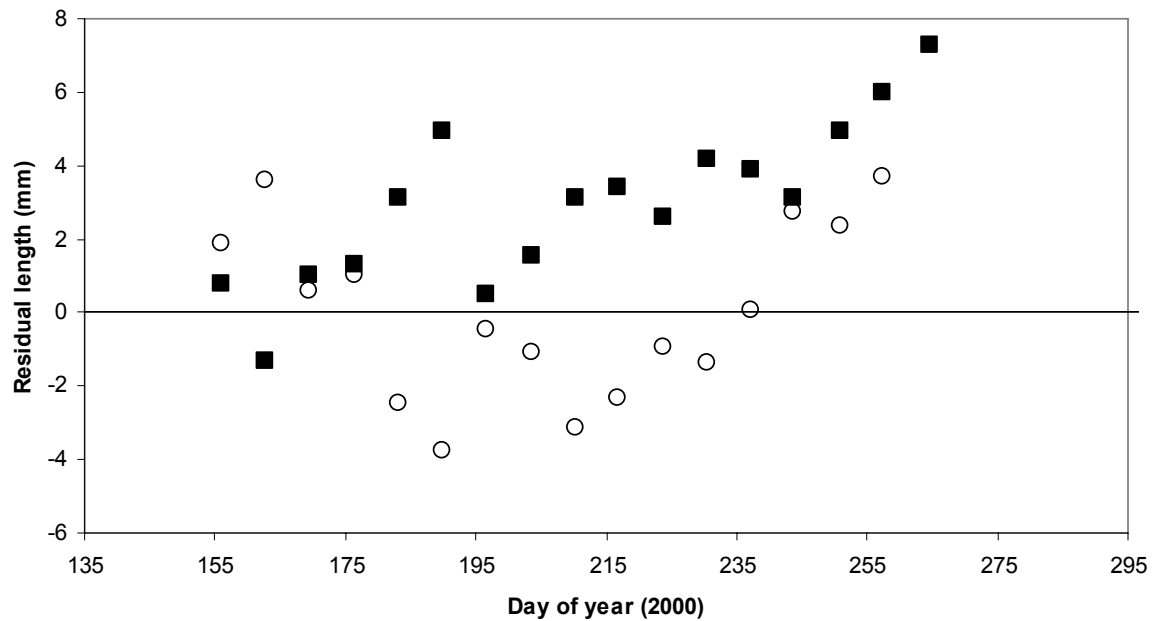
Figure 2.8: Residuals (mm) of the modified VBGF (Dion and Hughes 2004, filled squares) and GDD methods (open circles) for the 2000-year-class of age-0+ Arctic grayling. Mean square errors for the modified VBGF method and GDD method are 15.1 and 6.0 mm^2 respectively. The residuals from the modified VBGF method (Dion and Hughes 2004) demonstrate a significant trend (r^2=0.66; P<0.0001) while the residuals from the GDD method do not (P=0.66).

The GDD not only explains the variation in LaD among different year-classes in different years (above), it can also explain size-at-age variation among year-classes across multiple years as shown (Fig. 2.5kl) by the freshwater minnow in a north-temperate environment (Mills 1988). Here, calendar-time explains much of the evolution of LaD with a similar slope among year-classes but differing intercepts (Fig. 2.5k, ANCOVA, similar slopes P=0.85, different intercepts P=0.0014). The common-slope result (Mills 1988) is most likely related to the fact that there were limited differences in the GDD among years (coefficient of variation, CV=16%); i.e. limited differences in the thermal histories (thermal integrals) of the four year-classes over the 4 to 7 year period. The disparate intercepts may be related to the first sampling dates among year-classes in relation to the thermal histories of the fish. When the same fish are assessed in terms of their year-class (cohort) and GDD, a single relation emerges (Fig. 2.5l, ANCOVA, similar slopes, P=0.19 and marginally similar intercepts, P=0.032; Table 2.2). In summary, where the thermal environment varies little from one year to the next, calendar-time can be expected to explain much of the variation in LaD among year-classes, although in this case the GDD metric delivers slightly better explanatory power.

2.3.3 GDD in General

The above demonstrations of the ability of the GDD method to explain LaD variation in fishes is mirrored among the other datasets that I examined (58 in all, including those detailed above and below; Tables 2.1, 2.2) where the CV (51%) in slopes derived from LaD-*at*-GDD relations is smaller than that derived from the LaD-*at-calendar-time* relations (63%), demonstrating that physiological time is able to explain more of the variation in size-at-age in fishes among studies (temperatures, year-classes, species etc.) than does calendar time.

2.3.4 GDD in Other Aquatic Ectotherms

The explanatory power of the GDD appears to hold for other aquatic ectotherms. For example, and as shown above for herring and houting, spider crab (*Mithraculus forceps*) constant-temperature (25ºC and 28ºC) growth-trials (Penha-Lopes et al. 2006) demonstrate that calendar time explains much of the variation in carapace width (mm)

within a given trial (Fig. 2.5m) but each trial requires a different parameterisation, at least in the intercept (ANCOVA, similar slopes P=0.41, different intercepts P=0.01). However, when physiological time is employed, size-at-age relations between temperature trials are identical in slope and the intercepts are marginally the same (Fig. 2.5n, ANCOVA, similar slopes P=0.86, marginally similar intercepts P=0.031). The GDD method also proves useful for assessing size-at-age in the red king crab (*Paralithodes camtschatics*; Stevens 1990) where 92% of the variation in carapace length-at-age is a simple linear function of GDD (Linear regression, P<0.0001; Fig. 2.9). Stevens (1990) used a $\log_e$-linear fit to these data, presumably to avoid the arguably meaningless negative y-intercept provided here. The negative y-intercept may reflect an unresolved thermal constant related to early development (see Section 2.3.5 below).
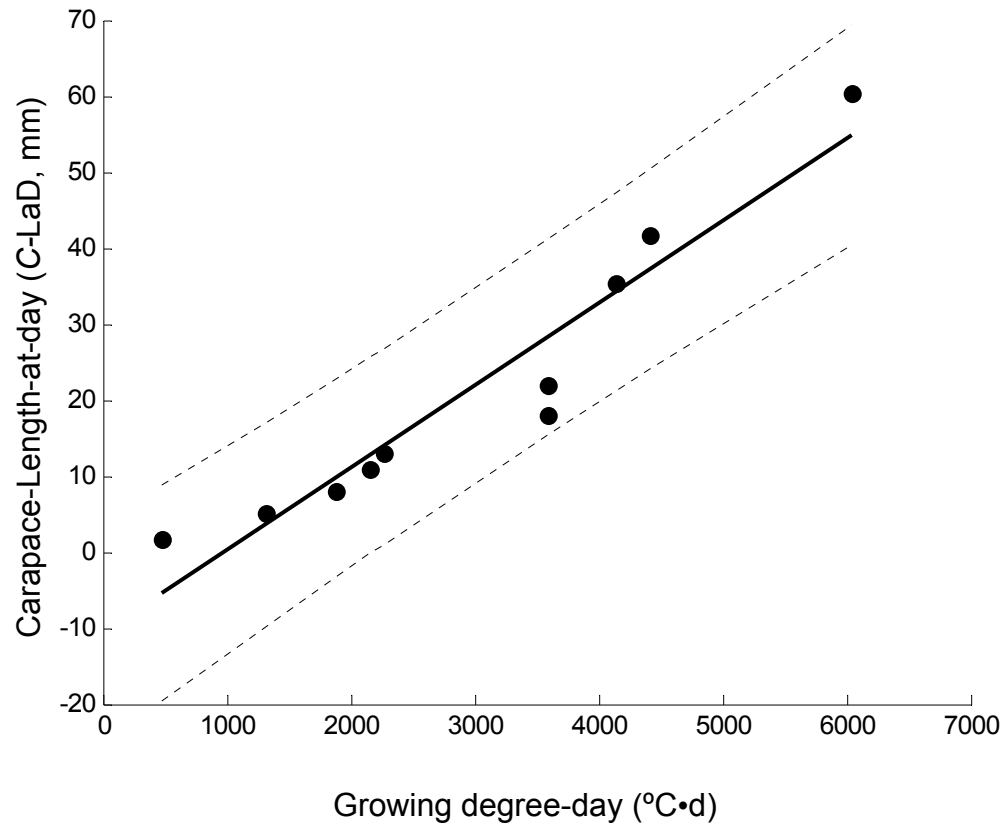
Figure 2.9: Carapace length-at-day (*C*-LaD, mm; filled circles) and GDD (ºC·day) for juvenile red king crab (*Paralithodes camtschatica;* Stevens 1990). Linear regression (solid line; *C*-LaD=0.011·GDD – 10.6mm; r^2=0.92; P<0.0001) and 95% prediction intervals (dashed lines) are provided.

2.3.5 GDD and Development

A corollary to the GDD is the thermal constant – the degree-days achieved to advance a given developmental stage – routinely used in agriculture and entomology to determine developmental time to stages such as emergence or maturation (Trudgill et al. 2005). This concept is applicable to fish (Lange and Greve 1997) including, for example, the development and hatching of chinook salmon (*Oncorhynchus tshawytscha*) eggs (Alderdice and Velsen 1978) incubated across a 16°C temperature range (Fig. 2.10a). Here, the GDD achieved for hatching to occur is 516 ± 40ºC·day regardless of incubation temperature (Fig.2.10b, Table 2.2) , thus reducing the CV in time-to-hatch from 65% (calendar time) to 7.8% (physiological time), though there are some outliers in the thermal constant estimates (see below). Time-to-hatch as a thermal constant is also noted in trout (*Salmo fario*) eggs (Gray 1928, Fig. 2.9a) near 493 ± 48ºC·day (Fig. 2.10b) and flounder (*Pleuronectes ferrugineus*) eggs (Benoit and Pepin 1999, Fig. 2.10c) near 52 ± 3 ºC·day (Fig. 2.10d) where the CV in time-to-hatch is reduced from 44% to 9.7% and from 32% to 6.4% respectively when GDD is used instead of calendar time. Again there are some outliers. The anomalously low thermal constants (outliers) generally appear at the extremes in the incubation temperature ranges, possibly indicating that the eggs are being incubated outside of the temperature range normally experienced by the organism where the metabolic response to changing temperature is expected to be near-linear. This may explain my examination of cod (*Gadus morhua*) eggs (Pepin et al. 1997, Fig. 2.10c) reared between 1 and 7ºC where the thermal constant for hatching appears to be near 66 ± 29 ºC·day with anomalously low estimates at the low end of the incubation temperature range (demonstrating an increase in CV from 25% to 44% for calendar time and GDD respectively, Fig. 2.10d); again suggesting incubation outside of temperature ranges within that which the organism has evolved or some other low-temperature physiology is involved (Valerio et al. 1992). Nevertheless, these examples (Fig. 2.10bd) illustrate that the GDD thermal constant may be useful in predicting the timing of life history development and transformation in fish. The substantial variation in thermal constants over large ranges in egg incubation temperatures for some species found in my study, and in that of Reibisch (1902), indicates that my greatly simplified assumptions regarding the

physiological responses to temperature may not explain all of the variation stemming from the complex processes involved.
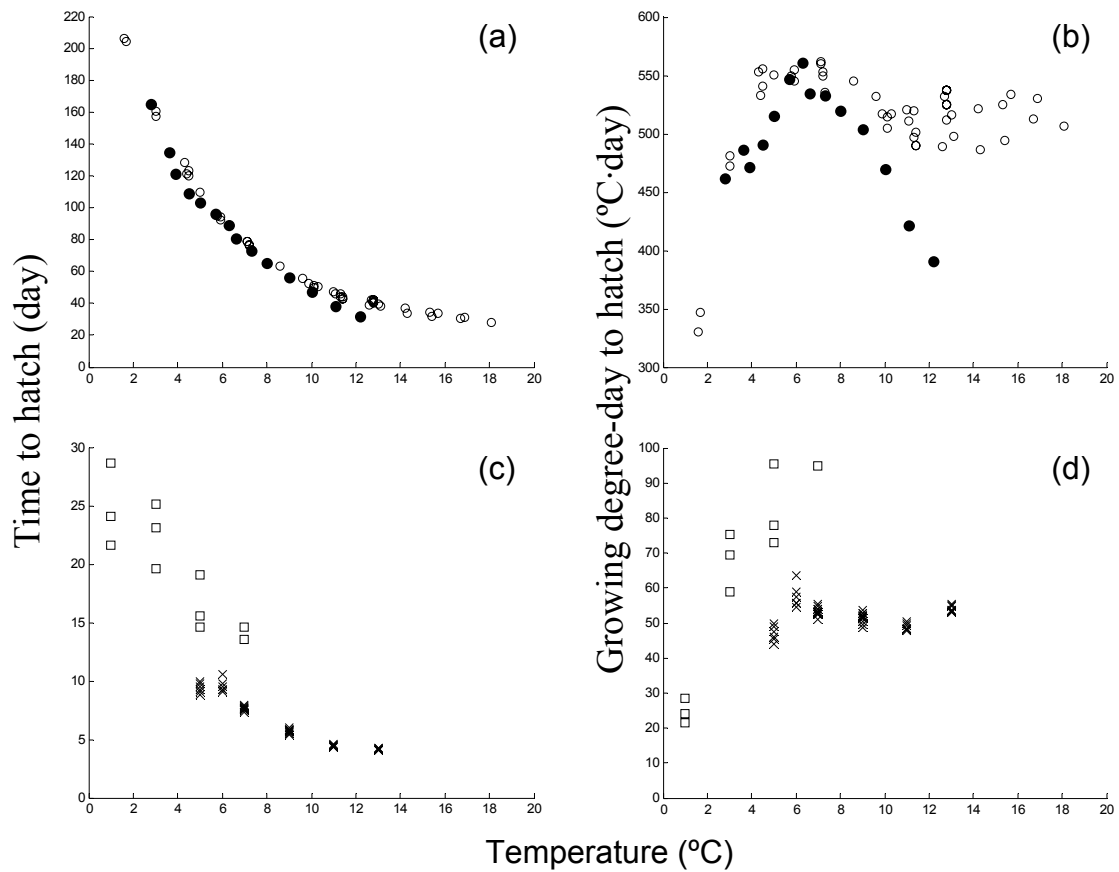
Figure 2.10: Egg development in calendar time to hatch (day, left panels) and in GDD to hatch (ºC·day, right panels) for incubation at constant temperatures (ºC) for: trout (Gray 1928; a,b, filled circles), chinook salmon (Alderdice and Velsen 1978; a,b, open circles), cod (Pepin et al. 1997; c,d, open squares) and flounder (Benoit and Pepin 1999; c,d, crosses).

In fish, life-history transformations (e.g. smoltification, maturation) are marked by changes in energy allocation from growth to other physiological demands and thus a discontinuity in LaD as a function of GDD is to be expected. Such discontinuities are observed in some of the multi-year data I examined (e.g. Atlantic salmon, *Salmo salar* and threespine stickleback, *Gasterosteus aculealtus*) and they appear to identify thermal constants that define the physiological time for life history transformation. For example, a discontinuity at approximately 1600ºC·day is apparent (Fig. 2.11) in Atlantic salmon growth trials (based on data from Jones et al. 2002) corresponding to an average LaD of approximately 114 mm – well within the standard deviation of the average LaD (124 ± 14mm, Hutchings and Jones 1998) reported for smoltification in the study area. Smoltification is associated with physiological changes involving salinity tolerance, hormone titre (thyroid activity), and olfaction (Specker et al. 2000), each presumably associated with a changing energy budget and thus a change in the LaD-at-GDD relation.
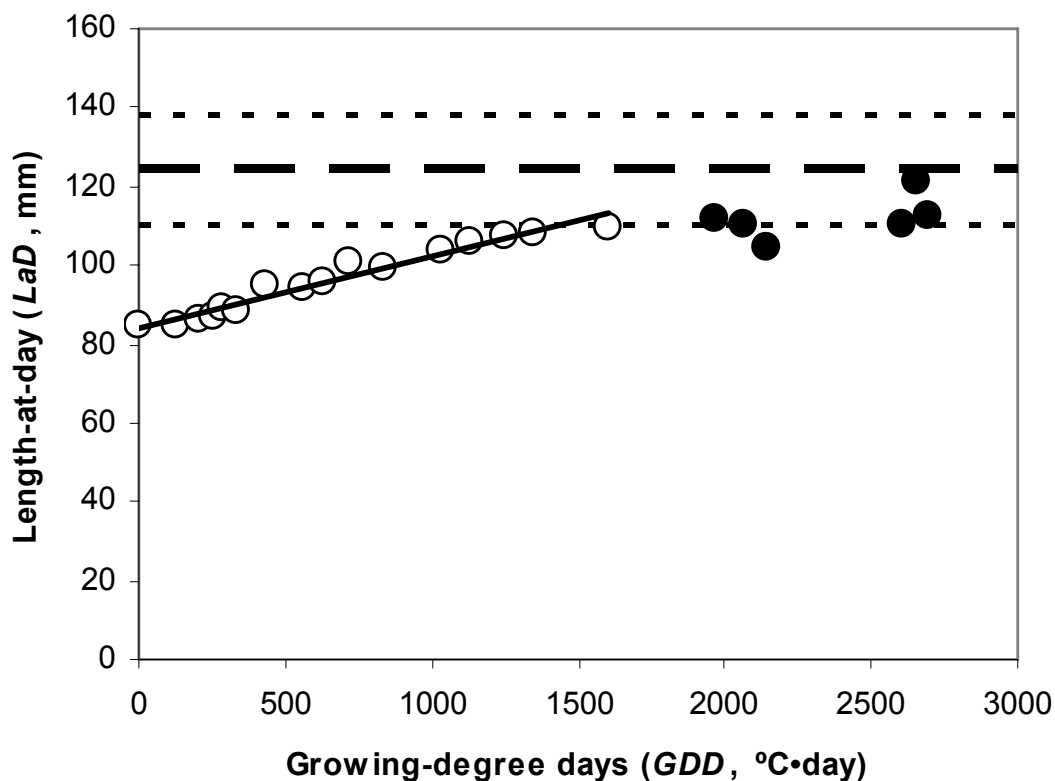
Figure 2.11: Length-at-day (mm) as a function of GDD (ºC·day) for juvenile Atlantic salmon (Jones et al. 2002). Open circles and solid line denote data included in GDD-LaD relation (LaD=0.019·GDD+83.6mm; r^2=0.97; P<0.0001), and filled circles those excluded. Dashed and dotted lines at 124 ± 14mm (standard deviation) illustrates the approximate size-at-smoltification for fish in the study area (Hutchings and Jones 1998).

2.3.6 GDD at Large Spatial Scales

To test the generality of the GDD measure in explaining size-at-age for fish over large spatial and temperature scales, I examined age-2 to -4 Atlantic cod and their associated long-term mean ocean temperature across their North Atlantic range using Brander's (1995) compilation. In doing so, I explicitly assume the variation in temperature among stocks is greater than that within. I am able to demonstrate that although there is a well known and near 3-fold range in length-at-age across the 17 stocks examined – a range attributable to differences in habitat temperature among the stocks (Brander 1995) – fully 93% of the variation in LaD is explained as a single linear function of GDD; i.e. the length of any cod, no matter its stock and habitat-temperature association, is very predictable (±19% being the 95% prediction interval; Fig.2.12) from the GDD metric, despite the fact that each stock has its own size-at-age (calendar time) relation due to differences in their thermally controlled growth rate. Such stock-specific length-at-age relations for many species abound in the literature.
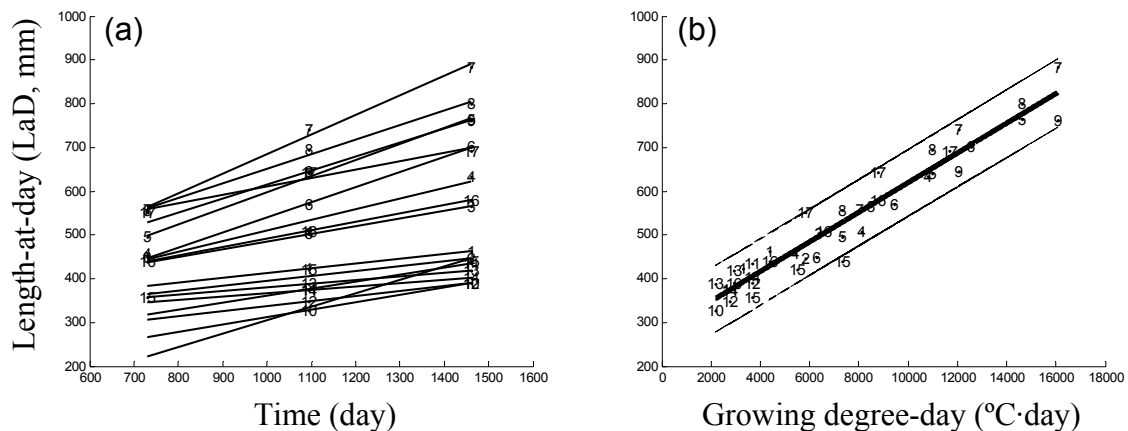
Figure 2.12: Length-at-day (mm) for 17 stocks of age-2 to -4 North Atlantic cod (Brander 1995) as a function of (a) calendar time (no significant relation among stocks, P=0.097); and as a function of (b) GDD (significant relation among stocks: LaD=0.034·GDD+280; r^2=0.93, P<0.0001 with 95% confidence intervals for the prediction, dashed lines). Data-labels are stock identifiers (cf. Brander 1995): East and West Greenland (1), Northeast Arctic (2), Iceland (3), Faroe (4), West Scotland (5), North Sea (6), Celtic Sea (7), Irish Sea (8), Eastern Channel (9), Labrador/Grand Bank (10), Southern Grand Bank (11), Northern Gulf of St. Lawrence (12), St. Pierre Bank (13), Southern Gulf of St. Lawrence (14), Eastern Scotian Shelf (15), Western Scotian Shelf (16), Georges Bank (17).

2.4 Critical Assumptions and Unresolved Questions

The temperature measures used to estimate GDD must be representative of that experienced by the organism. This ideally requires measurements at a sufficiently high frequency in the locale where the organism is growing. Much literature involving the application of the GDD metric to plant species has focused on microclimates near the plant (Wang 1960). Due to the high heat capacity of the aquatic environment, the time and space de-correlation scales are typically large relative to terrestrial locales, allowing temperature to be less-frequently estimated and at a larger spatial scale. Further, the thermal acclimation-limits of most aquatic ectotherms compromise their ability to move across thermal gradients (Claireaux et al. 1995). Nevertheless, evidence for the necessity of reliable local temperature estimates is found in a study (Kjellman et al. 2003) on perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*). There, differences in size-at-age among bay-specific populations disappear within species when a bay-specific GDD is used in place of bay-specific parameterisations based on local air temperature (Kjellman et al. 2003). Further, representative GDD must include the entire thermal history of the organism up to the point of interest (Trudgill et al. 2005); e.g. from hatch or spawning date to a given size or development stage. The more complete the temperature time series, the more the variation in LaD will be explained as it is the complete (i.e. integrated) thermal history of the fish that contributes to the size-at-age. For example, the New Zealand snapper (*Pagrus auratus*) data (Francis 1994) begin with a hatch-date (01 January) near the maximum spawning period and I am able to determine LaD as a strong function of GDD ($0.97 < r^2 < 0.98$) with statistically similar relations among year-classes (ANCOVA, similar slopes P=0.26, similar intercepts P=0.78). However, the burbot data (Kjellman and Eloranta 2002) begin at arbitrary starting-points in relation to the thermal history of the fish, and though the strength of the LaD-at-GDD relation is maintained ($0.98 < r^2 < 0.99$), the relations between the two year-classes are marginally different (ANCOVA, slopes P=0.058, intercepts P=0.035). It is difficult to know if the contrast between the snapper and the burbot examples are due simply to the choice of start date relative to the entire thermal history. It seems that the GDD method maintains strength in the face of temperature data that may be compromised by location, frequency or completeness of measurement. However, when care is made to optimize these criteria, the

GDD is frequently able to explain variation in LaD within as well as among different groups (e.g. locations, year-classes), something that calendar time cannot achieve unless the fish grow in an identical thermal environment. It is here that the increasing amount of archival tag data (e.g. Palsson and Thorsteinsson 2003) may provide unequivocal substantiation of the utility of the GDD measure due to the relatively high-frequency temperature measures provided over the recorded thermal history of the tagged fish, though getting a comparable length-at-age series may be challenging; micro-scale accelerometry offers a possible avenue of exploration and such development is now underway (D. King, VEMCO Ltd., 77 Chain Lake Drive, Halifax, NS).

2.5 Summary and Future Directions

Each of the above examples demonstrate that, with basic information on variation in the thermal environment, the physiological time-scaling provided by the GDD explains most of the temperature-related variation in length-at-age (inferred growth) prior to maturation and perhaps beyond. This appears to apply within and among stocks and populations of a given fish species – something that cannot be achieved using calendar time unless the thermal histories are very similar. It appears that the GDD has similar utility in explaining variation in life history development and stage transitions through the thermal constant. Thus, the GDD appears as an essential metric to explain a large amount of variation that is observed in fish growth and development; variation that is frequently attributed to temperature, but often with limited success or in an overly-complicated manner; simply because a physiologically-scaled temperature measure was not used. Such physiological scaling via GDD could be incorporated into fish simulation models and likely advance such models by avoiding the complications that result from different responses to time-varying and time-constant temperature environments (e.g. Neill et al. 2004). Indeed, identifying a correct physiological timescale through the use of GDD may advance many aspects of aquatic ectotherm research, from population-wide studies (e.g. timing of coral bleaching, Berkelmans 2002) to physiological timing within an individual. An example of the latter is the temperature-related variation in the rate of stomach evacuation associated with fish food consumption. In evacuation trials, the fish can be

held at different trial-specific constant temperatures and following the cessation of feeding, the reduction in stomach content (e.g. fullness index) over time is used as an estimate of evacuation. Miyasaka et al. (2005) used this method to determine stomach evacuation in freshwater sculpin (*Cottus nozawae*) held at constant temperatures of 2°C, 7°C and 12°C. For the evacuation trials variation in normalized stomach fullness index (nSFI) and variation in GDD (here, growing degree-hour, GDH) were compared and quantified through linear regression for each dataset, producing a relation of the form:

$$nSFI = \theta \cdot GDH + \rho \quad , \tag{3}$$

where θ is the slope (°C·hr)$^{-1}$ and ρ is the intercept of the nSFI-at-GDH relation (Table 2.3).

Table 2.3: A comparison of the relation between calendar time (days) and physiological time (GDH, ºC·hr) to normalized stomach fullness index (nSFI). Shaded values indicate statistical similarity among trials. Arrow indicates common linear relation among trials.

Species and relevant figures	Descriptors	Data (n)	Calendar time (hours)				Comparison	Physiological time (*GDH*; ºC·hr)				Comparison
			Linear regression: *nSFI= θ' ·Time + ρ'*					Linear regression: *nSFI= θ ·GDH + ρ*				
			Slope (θ) x 10^{-2} h^{-1}	Intercept (ρ)	r^2	P (α=0.05)		Slope (θ) x 10^{-3} (ºC·h)$^{-1}$	Intercept (ρ)	r^2	P (α=0.05)	
freshwater sculpin (*Cottus nozawae*) Miyasaka 2005 Fig. 2.12	2ºC	7	-1.6	1.0	0.85	0.0033	ANCOVA Different slopes P=0.0081	-8.2	1	0.85	0.003	Similar slopes P=0.49
	7ºC	7	-3.5	0.98	0.92	<0.0001		-4.9	0.98	0.92	0.0006	Similar intercepts P=0.92
	12ºC	6	-5.3	0.97	0.82	0.013		-4.4	0.97	0.82	0.013	
	Combined Trials		n/a					-4.6	0.97	0.88	<0.0001	←

As with my size-at-age analyses above, I show, in accord with Miyasaka et al. (2005), that calendar time requires 3 separate parameterisations – one for each trial (Fig. 2.13a, ANCOVA, different slopes, P= 0.0081). When assessed using the thermal integral (here using growing degree-hour, GDH) I can explain the variation in the normalized stomach fullness index (nSFI) within and among trials using a single parameterisation (ANCOVA, similar slopes P=0.49, similar intercepts P=0.92; nSFI= -0.0046·GDH+0.97; r^2=0.88; P<0.0001).   I offer this example simply to demonstrate that when the physiologically-relevant and short time-scale GDH is employed, it clearly explains the different rates in the physiological processes (digestion and evacuation) at the time and temperature scales at which they are occurring.
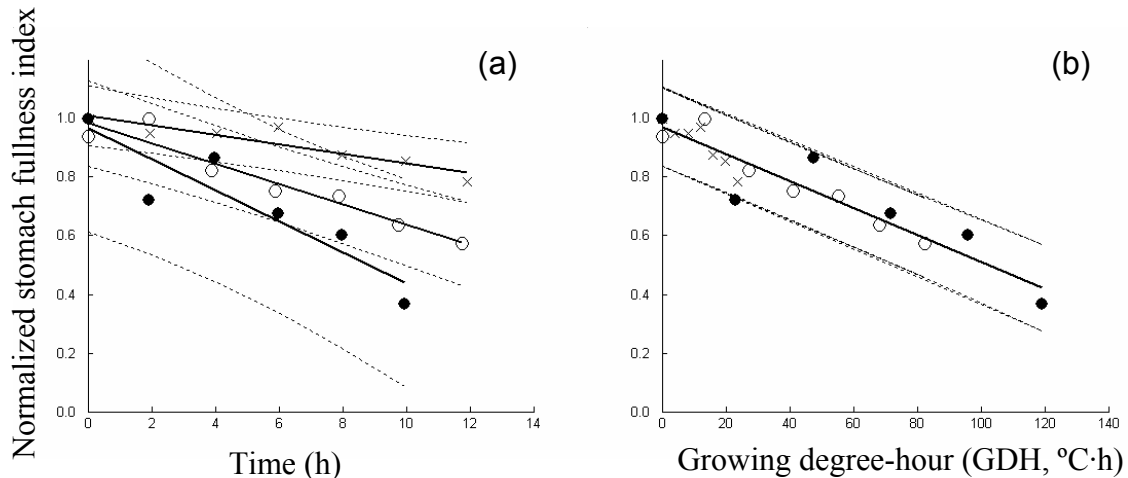
Figure 2.13: Normalized stomach fullness index (nSFI) as a function of (a) calendar time (h) and (b) as a function of growing degree-hour (GDH ; ºC·h) for freshwater sculpin held at 2ºC (crosses), 7ºC (open circles) and 12ºC (filled circles). SFI was calculated by Miyasaka et al. (2005) with SFI = $\log_e$[{1000· (dry mass of stomach contents)/(dry mass of fish body)} +1]. I have normalized the SFI within temperature trials where nSFI = SFI/(maximum SFI). The linear regression (solid line) and 95% prediction intervals (dashed lines) are provided for each (see Table 2.3 for details).

In addition to its applications with physiological rates in individuals (previous example) the GDD metric may prove useful in defining a physiologically-relevant time scale for ecological rates of populations. For example, Griffiths and Harrod (2007) examined relations between variation in growth rate, temperature and natural mortality reported as M (instantaneous mortality rate), converted here to an annual mortality rate as per cent (A, %·yr^{-1}) of population size (Ricker 1975; $A = 1 - e^{M}$) among 173 fish species. As in Griffiths and Harrod (2007) the mean annual mortality rate demonstrates a significant increase with mean habitat temperature, T in ºC, (Fig. 2.14a, linear regression, $A = 2.6$ %yr^{-1}ºC^{-1} · T - 3.0 %·yr^{-1}, r^2=0.99, P=0.0068). However, estimating mortality in this way (i.e. calendar time) assumes all fish physiologically "experience a year" at the same rate. This does not hold for ectotherms living in different and/or varying temperature conditions. Accordingly, mortality rates should be calculated on a time scale that is physiologically-relevant. When I convert the mean annual mortality estimates (%·yr^{-1}) to growing degree-year mortality (GDY mortality, %·GDY^{-1}), *GDY* mortality $= \dfrac{A}{T}$, the mean mortality among habitats is constant (Fig. 2.14b, P=0.52) at 2.4 ± 0.1%·GDY^{-1}, and represents a decrease in the coefficient of variation from 22% using calendar-time mortality to 3.2% using GDY-mortality. Thus, much of the variation in mortality rates among habitats is explained when mortality rates are explored on a time-scale relevant to the fish. It follows that estimating physiologically-related rates using physiologically-meaningful times may apply to fishing mortality as well. Sustainable harvest rates may be more successfully estimated for populations inhabiting varying temperatures if a physiologically relevant time is used. Similar exploitation rates (physiological time) could be defined among fish populations that span a wide temperature range, translating to the well-known higher exploitation rates (calendar time) in warm-water populations and lower exploitation rates (calendar time) in cold water populations. Moreover, physiologically-based rates can be easily scaled to new situations when novel temperature variation arises (e.g. climate change, population discovered in a new area) without the need for tedious temperature-specific parameterisations.
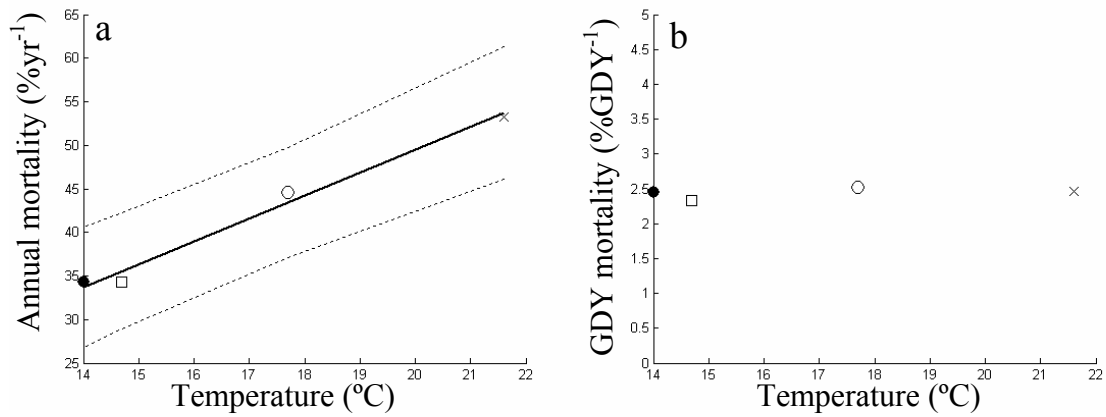
Figure 2.14: Mean natural mortality among species as a, annual mortality (A, %·yr^{-1}, Griffiths and Harrod 2007) and as b, growing degree-year mortality (GDY mortality, %·GDY^{-1}) at mean habitat temperature (T, ºC) for four habitats: reef (cross), pelagic (open circle), demersal (square) and benthopelagic (filled circle). The linear regression (solid line) and 95% prediction intervals (dashed lines) are provided for annual mortality and mean habitat temperature, $A = (2.6\ \%yr^{-1}ºC^{-1})·T - 3.0\ \%·yr^{-1}$ (r^2=0.99, P=0.0068). There was no significant linear regression for GDY mortality and mean habitat temperature (P= 0.52).

The implications of not using a physiologically-scaled temperature become apparent when I examine the effect of a small increase in daily temperature on a predicted LaD. By example, when the daily temperatures for the 2000 year-class of age-0+ Arctic grayling (Fig. 2.5i,j) are uniformly raised by 0.6°C or less, I cannot statistically detect a significant difference between the means of the original and elevated temperature series (neither normal, Wilcoxon Rank Sum, P=0.096, Fig. 2.15) because the variance within each temperature series is greater than among. However, the GDD method predicts a significant ~5% increase (89 to 93 mm) in the length-at-day of the grayling at the end of their first growing season based on the elevated temperature record; a change in size that cannot be explained by the change (not significant) in the mean temperature. The LaD estimates from the two series diverge because the original and adjusted temperature-based GDD series diverge as the heat transferred from the environment to the fish accumulates. Moreover, the effect (expected LaD) will magnify with time (age) as the temperature difference between the two series is integrated in time. Therefore, this physiologically-relevant measure of temperature (heat integral) is essential in predicting the response of fish size-at-age to even small changes in temperature, simply because the changes are integrated by the fish over time. Thus, the GDD metric may prove relevant in resolving size-at-age changes in relation to small changes in ocean temperature (e.g. 0.3 °C increase in the 0-300 m ocean stratum from the 1950s to 1990s, Levitus et al. 2000) being reported as a result of climate change (e.g. Thresher et al. 2007).
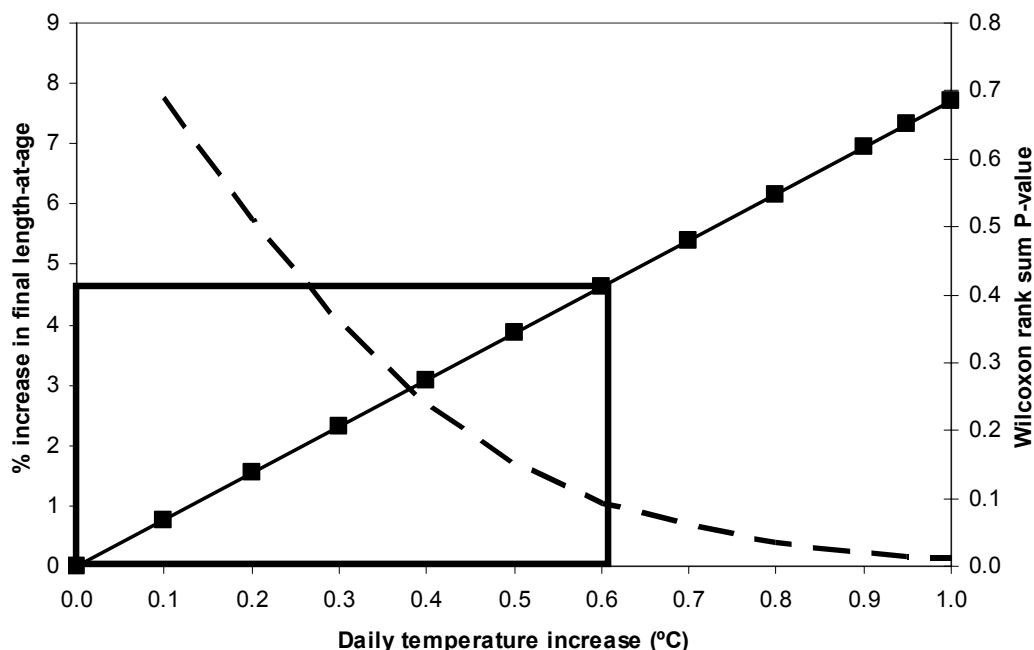
Figure 2.15: Per cent increase in predicted final length-at-age (mm, squares and solid line) for the 2000 year-class age 0+ Arctic grayling (Dion and Hughes 2004) as a function of GDD when the daily temperature series is uniformly increased between 0.1ºC and 1.0 ºC in 0.1ºC increments. The dashed line defines the P-value of Wilcoxon Rank Sum test assessing the difference between the mean temperature of each elevated series relative to the original series. The boxed region indicates the predicted increase in length-at-age that cannot be predicted from differences (not significant) in the mean temperature (i.e. mean temperature of original and perturbed temperature series are statistically similar at a conservative P>0.09).

Although the GDD method has a proven record in explaining growth and development variation among ectotherms for some considerable time (decades to centuries) I know of no previous demonstrations that show GDD to be equally and generally applicable in explaining growth variation (size-at-age) in a variety of fish species and environments, in control and field studies, over large and small spatial and temporal scales.

The GDD appears to have greater explanatory power than contemporary fish-growth models. Clearly, "If the life-table, or population model, is to predict the population dynamics correctly, it must work on the correct time-scale. In the case of homeotherms, the correct time-scale is, clearly, calendar time. . . If we base [a fish] population model on calendar time, we must allow for the effect of temperature. But it is much simpler to base the model on the [fish's] own 'physiological' time-scale, which is a combination of calendar time and temperature." (Gilbert et al. 1976, pp15–16). While physiological rates for endotherms (including humans) are generally independent of environmental temperature due to homeostasis, the rates for most fish (and other ectotherms) are a function of their thermal environment. As demonstrated above, rates measured in calendar time are aliased by our 'endothermocentric' view of time that is physiologically meaningless among fishes that have different thermal histories. In the future, temperature by itself, and time by itself should fade away as only a union of the two will preserve an independent reality for ectotherms (cf. Minkowski 1908). Thus, I challenge others to test the GDD metric in all aspects of fish and aquatic invertebrate physiology, growth and development. I set this challenge because most ectotherms use similar chemical constituents and thermally-controlled reaction rates to create an amazing variety of forms across large time and temperature scales. The question has been asked: "Do biological phenomena obey underlying universal laws of life that can be [parameterised] so that biology can be formulated as a predictive, quantitative science?"(West and Brown 2004). Perhaps a convergence of fish physiology, growth and development, under the scaling of physiological time as provided by the GDD metric, with that already established in agricultural and entomological research, will provide a significant step toward such an underlying law for ectotherm growth and development.

Chapter 3

Fishing Selection and Size-at-Age in Scotian Shelf Haddock (*Melanogrammus aeglefinus*) – Application of the Growing Degree-Day Metric

A portion of this chapter is accepted for publication in:

Neuheimer, A.B., C.T. Taggart, and K.T. Frank. Size-at-age in haddock (*Melanogrammus aeglefinus*): Application of the growing degree-day (GDD) metric. In: G.H. Kruse, K. Drinkwater, J.N. Ianelli, J.S. Link, D.L. Stram, V. Wespestad, and D. Woodby (eds.), Resiliency of gadid stocks to fishing and climate change. Alaska Sea Grant, University of Alaska Fairbanks.

3.1 Introduction

Most fishing gear is size-selective (Sinclair et al. 2002). If a portion of the phenotypic variation in size-at-age is rooted in genetic variation, it is possible that fishing mortality (often exceeding natural mortality by a factor of 2 or 3) may represent a strong genetic selection on a population (Engelhard and Heino 2004; Hutchings 2005) resulting in evolutionary changes in growth and maturation (Law 2000; Stokes and Law 2000). Evidence of these changes in growth dynamics often accompanies periods of exploitation (Grift et al. 2003, Olsen et al. 2004, Hutchings 2005) and have been shown to have a genetic link for Atlantic cod (Swain et al. 2007). Changes in mean growth dynamics affect population growth and recovery rates through decreased age- and size-at-maturity, fecundity and egg size (Hutchings 2005). Thus, evaluating fishing pressure and its effects on fish size-at-age is instrumental in predicting the production capabilities of a population for successful fisheries management.

Management strategies differ depending on the sources of the variation in size-at-age, requiring the causal mechanisms to be identified before management can be successful (Sinclair et al. 2002). Indeed, "failure to simultaneously consider alternative mechanisms, especially size-selective mortality, can lead to incorrect conclusions about the role of environmental factors in determining growth of fishes" (Sinclair et al. 2002).

Thus the ability to assess the effects of fishing pressure on the variation in size-at-age of a population lies in the ability to disentangle those effects from other possible sources of size-at-age variation (e.g. temperature, food consumption, food quality, genotype, phenotype, etc.). Of the fishing-independent factors impacting variation in fish size-at-age, temperature is a controlling factor governing the reaction rates at the cellular level (Fry 1971) and affecting growth processes directly (e.g. cell growth) and indirectly (e.g. digestion). To quote Brander (1995, p. 9) "*Of course, other factors, such as food availability, maturation, and size-selective mortality or migration will affect observed* [length]-*at-age, but the effect of temperature should be allowed for before too much effort is invested in the alternatives.*" Therefore the impact of temperature on size-at-age variation must be examined foremost (Brander 1995) and in a manner that is physiologically-meaningful for the fish.

As change in size-at-age is not an instantaneous process, it cannot be described by an instantaneous measure of temperature. Instead the growth integral (size-at-age) is best examined using the time-based integral of the heat available for growth as demonstrated in Neuheimer and Taggart (2007) and **Chapter 2**. For up to 270 years in some areas of ectotherm research (e.g. agriculture and entomology, Seamster 1950; Atkinson 1994; Bonhomme 2000) and recently in fish research (Neuheimer and Taggart 2007 and **Chapter 2**), the approximation of the thermal integral employed to describe size-at-age is the growing degree-day (GDD, ºC·day). The GDD metric is simply the time integral of the daily temperature measured above a given temperature threshold and in fish it has been shown to explain between 92 and 99% of variation in fish size-at-age over a range of species among environments, temperature regimes, laboratory and field studies represented by 58 datasets. Moreover, the GDD metric explains that portion of the size-at-age variation among datasets that results from variation in the integrated thermal history of the fish. The GDD metric compares fish size-at-age variation on a physiologically-relevant time-scale thereby disentangling size-at-age variation due to variation in temperature from that which may be attributable to other factors such as food availability, genetic composition, etc. as required by Brander 1995.

In this chapter I employ the GDD metric to examine variation in length-at-age (mm) of the eastern Scotian shelf (Northwest Atlantic Fisheries Organization, NAFO,

statistical division 4VW) haddock (*Melanogrammus aeglefinus*) stock for the mature ages 5 through 10 over the period 1970 through 2003. This stock is considered to be a challenge for the utility of the GDD metric in explaining size-at-age variation given the profound reduction in size-at-ages 3+ that has occurred over the past 30 years coincident with high fishing pressure and changing environmental conditions (Frank et al. 2001). Further, I explore the variation in length-at-age unexplained by GDD and the role fishing selection may have played in influencing it. In addition I examine the implications of the effects of fishing selection on the interpretation of condition (*K*), a "health" index based on the weight-at-length relation often employed when examining variation in fish size-at-age.

3.2 Methods

Haddock length-at-age (i.e. length-at-day, LaD, mm, Fig. 3.1) for the NAFO-4VW statistical division (Fig. 3.2) from 1970 through 2003 were obtained from the summer groundfish-trawl research vessel (RV) survey conducted annually by Fisheries and Oceans Canada. I restrict my analyses to mature haddock (ages 5 through 10; Fig. 3.3) to avoid the allometry and discontinuities in LaD as a function of GDD that occur when life-history transformations such as maturation are marked by a change in energy allocation from growth to other physiological demands (e.g. **Chapter 2**, Fig. 2.10).
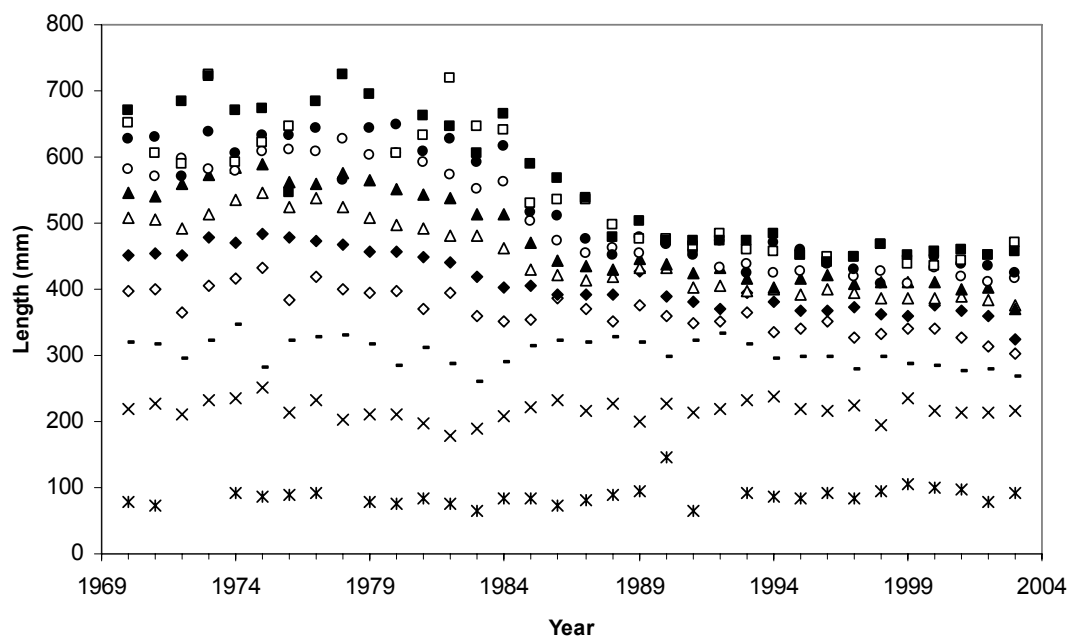
Figure 3.1: Variation in length-at-age (mm) for 4VW haddock from 1970 to 2003 (Frank et al. 2001). Symbols indicate age-0 (star), -1 (cross), -2 (horizontal line), -3 (open diamond), -4 (filled diamond), -5 (open triangle), -6 (filled triangle), -7 (open circle), -8 (filled circle), -9 (open square), -10 (filled square).
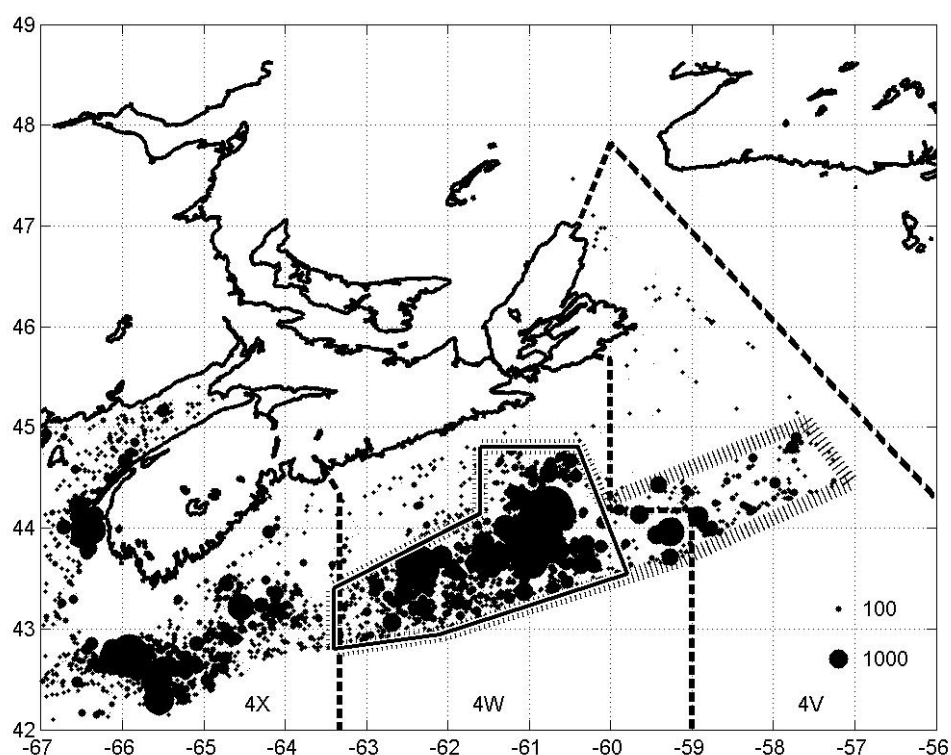
Figure 3.2: Chart showing the Northwest Atlantic Fisheries Organization (NAFO) statistical divisions 4V, W, and X (dashed lines) on the Scotian Shelf off Nova Scotia, Canada with location of RV survey sampling stations with highest abundance of haddock (i.e. upper 3 quartiles of log-transformed effort-adjusted abundance, filled circles) and polygons outlining area wherein temperature was extracted from the Bedford Institute of Oceanography hydrographic database (polygon 1, hatched line, preliminary evaluation including divisions 4VW; polygon 2, solid black line, subsequent evaluation including division 4W; see Section 3.4).
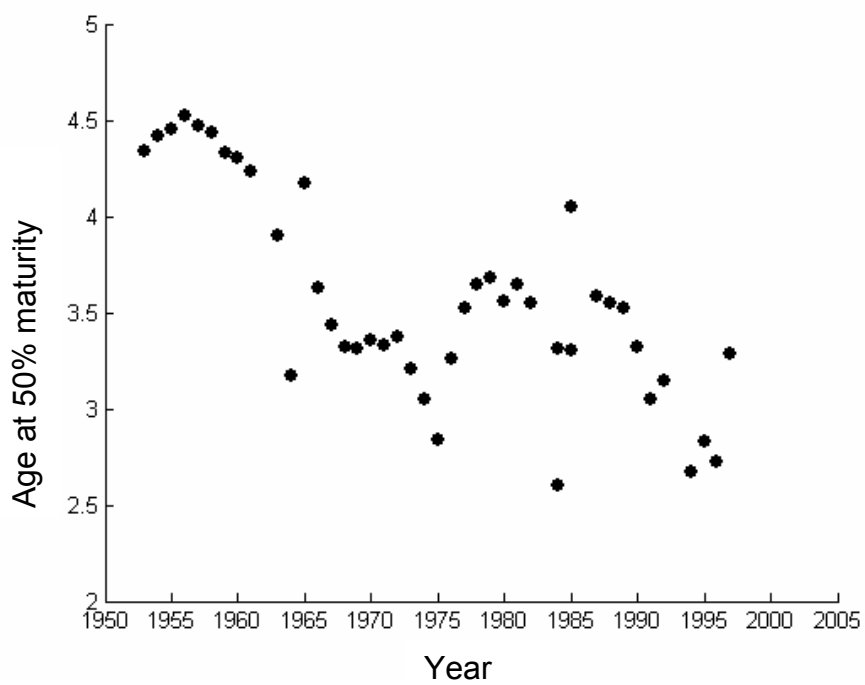
Figure 3.3: Age at 50% maturity for 4VW haddock from 1950 through 2000 (linearly interpolated from Mohn and Simon 2002).

Monthly mean temperature data was extracted from the Bedford Institute of Oceanography hydrographic database for 1960 through 2006 and the 75 ± 25m depth stratum over the area on the Scotian Shelf that encompasses the majority of trawl locations and depths in the summer RV survey with highest haddock abundance estimates; i.e. upper 3 quartiles of log-transformed effort-adjusted abundance (Fig. 3.2, polygon 1).   The mean monthly temperature estimates were linearly interpolated (month to month) where necessary (Fig. 3.4).   The interpolated monthly temperature series was then smoothed using a 25-month uniformly-weighted, centred moving average (to reduce bias due to incomplete time series) and subsequently used to interpolate daily (T_i) estimates. A 25-month moving average was thought to be acceptable as we are concerned with only low-frequency (yearly) LaD measures.   In addition, analysis performed with 13-month, 37-month and 61-month moving averages (to examine the influence of moving average extent) led to similar results in all cases.   The GDD at day n (°C·day) was then calculated as

$$GDD(n) = \sum_{i=1}^{n} (T_i - T_{Th}) \cdot \Delta d, \quad T_i \geq T_{Th} \quad , \tag{1}$$

where T_i is the interpolated mean daily temperature at day i, T_{Th} is the predetermined threshold temperature ($T_{Th} = 0$°C, see **Chapter 2** and Neuheimer and Taggart 2007) and Δd is a set time step (sampling frequency, i.e. 1 d).   Variation in LaD and GDD for each year-class was compared and quantified through linear regression (see **Chapter 2**) according to:

$$LaD = \beta \cdot GDD + \alpha \; , \tag{2}$$

where β is the slope, mm·(°C·day)$^{-1}$, and α is the intercept, mm, of the LaD-at-GDD relation.
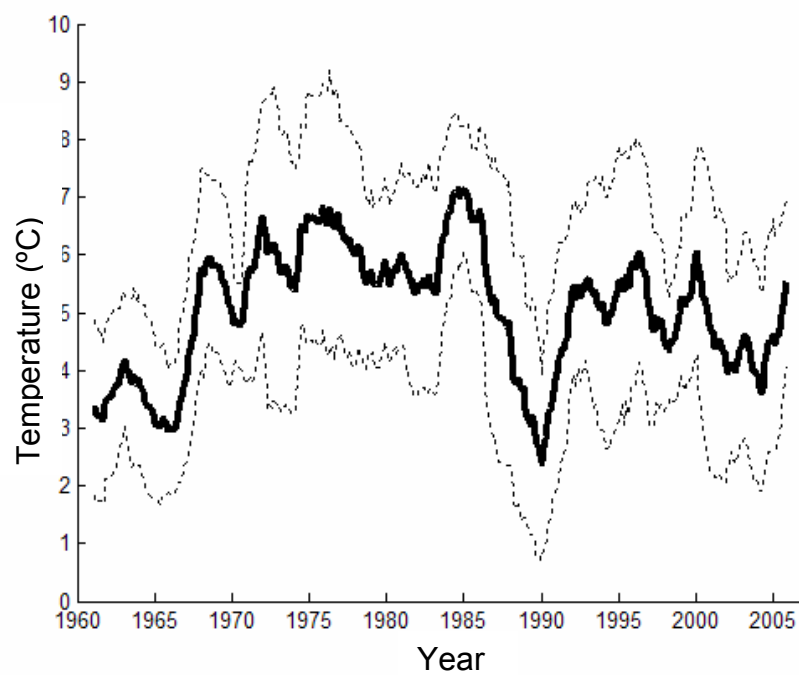
Figure 3.4: Smoothed (25-month moving average) interpolated monthly mean temperature (ºC, solid line) ± one standard deviation (ºC, dotted lines) for polygon 1 in Fig. 3.2. Source data obtained from the Bedford Institute of Oceanography hydrographic database.

Prior to the 1993 fishery closure, 4VW haddock were subject to an extensive fishery with maxima in total landings followed by sharp declines occurring in the mid-1960s and mid-1980s (Frank et al. 2001, Grift et al. 2003, Engelhard and Heino 2004, Walsh et al. 2006). As a measure of temporal variation in size-selective fishing pressure, the annual length-at-maximum-fishing-mortality (mm) from 1970 through 2000 was estimated using annual fishing-mortality-at-age and length-at-age estimates for this stock provided by Frank et al. (2001).

Yearly mean relative condition was estimated for the haddock from 1970 through 2000. Condition (K) is based on the weight-at-length equation (Fig. 3.5)

$$W = aL^b \qquad , \tag{3}$$

where L is length (cm), W is weight (g) and a (g·cm^{-b}) and b are fitted parameters with "good" condition fish being those that fall above the weight-at-length relation and "poor" condition fish being those that fall below. A relative estimate of condition can simply be made using the residuals of the weight-at-length relation (i.e. positive residuals are "good condition", negative residuals are "poor condition"). More commonly, Equation (3) is rearranged to give an estimate of 'relative condition' (K_n) as

$$K_n = \frac{W}{aL^b} \quad \text{(Le Cren 1951).} \tag{4}$$

As a is often very small (10^{-5} to 10^{-3} g·cm^{-b}), 'relative condition' is often reported as

$$K_n = \frac{1}{a} \cdot \frac{W}{L^b} \quad . \tag{5}$$

This formula has been generalized in many studies with a approximated to 0.01 (a^{-1}=100) and b=3 (assuming isometric growth, "cube-law"). This gives us the formula for the more widely used cube-law condition, (K_3):

$$K_3 = 100 \cdot \frac{W}{L^3} \qquad .$$
(6)

However, when examining a specific population, the weight-at-length relation is often known and therefore more accurately estimates of a and b are available. The weight-at-length relation for this stock is

$$W = 0.0054 \cdot L^{3.16},$$
(7)

(Fig. 3.5) making the relative condition (K_n),

$$K_n = 185 \cdot \frac{W}{L^{3.16}} \qquad .$$
(8)

For 4VW haddock K_3 continually underestimates K_n (Fig. 3.6a). As well, the distribution of K_n is more closely centred on 1 (median = 1.00, Fig. 3.6b) than that of K_3 (median = 1.02, Fig. 3.6b) inferring that K_n allows for an estimate of condition normalized to the study population and, subsequently, more accurate comparisons of condition may be made among populations using population-specific parameterizations of K_n.

The time-series (1970 through 2000) of annual mean K_n for ages-5 through -10 was estimated from (8) and examined for discontinuities based on the procedure outlined in Legendre and Legendre (1998). All statistical analyses were performed using Matlab (Version 6.5, MathWorks Inc.). Statistical significance was evaluated at significance level = 0.05 unless otherwise stated.
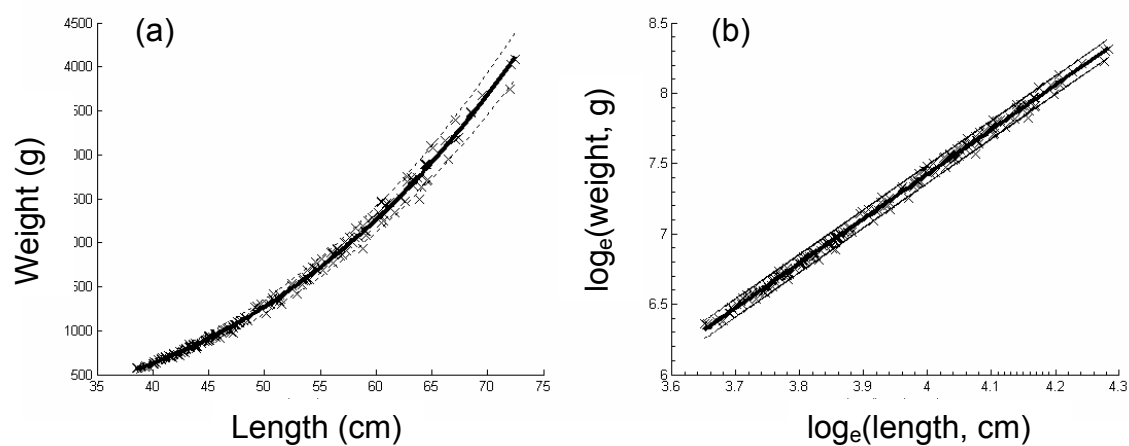
Figure 3.5: The weight-at-length relations for 4VW haddock over 1970 through 2003 (crosses, a) arithmetic: linear regression, black solid line, $W=0.0054 \cdot L^{3.16}$, $r^2=0.99$, $P<0.0001$, with 95% confidence intervals for the prediction, dashed lines; b) geometric: linear regression, black solid line, $\log_e W = -5.23 + 3.16 \cdot \log_e L$, $r^2=0.99$, $P<0.0001$, with 95% confidence intervals for the prediction, dashed lines).
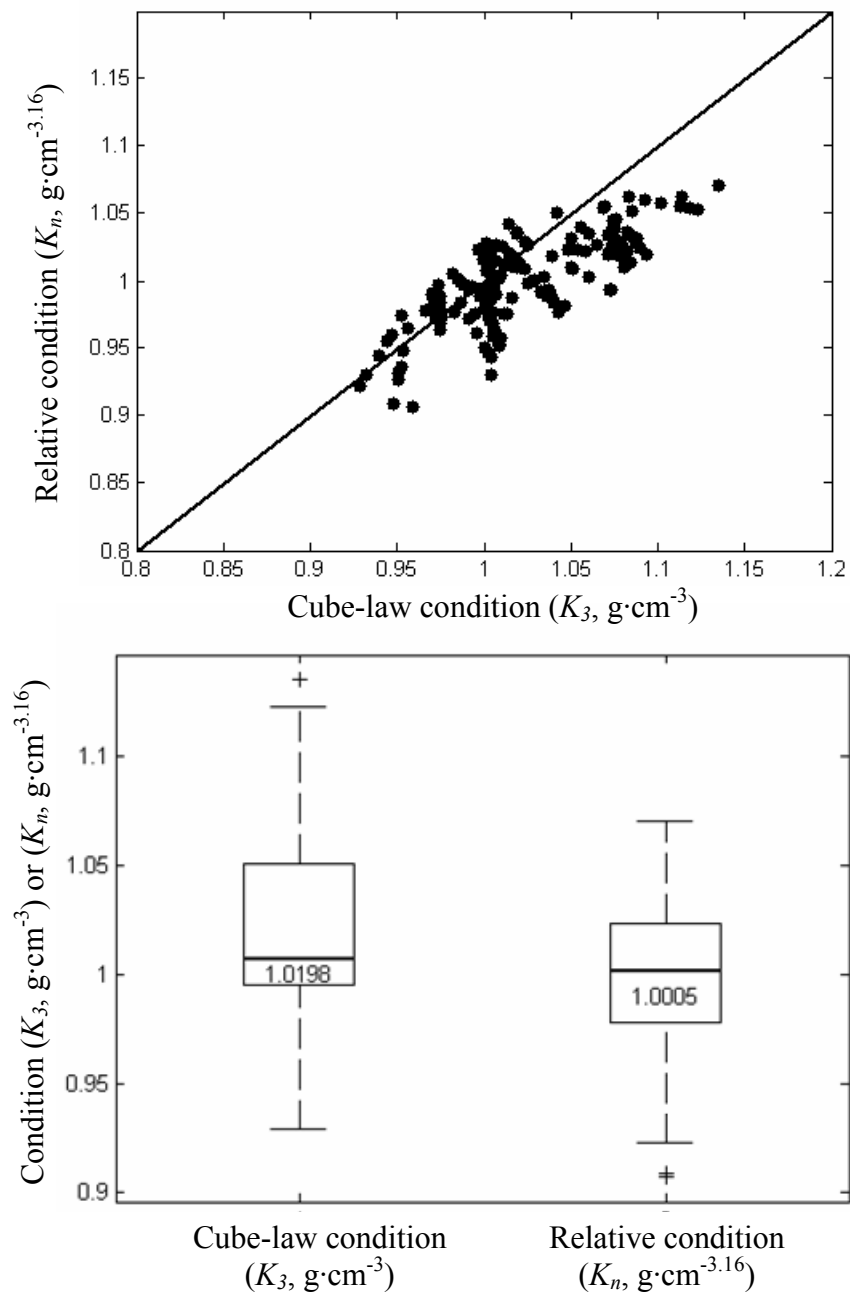
Figure 3.6: a) Relative condition (K_n) and Cube-law condition (K_3) for 4VW haddock ages-5 to -10. Solid line is 1:1 line. b) Box and whisker plots of relative condition (K_n) and Cube-law condition (K_3) Vertical lines are lower quartile, median (value labeled) and upper quartile while whiskers denote extent of data with outliers as +.

3.3 Results

NAFO-4VW haddock show a significant decline in length-at-age for ages 3+ from the mid-1970s to the early 1990s with the highest rate of decline occurring over the 1982 through 1989 period (Fig. 3.2, Table 3.1). The decline in length-at-age with year (slope, mm·yr^{-1}) increased with age (Table 3.1). Length-at-age for age-0 and -1 show no trend over time and for age-2 the relation is marginal as time (year) explains 22% of the length-at-age variation relative to >73% for age-classes 3+ and older (Table 3.1).

Table 3.1: Parameters of linear regression for length-at-age (mm) of NAFO division 4VW haddock as a function of year from 1970 through 2003.

Age	Slope (mm·yr^{-1})	Intercept (mm) x 10^3	r^2	P-value
0				0.09
1				0.80
2	-1.0	2.3	0.22	0.005
3	-2.8	5.9	0.76	<0.001
4	-4.2	8.7	0.87	<0.001
5	-5.3	11.0	0.87	<0.001
6	-6.7	13.7	0.87	<0.001
7	-7.2	14.9	0.84	<0.001
8	-7.8	16.0	0.80	<0.001
9	-7.7	15.8	0.73	<0.001
10	-9.3	19.1	0.81	<0.001

Bathypelagic (75±25m) water temperature within the domain of high haddock abundance on the eastern Scotian Shelf exhibited rapid cooling during the mid- to late-1980s followed by a warming in the early 1990s (Fig. 3.4). Contrary to expectations, variation in GDD within the stock, at shelf scales, did not explain the majority of variation in length-at-day among haddock year-classes as it does, for example, among 17 cod stocks at ocean basin scales (**Chapter 2**, Fig. 2.11). There is nearly as much variation in LaD as a function of physiological time (GDD) across haddock year-classes as there is LaD as a function of calendar time (Fig. 3.7). There was significant variation among LaD-at-GDD relations for the 1965 through 1996 year-classes (Fig. 3.7b, ANCOVA, different slopes P<0.0001). On inspection (Fig. 3.7), the year-classes can be aggregated into two periods, prior to 1979 and 1979 and later, to compare the LaD-at-GDD relations (i.e. slope and intercept, Fig. 3.8). The LaD as a function of GDD relations among the <1979 year-classes demonstrate statistically similar slopes (P=0.43) and differing intercepts (P=0.0018) as shown in Figure 3.8 and there is no time-dependent trend in the intercepts (Fig. 3.8b, linear regression, P=0.71). The LaD as a function of GDD relations among the ≥1979 year-classes also demonstrate (Fig. 3.8) statistically similar slopes (P=0.17) and differing intercepts (P<0.0001) but unlike with the earlier year-classes there is significant and near-systematic year-class dependent decay in the intercepts of the LaD-at-GDD relations (Fig. 3.8b. linear regression, r^2=0.50, P=0.003). Further, the mean slope of the LaD-at-GDD relation for the <1979 year-classes is 0.013 ± 0.0009 mm·(ºC·day)$^{-1}$ and is nearly twice that (Fig. 3.8a, Shapiro-Wilk normality test: P>0.62; Two-sample T-test: P<0.0001) estimated for the ≥1979 year-classes at 0.007 ± 0.0004 mm·(ºC·day)$^{-1}$. Of the 18 year-classes (1960 through 1964, 1966, 1970, 1973, 1976 through 1978, 1983, 1985, 1986, 1997 through 2000) that did not demonstrate significant (P > 0.05) LaD-at-GDD relations, a few were marginally significant (P < 0.15, 1964, 1973 and 1985) while others suffered from limitations in series length (i.e. many of the older ages for the most recent, 1997 through 2000, year-classes were absent).
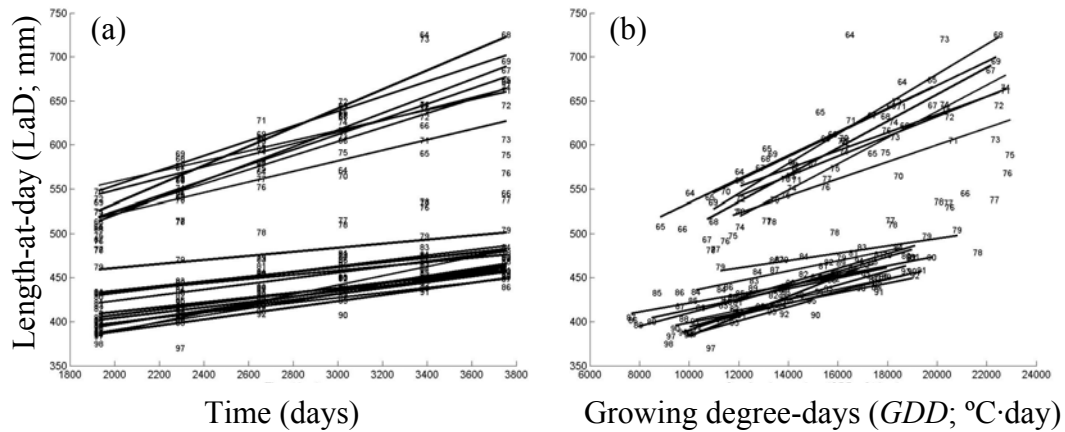
Figure 3.7: Length-at-day (mm) for 4VW haddock ages-5 to -10 as a function of a) calendar time (days, no significant relation among year classes, ANCOVA, different slopes P<0.0001); and as a function of b) GDD (ºC·day, no significant relation among year classes, ANCOVA, different slopes P<0.0001). Data-labels denote year-class decade and year in the 1900s. Year-classes with non-significant (P>0.05) LaD-at-GDD relations are omitted (1960 through 1964, 1966, 1970, 1973, 1976 through 1978, 1983, 1985, 1986, 1997 through 2000)
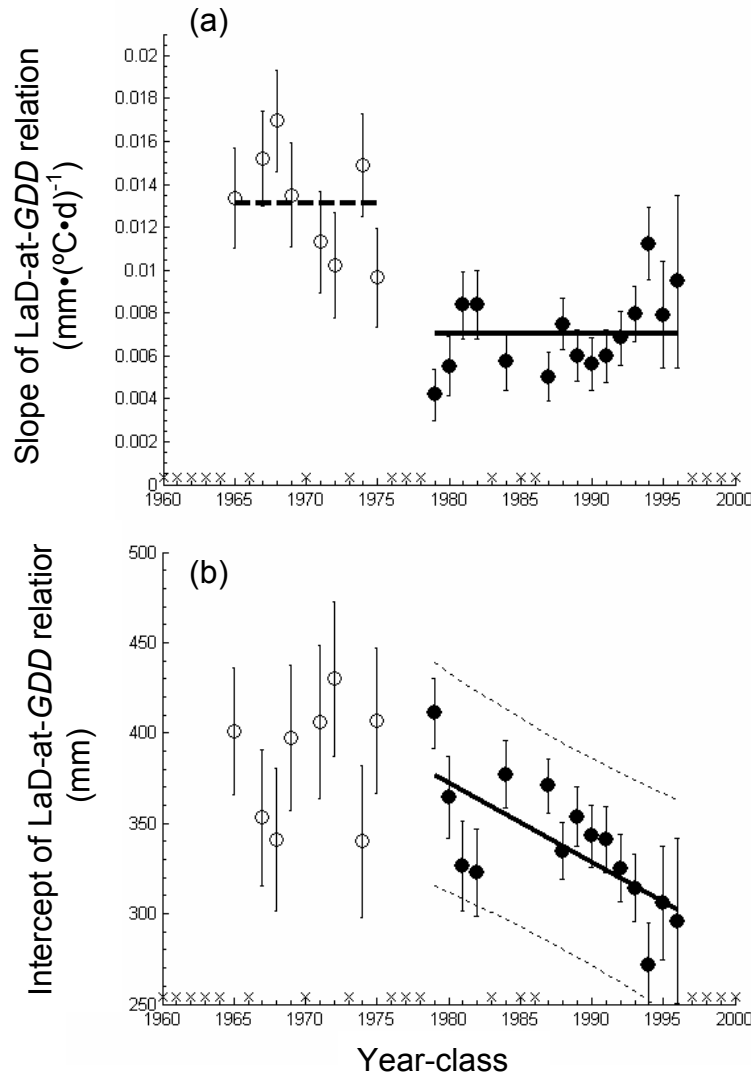
Figure 3.8: Parameters of the LaD-at-GDD relation for early (< 1979, open circles) and late (≥ 1979, filled circles) year-classes.   a) Slopes, mm·(°C·day)$^{-1}$, and associated standard error of the LaD-at-GDD relations are statistically similar within early (open circles, dashed horizontal line, ANCOVA, similar slopes P=0.43) and late (filled circles, solid horizontal line, ANCOVA, similar slopes P=0.17) year-classes. Slopes of the LaD-at-GDD relations are statistically higher in early, 0.013 ± 0.0009 mm·(°C·day)$^{-1}$, year-classes than late 0.007 ± 0.0004 mm· (°C·day)$^{-1}$, year-classes (Shapiro-Wilk normality test: P>0.62; Two-sample T-test: P<0.0001). b) Intercepts, mm, and associated standard error of the LaD-at-GDD relations are statistically different within early (ANCOVA, different intercepts P=0.0018) and late (ANCOVA, different intercepts P=0.17) year-classes. There was a significant decline in intercept among late year-classes (solid line, linear regression, Intercept = -4.3·Year-class + 1x10^{3}mm, r^2=0.50, P=0.003, dashed lines indicate 95% confidence intervals around the prediction) but not early year-classes (linear regression, P=0.71). Crosses denote year-classes with non-significant (P>0.05) LaD-at-GDD relations.

Instantaneous fishing mortality systematically targeted the largest fish in the population (Fig. 3.9a), consistently greater than 400 mm and age-6 (Fig. 3.9b) throughout the study period (1970 through 2000). There was a significant decline in length-at-maximum-fishing-mortality (mm) with year as the size at maximum fishing mortality followed the largest fish in the stock through time (linear regression, length-at-maximum-fishing-mortality = -0.043·Year + 86, r^2=0.31, P=0.0011; Fig. 3.9b).
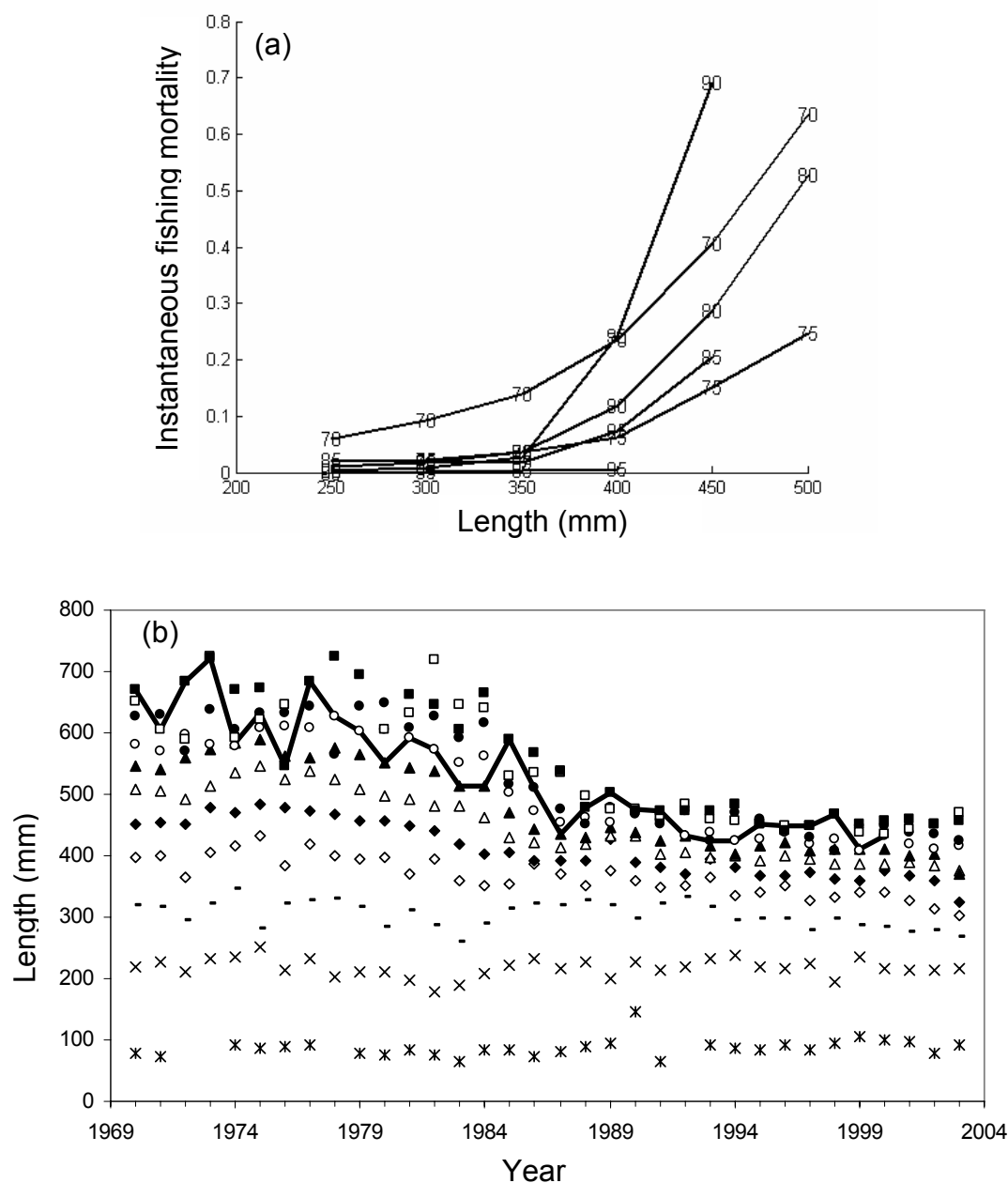
Figure 3.9: a) Variation in mean instantaneous fishing mortality (Frank et al. 2001) at length (mm) grouped in 5-year periods: "70": 1970-1974, "75": 1975-1979, "80": 1980-1984, "85": 1985-1989, "90": 1990-1994, "95": 1995-1999. b) Variation in length-at-maximum-fishing-mortality (mm, solid line) and length-at-age (mm, symbols, Frank et al. 2001) for 4VW haddock from 1970 to 2003. Symbols indicate age-0 (star), -1 (cross), -2 (horizontal line), -3 (open diamond), -4 (filled diamond), -5 (open triangle), -6 (filled triangle), -7 (open circle), -8 (filled circle), -9 (open square), -10 (filled square).

The annual time series of mean relative condition (K_n, Fig. 3.10a) for haddock ages-5 through -10 from 1970 through 2000 exhibited a significant discontinuity about 1982 and 1983 (Fig. 3.10b, discontinuity analysis, P>0.10) with significantly higher condition (Shapiro-Wilk normality test: P>0.42; Two-sample T-test: P=0.0052) for years prior to 1982 (mean = 1.02 ± 0.029 g·cm$^{-3.16}$) than after (mean = 0.99 ± 0.025 g·cm$^{-3.16}$).
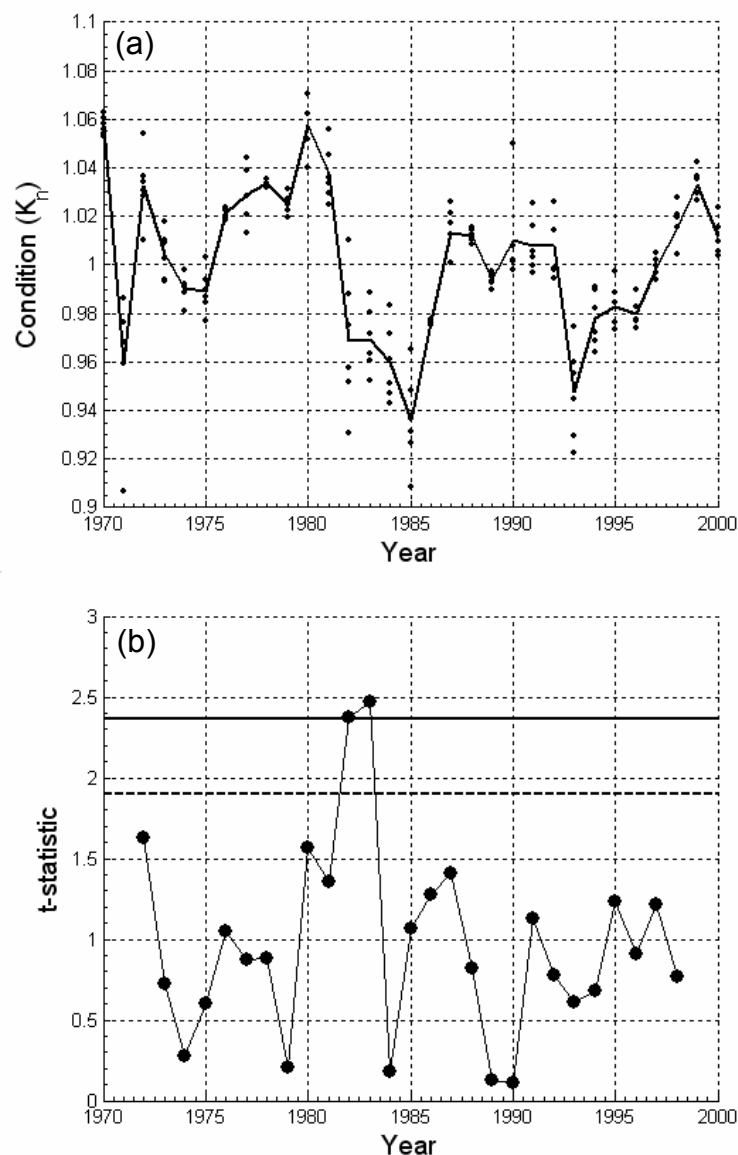
Figure 3.10: a) Relative condition (K_n) of 4VW haddock ages-5 through -10 (filled circles) and annual mean K_n (solid line) for 1970 to 2000. b) Discontinuity analysis for the time series (1970-2000) of mean annual relative condition of haddock. Horizontal lines indicate t-statistic at P=0.10 (broken line) and P=0.05 (solid line). Window extent = 4 years.

3.4 Discussion

The NAFO-4VW haddock stock experienced a decline in LaD in the 1980s that was coincident with variation in a number of factors affecting fish growth, as inferred through population size-at-age; factors that included a doubling of the fishing effort and a decrease in water temperature (Zwanenburg 2000). As a first step toward disentangling the various factors that could potentially explain the variation in haddock length-at-age, I turned to temperature (as Brander 1995 suggests I must) and examined variation in LaD (mm) with GDD (°C·day) as a function of variation in year-class thermal history; i.e. the physiologically-relevant measure of temperature. In doing so I find the thermal integral explains only a small portion of the variation in LaD among 4VW haddock year-classes.

A major requirement for employing the GDD metric is that the temperature measure used is representative of that experienced by the organism over the growth period of interest (**Chapter 2** and Neuheimer and Taggart 2007). Over the period I examine here, the distribution of the 4VW haddock generally shifted from an area restricted primarily to 4W (polygon 2, Fig. 3.2) for the 1965 through 1974 year-classes to an area generally including divisions 4VW (polygon 1, Fig. 3.2) for the 1975 through 1984 year-classes, and then back to division 4W for the 1985 through 1994 year-classes. Bathypelagic (75±25m) water temperatures for polygon-1 and -2 demonstrated similar cooling in the mid- to late-1980s and warming in the early 1990s (Fig. 3.11a), and though the uncertainties (standard deviations) are large in either case (Fig. 3.11a), the temperature in polygon-2 was warmer than that in polygon 1 (Fig. 3.11b) for most of the time. During both the early (<1979) and late (≥1979) periods of year-class groupings, the majority of the stock as revealed by the survey was restricted to division 4W (polygon 2, Fig. 3.1). Consequently, I ask, if I limit my temperature analyses to the polygon-2 temperature estimates, do I find that GDD was better able to explain the variation in LaD among the early and late year-classes? The answer was unequivocally no, as I resolved similar relations among year-classes as with the polygon-1 temperature data. The only difference was a slightly lower slope in the mean LaD-at-GDD relation for the late year-classes (≥1979) using the polygon-2 temperature data, 0.006 ± 0.0004 mm·(°C·day)$^{-1}$, relative to that of polygon-1, 0.007 ± 0.0004 mm·(°C·day)$^{-1}$; each nearly half that exhibited for the earlier year-classes (see above). Thus, my examination of temporal

changes in the geographic distribution of the stock in relation to thermal habitat does not appear to explain the expected temperature-dependent variation in LaD among year-classes when spatial variation over time is incorporated into the analyses.
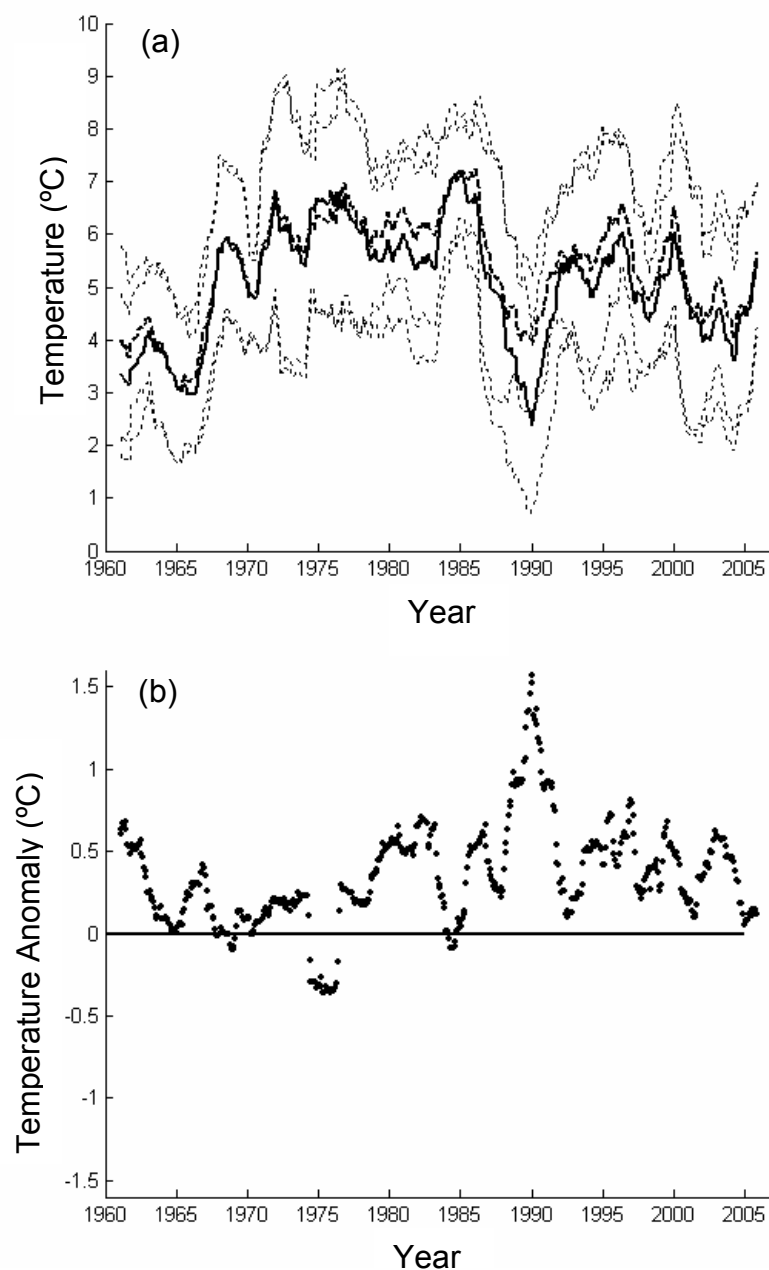
Figure 3.11: a) Smoothed (25-month moving average) interpolated monthly mean temperature (ºC) ± one standard deviation (ºC, dotted lines) for polygon-1 (solid line) and polygon-2 (dashed line) in Fig. 3.1. b) Temperature anomaly for polygon-1 relative to polygon-2 (i.e. temperature in polygon 1 − temperature in polygon 2, ºC). Source data obtained from the Bedford Institute of Oceanography hydrographic database.

The above analyses show that the variation in thermal history (GDD) was unable to explain the majority of variation in LaD among 4VW haddock year-classes on the Scotian Shelf despite the fact that cooler water is often given as the primary source of size-at-age decline in this stock (e.g. Trippel 1995). Such an argument is most easily attributed to observations of the decline in temperature on the Shelf occurring more-or-less coincidently with the decline in LaD for this stock. However, the decline in size-at-age precedes that of temperature by approximately 3 years (Fig. 3.12). Furthermore, when temperatures return to near-normal in the 1990s, the size-at-age does not return to near-normal but continues to decline (see also Zwanenburg 2000; Drinkwater and Frank 2001). These conclusions remain if I employ time to examine LaD or the integrated temperature measure (GDD); the preferred metric particularly when various year-classes with different growth (and thermal) histories are involved and when spatially different thermal histories related to distributional changes in the stock are considered. Further, and perhaps the most compelling argument is based on the evidence that LaD for 4VW haddock ages, 0, 1 and marginally so for 2, remain unchanged regardless of the thermal environment (integrated or not). Age-0 haddock occupy pelagic waters for approximately four months before becoming bathypelagic along with older age-classes (DFO 2001). If temperature was the major source of variation in LaD, one would expect the youngest ages to be equally affected (Drinkwater and Frank 2001) and this is not the case (Fig. 3.2, Table 3.1).
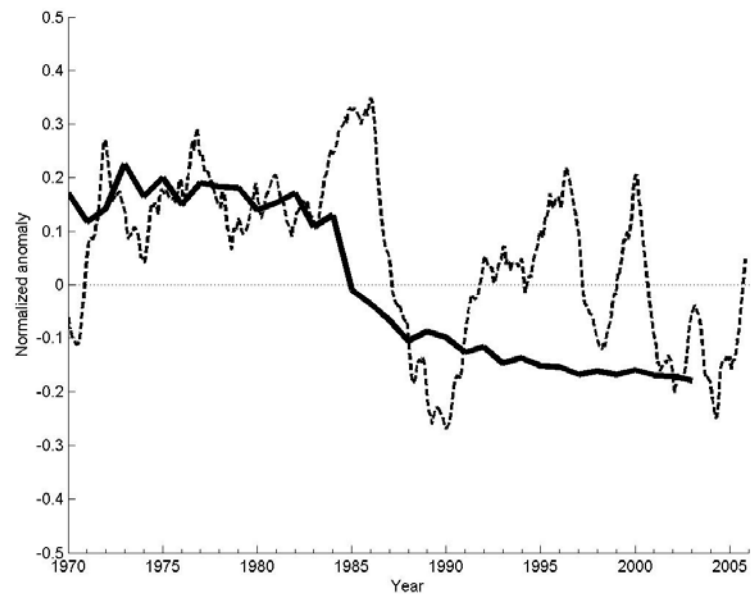
Figure 3.12: Normalized anomalies of mean length for ages-5 through -10 (solid line) and smoothed (25-month moving average) interpolated monthly mean temperature (dashed line) where $\dfrac{Normalized\ Anomaly}{} = \dfrac{Anomaly - (Mean\ Anomaly)}{Mean\ Anomaly}$.

It is clear that temperature variation, as parameterized through the thermal integral, does not explain the decline in 4VW haddock size-at-age over the study period. However, it has been shown elsewhere that temperature can explain LaD among fish, within species, in many environments if the comparisons are made using the same physiological timescale (i.e. GDD) and where it does not it is an indication that contributions to the variation in LaD may be attributed to other factors (**Chapter 2** and Neuheimer and Taggart 2007). Here I have employed the GDD metric to identify the portion of variation in size-at-age that is attributable to variation in thermal history. The question becomes – what other factors may explain the remaining size-at-age variation in the 4VW haddock; i.e. the variation in slopes and intercepts of LaD-at-GDD relations among year-classes shown in Fig. 3.8?

The year-class LaD-at-GDD relations demonstrate declines in slope and intercept with increasing year-class that are unrelated to temperature variation (Fig. 3.8ab). The smaller LaD-at-GDD slope of the late ($\geq$1979) year-classes relative to the early (<1979) may be inferred as slower growth in the late year-classes. The decline in intercepts among the late year-class LaD-at-GDD relations may result from either 1) slower growth prior to maturation (Fig. 3.13a) or 2) earlier maturation (Fig. 3.13b). As LaD for immature fish (age-0 to -1 and marginal for -2) show no significant change over time (Linear regression, age-0: P=0.09, age-1: P=0.80, age-2: P=0.005, r^2=0.22, Table 3.1), there is no evidence for slower growth in immature fish. Conversely, evidence for earlier maturation and maturation at smaller size is found in this stock as 4VW haddock show a significant decline in length at 50% maturity (Fig. 3.14a, linear regression, length at 50% maturity = -4.3 · Year + 8900 mm, r^2=0.68, P<0.0001) and marginal decline in age at 50% maturity (Fig. 3.14b, linear regression, age at 50% maturity = -0.024·Year + 50, r^2=0.14, P=0.088) from approximately 480 mm and 3.5 yr in 1980 to 300 mm and 3.2 yr in 2001 (Drinkwater and Frank 2001, Frank et al. 2001). The onset of maturation is accompanied by a decrease in growth rate as a portion of energy previously allocated to growth is redirected to reproduction. Therefore, earlier maturation (decrease in LaD-at-GDD intercepts among year-classes) in concert with the slower growth (decrease in LaD-at-GDD slopes among year-classes) appears to be the most parsimonious explanation for the decrease in LaD in this stock. But what is responsible for this trend towards earlier

maturation and slower growth? Here I turn to my index of size-selective fishing (length-at-maximum-fishing-mortality).
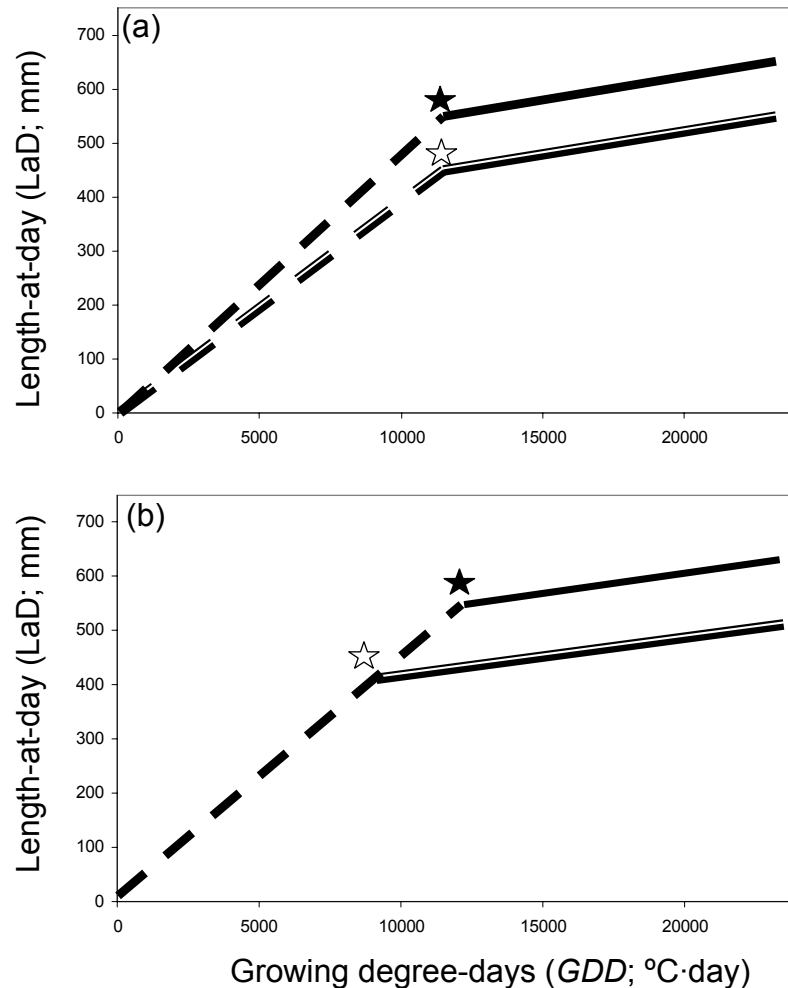
Figure 3.13: Illustrations of the possible mechanisms resulting in a decrease in intercept of the LaD-at-GDD relation for mature fish. The slope of the LaD-at-GDD relation for mature fish (solid line) is typically lower than that of immature fish (dashed line) with a change in slope occurring at maturation (filled star). A decrease in the intercept of the LaD-at-GDD relation for mature fish (e.g. $\geq$ 1979 year-classes, solid double line) may result from either a) slower growth prior to maturity - the slope of the LaD-at-GDD relation for immature fish (open squares, dashed double line) is lower while maturation (open star) remains at the same physiological time, or b) earlier maturation - the slope of the LaD-at-GDD relation for immature fish remains the same while maturation (open star) occurs earlier in physiological time.
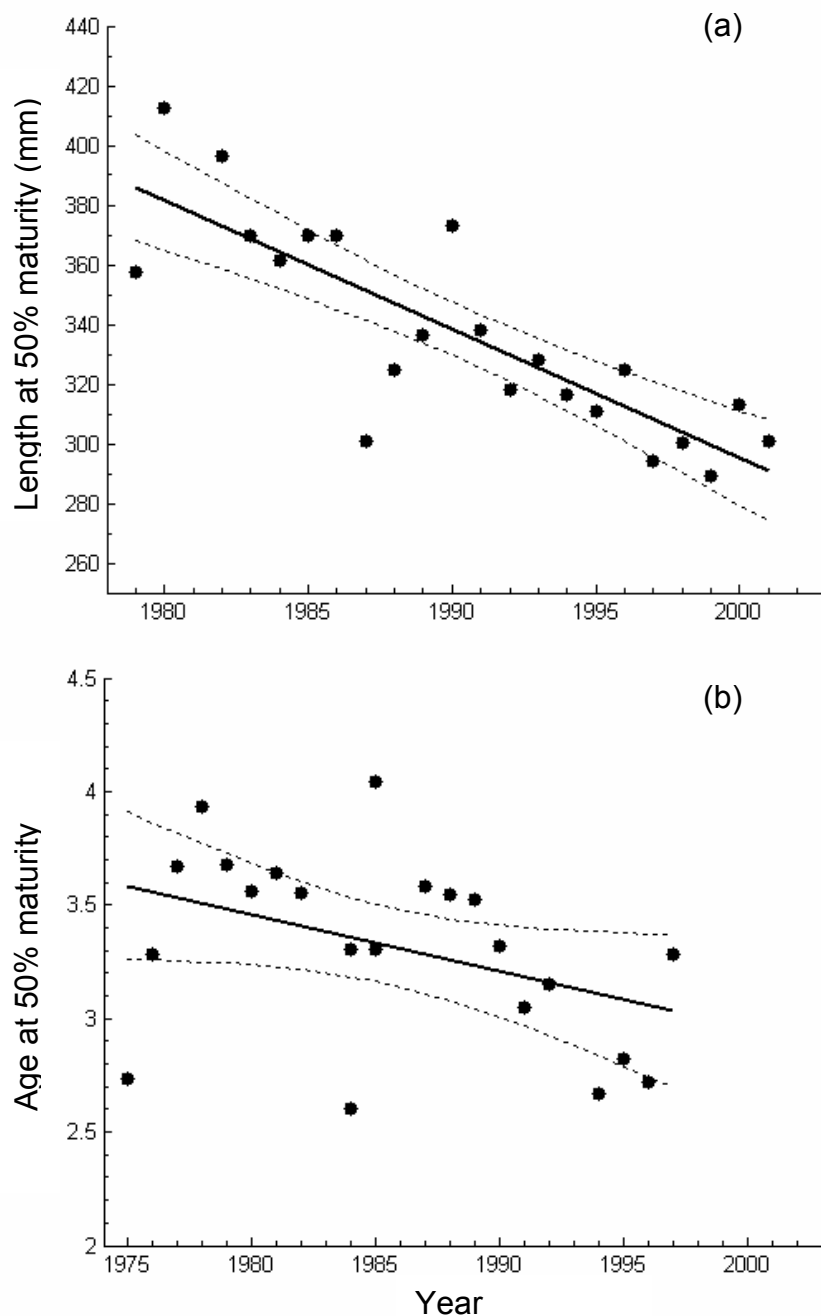
Figure 3.14: a) Linearly interpolated length (mm) at 50% maturity for 4VW haddock (source data from Frank et al. 2001). Solid line indicates significant trend (linear regression, length at 50% maturity = -4.3 · Year + 8900 mm, r^2=0.68, P<0.0001), dashed lines indicate 95% confidence intervals around the prediction. b) Interpolated age at 50% maturity for 4VW haddock (source data from Frank et al. 2001). Solid line indicates marginal trend (linear regression, age at 50% maturity = -0.024 · Year + 50, r^2=0.14, P=0.088), dashed lines indicate 95% confidence intervals around the regression.

Prior to the 1993 fishery closure, 4VW haddock were subject to an extensive and intensive fishery that was size-selective simply because fishing pressure concentrated on the largest haddock throughout the study period (Fig. 3.9ab). This selection is typical of most fishing gear where minimum mesh (or hook, etc.) size is employed to allow the smallest fish to escape (Sinclair et al. 2002). What effect might selecting for large fish have on the growth characteristics of the population? This question can be explored by first identifying the strategies that allow individual fish to grow large relative to the mean of the population. These are 1) faster growth overall and 2) later maturation (to maximize time spent at the faster, immature growth). By preferentially removing the largest fish, that section of the population that is late-maturing and fast-growing is removed preferentially. If I illustrate the variation in growth rate and time to maturation of a population by normal probability density functions (Fig. 3.15ac), I can show that, by removing the late-maturing, fast-growing fish, I drive the growth and maturation distributions to the left, resulting in a population disproportionately represented by slower-growing, earlier-maturing fish. Thus, sustained exploitation selecting for large fish offers a simple mechanism that results in declines in growth (slope of the LaD-at-GDD relation) and age-at-maturity (intercept of the LaD-at-GDD relation) over time; as observed for this stock. Indeed, comparing the 1971-1981 and 1982-2000 time periods, I find a significant decline in median growth rate (mm·yr^{-1}, Fig. 3.15b, Median test, P<0.0001) for this stock. The median age at 50% maturity also appears to be declining though not significantly (Fig. 3.15d, Median test, P=0.70) and may reflect the added uncertainty in estimating both age and maturity.
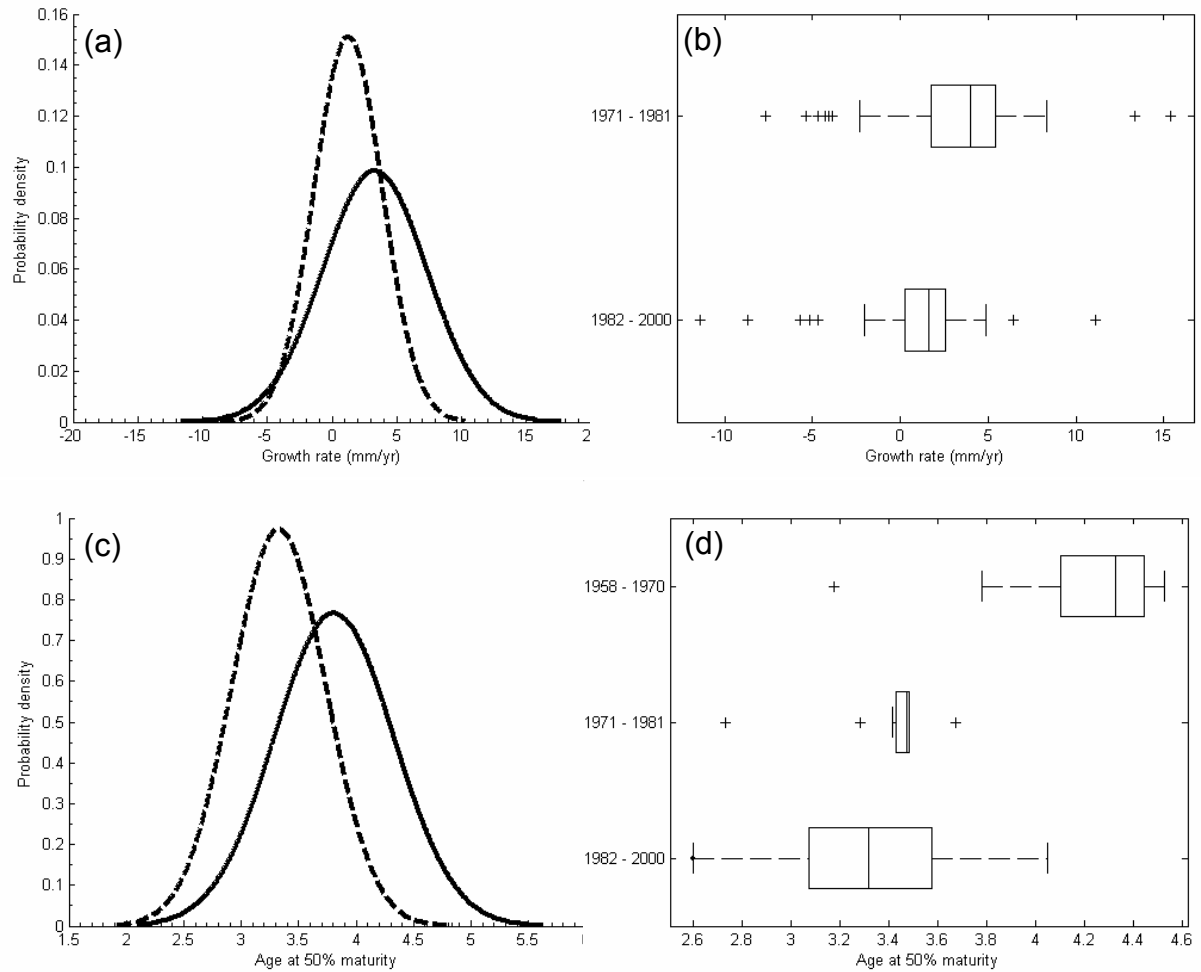
Figure 3.15: Theoretical normal probability density functions for a) growth rate (mm·yr^{-1}, solid line: 1971 through 1981, dashed line: 1982 through 2000, parameterized from length-at-age (mm) data in Frank et al. 2001) and c) age at 50% maturity (yr, solid line: 1958 through 1981, dashed line: 1982 through 2000, parameterized from age at 50% maturity data in Frank et al. 2001). Also shown are box and whisker plots of b) growth rate (mm·yr^{-1}) for 1971 through 1981 and 1982 through 2000 (from length-at-age (mm) data in Frank et al. 2001) and d) age at 50% maturity (yr) for 1958 through 1981, 1971 through 1981 and 1982 through 2000 (from Mohn and Simon 2001 and Frank et al. 2001). Vertical lines are lower quartile, median and upper quartile while whiskers denote extent of data with outliers as +.

Evidence for these impacts of size-selective fishing is noted elsewhere in the North Atlantic; greater reductions in size-at-age are found in target than in non-target species (Zwanenburg 2000) and similar trends toward earlier maturation are found in other exploited populations including Northeast Arctic cod, *Boreogadus saida*, North Sea plaice, *Pleuronectes platessa*, Atlantic halibut, *Hippoglossus hippoglossus*, and Atlantic cod, *Gadus morhua*, (Hanson and Chouinard 1992; Law 2000; Sinclair et al. 2002).

A change in the growth dynamics of the stock brought on by size-selective fishing pressures can influence the interpretation of the condition metric, a widely-used metric in examining the "health" of fish populations. Most fish species on the Scotian Shelf show "good" condition up to 1982 with "poor" condition after (DFO 2003) mirroring the trend found in my analysis of temporal variation in condition for NAFO-4VW haddock (Fig. 3.10). As variables favourable to growth were strong at this time (i.e. low groundfish abundance, high prey abundance since approximately 1990), "the persistent reduced condition of a variety of groundfish species…is perplexing to say the least" (DFO 2003). As the 1982 discontinuity marked a switch from consistently positive to consistently negative weight-at-length residuals, I hypothesized that the apparent decrease in condition may be evidence of a switch in weight-at-length relation for this stock, i.e. the parameterization of the condition index has changed. By grouping the haddock condition data into the "pre" (<1982) and "post" ($\geq$ 1982) years I find evidence for such a switch as the weight-at-length relations for the two periods differ statistically (pre: $\log_e W = 3.08 \cdot \log_e L - 4.89$, $r^2 = 0.99$, P<0.0001; post: $\log_e W = 3.03 \cdot \log_e L - 4.73$, $r^2 = 0.99$, P<0.0001; ANCOVA, similar slopes P=0.16, different intercepts P<0.0001, Fig. 3.16). To normalize the condition estimates between periods, I used the respective weight-at-length relations as according to LeCren 1951 (Section 3.2) to reformulate the relative condition for the 'pre' (K_{n_pre}) and 'post' (K_{n_post}) years,

$$K_{n\_pre} = 133 \cdot \frac{W}{L^{3.08}} \quad , \tag{9}$$

$$K_{n\_post} = 113 \cdot \frac{W}{L^{3.03}} \quad . \tag{10}$$

When I re-evaluate the time-series in annual mean relative condition with the normalized formulations (Fig. 3.17a) I find the discontinuity at 1982 no longer significant (Fig. 3.17b, P>0.05) and the mean condition for the pre and post periods are statistically similar (mean = 1.00 ± 0.028 g·cm$^{-3.08}$ and 1.00 ± 0.022 g·cm$^{-3.03}$ respectively; Shapiro-Wilk normality test: P>0.11; Two-sample T-test: P=0.97). Thus, by employing the relative condition, K_n, metric no temporal discontinuity in condition is found, indicating that the observed discontinuity in cube-law condition, K_3, (Fig. 3.10) is likely resulting from changes in the population mean growth dynamics (weight-at-length relation), most parsimoniously explained by fishing. Therefore, changes in condition that may be inferred as representing changes in food availability or quality may in actual fact be only an artifact (i.e. a product of human conception rather than an inherent element) of the changes in growth dynamics explained by size-selective fishing. It would be interesting to examine the same phenomenon in condition of other exploited fish stocks on and off of the Scotian shelf. I hypothesize that strong switches in condition in exploited fishes may simply be another indicator of the changing growth dynamics most parsimoniously explained by fishing selection.
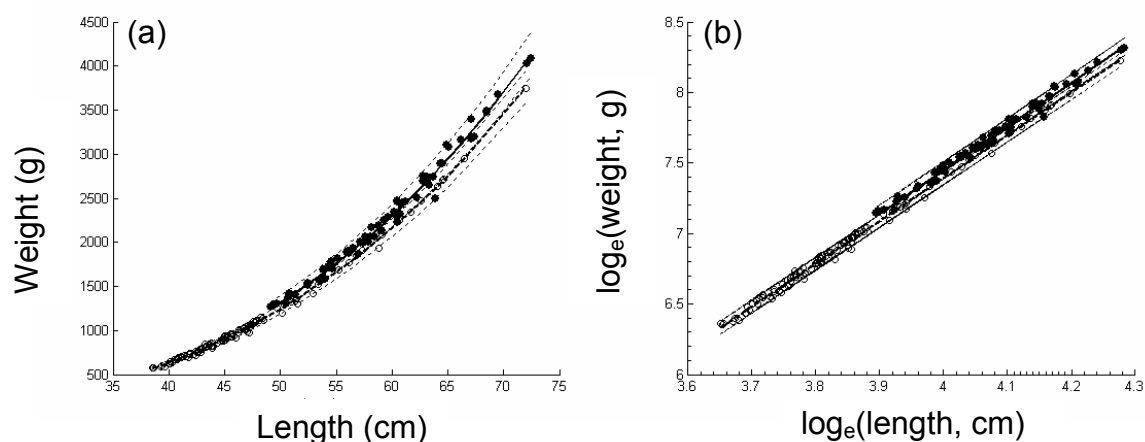
Figure 3.16: The weight-at-length relations for 4VW haddock over 1970 through 1981 ("pre" group, filled circles, linear regression, solid line, $\log_e W = 3.08 \cdot \log_e L - 4.89$, $r^2 = 0.99$, P<0.0001) and 1982 through 2000 ("post" group, open circles, linear regression, dashed line, $\log_e W = 3.03 \cdot \log_e L - 4.73$, $r^2 = 0.99$, P<0.0001). Weight-at-length relations are significantly different between "pre" and "post" groups (ANCOVA, similar slopes P = 0.16, different intercepts P < 0.0001). Dashed lines indicate 95% confidence intervals around the prediction.
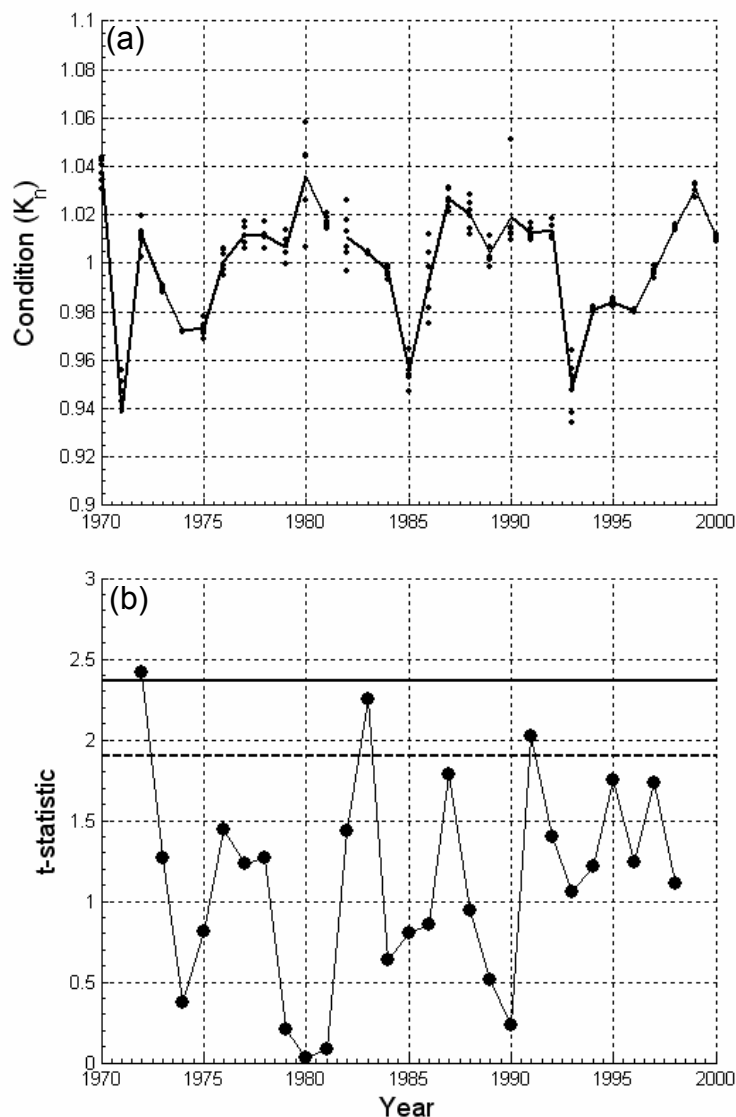
Figure 3.17: a) Relative condition (K_n) of 4VW haddock ages-5 through -10 (filled circles) and annual mean K_n (solid line) for 1970 to 2000 evaluated 'pre' and 'post' the 1981/1982 discontinuity (see Discussion). b) Discontinuity analysis for the time series (1970-2000) of mean annual relative condition of haddock evaluated 'pre' and 'post' the 1981/1982 discontinuity. Horizontal lines indicate t-statistic at P=0.10 (broken line) and P=0.05 (solid line). Window extent = 4 years.

Changes in size and maturation can result in genetic shifts in a population (Trippel 1995, Grift et al. 2003) that may not be readily reversible, unlike phenotypic changes such as those resulting from the influence of temperature or food availability (Grift et al. 2003) particularly considering the low strength of natural selection relative to fishing selection (Sinclair et al. 2002, Swain et al. 2007).   These shifts may reduce a population's capacity to recover from high exploitation as the overall effect of selective fishing is to select against those traits that allow for the conversion of energy into population growth (Walsh et al. 2006). Evidence for the recovery potential of the 4VW haddock will begin to become apparent as monitoring of the stock's size-at-age continues, especially if the GDD metric is employed to explain temperature effects and allow for year-class comparisons on a physiologically-relevant time-scale. I can not reject other possible factors (e.g. food availability and quality) playing a role in the observed changes in size-at-age in this stock.   However, I argue size-selective fishing provides the most parsimonious mechanism for the changes, able to explain the changes in size-at-age, age- and length-at-maturity as well as the temporal variation in condition observed in this stock.

Chapter 4

Variation in Growing Degree-Day and Size-at-age in Southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*)

4.1 Introduction

Explaining variation in fish size-at-age requires disentangling the influence of a number of different factors including temperature, food consumption and fishing mortality. Of these factors temperature is a controlling force for all ectotherms and must be examined foremost to accurately quantify the effects of other, temperature-independent factors. In **Chapters 2** and **3** (as well as Neuheimer and Taggart 2007) I argue that the appropriate metric for measuring the thermal history of fish is the growing degree-day (GDD) as the integrated formulation allows one to include variation in temperature on a physiologically relevant time scale comparable to changes in size-at-age. However the use of the growing degree-day metric requires temperature measurements that are relevant to the animal; i.e. representing the variation in temperature actually integrated by the fish. The decorrelation scale for temperature in aquatic environments can be much larger than that of terrestrial environments due to the high heat capacity of water. Thus temperature measurements for studies involving aquatic ectotherms need not be made as locally or frequently as that for terrestrial organisms (**Chapter 2**; Neuheimer and Taggart 2007). However, by optimizing the temperature measurements sufficiently local to the stock one can have more confidence that the variation in temperature integrated by the fish is captured and the temperature-independent differences among year-classes can be explored.

While measuring relevant temperature variation is relatively straightforward for freshwater fish occupying a closed system (e.g. lake), marine fish, some highly migratory, present a challenge to the estimation of the fish's thermal environment. One such challenge is found with the Atlantic cod (*Gadus morhua*) of the southern Gulf of St. Lawrence (sGSL; Northwest Atlantic Fisheries Organization, NAFO, statistical division 4T). Cod occupy the sGSL during the spring and summer where they reproduce and feed

intensively (Comeau et al. 2002). In autumn, cod leave their feeding grounds in dense aggregations (Rose 1993) and migrate up to 650 km to overwinter along the southern edge of the Laurentian channel in the Cabot Strait and the eastern Scotian Shelf where they mix with other stocks (Ruzzante et al. 2000). In the spring they migrate back to their spawning and feeding grounds inside the sGSL (Fig. 4.1; Comeau et al. 2002). In addition, the stock is vertically stratified based on age with older cod found at depth (Tremblay and Sinclair 1985; Swain 1993; Swain and Kramer 1995). Thus, sGSL cod exhibit temporal and age-dependent variations in space, both horizontally and vertically, requiring a characterization of migration timing and temperature estimates from a variety of locations to ensure the estimation of representative thermal histories. In this chapter I examine the ability of the GDD metric to explain size-at-age variation in the highly migratory sGSL cod. My goal is to identify that portion of variation in sGSL cod size-at-age that is due to variation in temperature to allow for the examination of remaining variation in size-at-age among year-classes that may be attributable to other factors.

4.2 Methods

The sGSL (Northwest Atlantic Fisheries Organization, NAFO, statistical division 4T; Fig. 4.1) Atlantic cod length-at-age (i.e. length-at-day, LaD, mm, Fig. 4.2) from 1970 through 2005 were obtained from the summer groundfish-trawl research vessel (RV) survey conducted annually by Fisheries and Oceans Canada (Chouinard et al. 2006). Temporal trends in length-at-ages-1 through 14 were quantified through linear regression. During the spring and summer, 4T cod occupy the sGSL ("In", Fig. 4.1). During the autumn cod migrate to overwinter along the southern edge of the Laurentian channel in the Cabot Strait and the eastern Scotian Shelf representing portions of NAFO statistical divisions 3Pn, 3Ps, 4R, 4Vn, and 4Vs ("Out", Fig. 4.1).
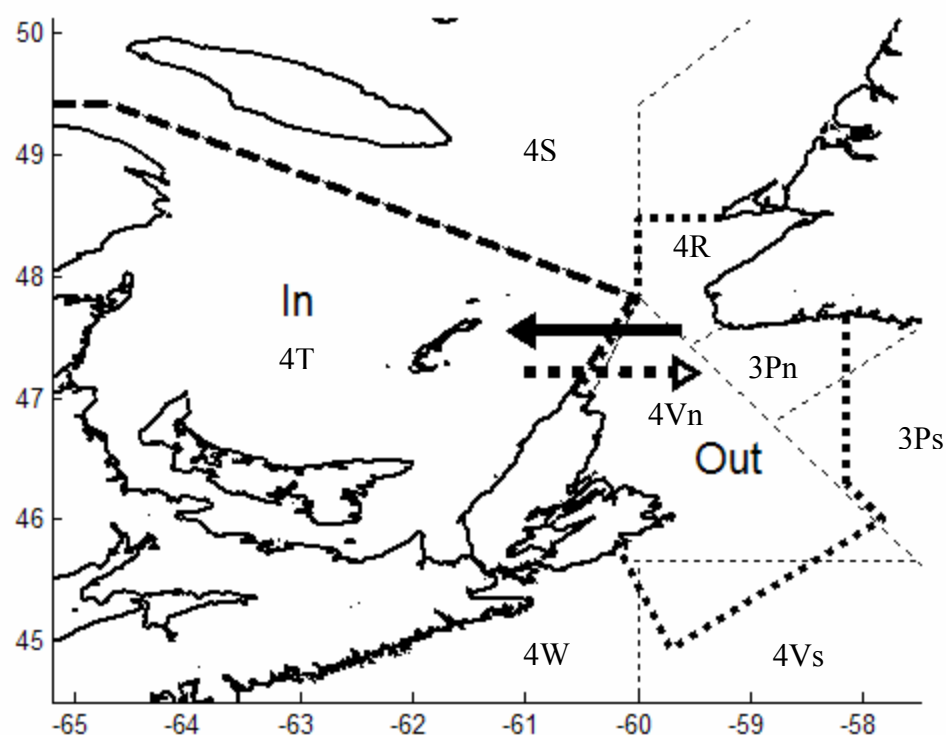
Figure 4.1: Chart of the southern Gulf of St. Lawrence (sGSL) indicating areas occupied by the NAFO 4T cod. sGSL cod migrate in to the sGSL (area indicated by dashed line, NAFO subdivision 4T) during the spring (May, solid arrow) and out of the sGSL (area indicated by dotted line) in the autumn (November, dashed arrow). Alphanumeric labels are NAFO subdivisions.
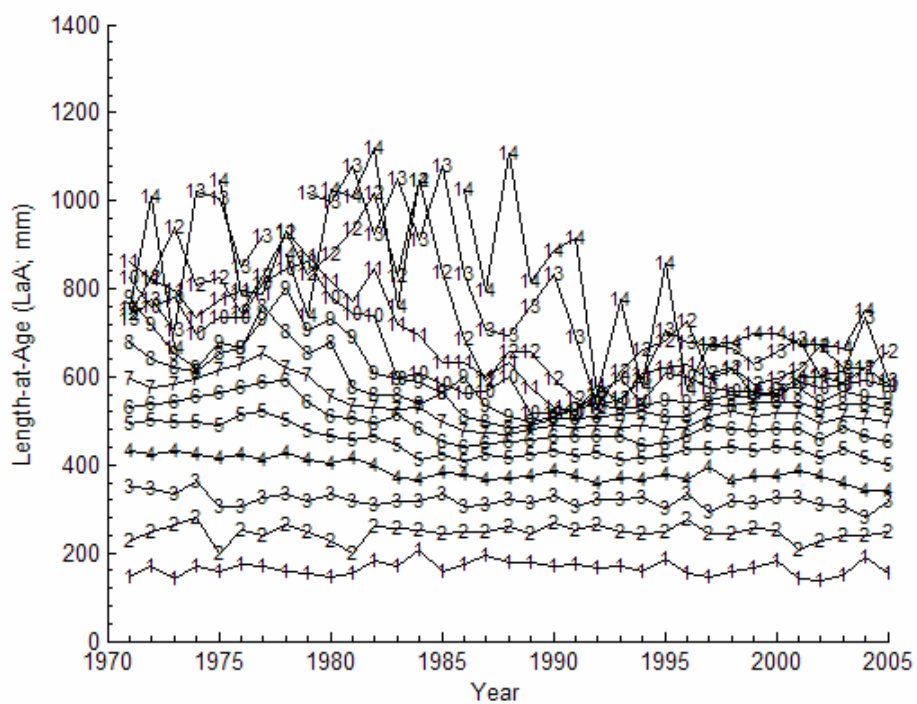
Figure 4.2: Variation in length-at-age (mm) for 4T cod from 1970 to 2005 (from Chouinard et al. 2006). Numerals indicate age.

Age-of-50% maturity decreased from 6 to 3.5 yr during the 1960s and 1970s (Beacham 1987). Accordingly mean length-at-ages were grouped as immature (ages-1 to -4) and mature (ages-6 to -14) by year-class to manage the allometry and discontinuities in LaD as a function of GDD that may occur when life-history transformations such as maturation are marked by a change in energy allocation from growth to other physiological demands (**Chapter 2** and Neuheimer and Taggart 2007). As well, the immature/mature division aids in the estimation of relevant temperature variation (and subsequent relevant thermal histories) as the two stages occupy different depths and potentially different thermal environments (Hanson 1996).

Monthly mean temperature data were extracted from the Bedford Institute of Oceanography hydrographic database for 1955 through 2006 and the waters occupied by immature (stage = immature; ages-1-4) and mature (stage = mature; ages-6-14) cod inside (area = in; Fig. 4.1; immature depths = 0-50m, mature depths = 50-350m, Hanson 1996) and outside (area = out, Fig. 4.1; immature depths = 100-200m, mature depths = 200-550m, Hanson 1996) the sGSL, with linear interpolation (month to month) where necessary. The interpolated monthly temperature series were smoothed using uniformly-weighted and centred 25-month moving averages (to reduce bias due to incomplete time series) and subsequently used to interpolate temperature ($T_{area,i}^{stage}$) estimates at day (i) for each stage (immature, $T_{area,i}^{immature}$, or mature, $T_{area,i}^{mature}$) and area (in, $T_{in,i}^{stage}$, or out, $T_{out,i}^{stage}$, of the sGSL, Fig. 4.1). Analysis performed with 13-month, 37-month and 61-month moving averages (to examine the influence of moving average extent) led to similar results in all cases.

A continuous temperature series (T_i^{stage}) at day i was determined for each stage (stage = immature or mature) by shifting between the stage-specific temperature series for inside ($T_{in,i}^{stage}$) and outside ($T_{out,i}^{stage}$) the sGSL based on the timing of seasonal migration (illustrated in Fig. 4.3). The inter-annual variability in timing of seasonal migrations for sGSL cod is small with the spring migration occurring on May $3^{rd} \pm 8$ days (day of year 115 to 131, 1970 through 1992) with some variation depending on ice leaving the sGSL (Comeau et al. 2002). Cod initiated autumn migration progressively earlier since the 1980s with migration occurring near 30 November for 1970 through 1985, 14 November

for 1986 through 1992 and 1 November for 1995 through 1999 (Comeau et al. 2002). Thus, the summer migration (i.e. switch from $T_{out,i}^{stage}$ to $T_{in,i}^{stage}$) was estimated at 3 May (day of year 123) for 1955 through 2004 while the winter migration (i.e. switch from $T_{in,i}^{stage}$ to $T_{out,i}^{stage}$) was estimated at 30 November (day of year 334) for 1970 through 1985, 14 November for 1986 through 1995 (day of year 318), and 1 November (day of year 305) for 1996 through 2004 (Fig. 4.3).
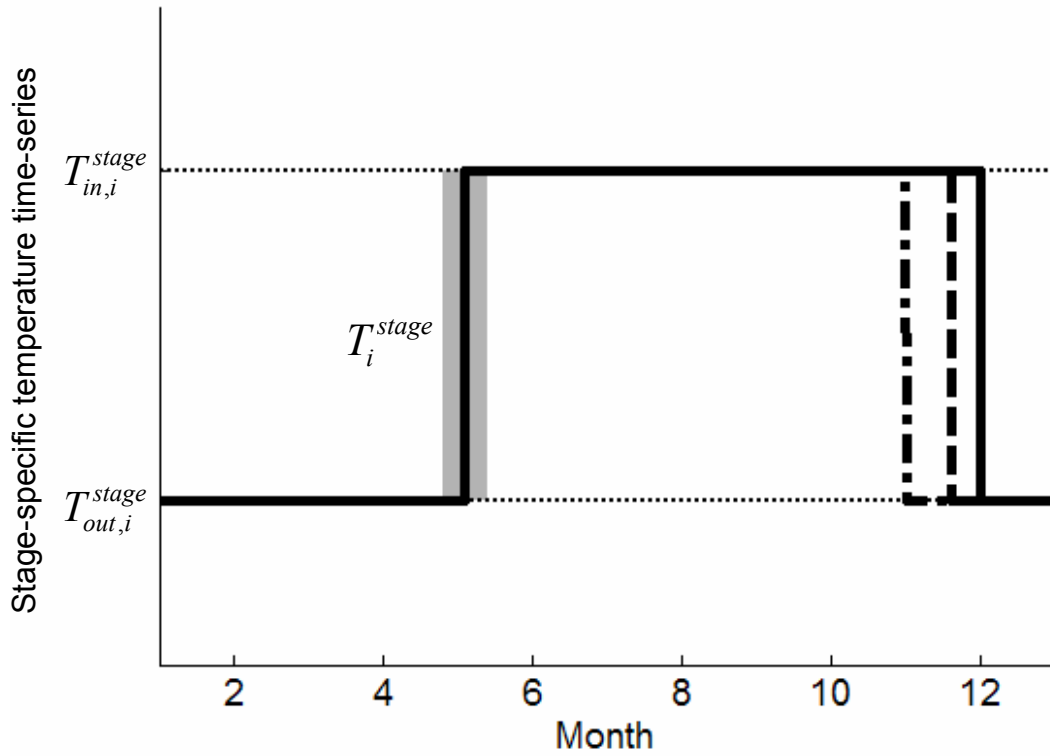
Figure 4.3: An illustration of the stage-specific temperature series (T_i^{stage}, solid line) at day i determined for each stage (stage = immature or mature) by shifting between the depth-specific temperature series for inside ($T_{in,i}^{stage}$) and outside ($T_{out,i}^{stage}$) the sGSL based on the timing of seasonal migration. Variation in the spring migration is shaded in grey (3 May ± 8 days). The autumn migration advanced from 30 November (solid line) in 1970 through 1985 to 14 November (dashed line) for 1986 through 1992 to 1 November (dash-dot line) for 1996 through 2004 (Comeau et al. 2002).

The GDD at day n (°C·day) was calculated for each year-class as:

$$GDD(n) = \sum_{i=1}^{n} \left(T_i^{stage} - T_{Th} \right) \cdot \Delta d, \qquad T_i^{stage} \geq T_{Th} \quad , \tag{1}$$

where T_i^{stage} is the interpolated mean daily temperature at day i for stage = immature or mature, T_{Th} is the predetermined threshold temperature (T_{Th} = 0°C, see **Chapter 2** and Neuheimer and Taggart 2007) and Δd is a set time step (sampling frequency, i.e. 1 day). Variation in LaD and time for the immature and mature fish of each year-class were compared and quantified through linear regression according to:

$$LaD = \beta' \cdot Time + \alpha' \quad , \tag{2}$$

Where β' is the slope, mm·(day)$^{-1}$, and α' is the intercept, mm, of the LaD-at-Time relation. Variation in LaD and GDD for the immature and mature fish of each year-class was compared and quantified through linear regression according to:

$$LaD = \beta \cdot GDD + \alpha \quad , \tag{3}$$

where β is the slope, mm·(°C·day)$^{-1}$, and α is the intercept, mm, of the LaD-at-GDD relation. All statistical analyses were performed using Matlab (Version 6.5, MathWorks Inc.). Statistical significance was evaluated at significance level = 0.05 unless otherwise stated.

4.3 Results

SGSL cod show a significant decline in length-at-age for ages 4+ from the mid-1970s to the early 2000s with the highest rate of decline occurring over the late 1970s through the 1980s (Fig. 4.2, Table 4.1). Length-at-age for age-1 and -2 show no trend over time and the relations for age-3 and -14 are not as strong as other ages as time (year) explains 24% and 25% of the length-at-age variation respectively relative to >43% for ages-4+.

Table 4.1: Parameters of linear regression for length-at-age (mm) of sGSL cod as a function of year from 1970 through 2005.

Age	Slope	Intercept (x10^3)	r^2	P-value
1				0.97
2				0.92
3	-0.78	1.9	0.24	0.0026
4	-2.11	4.6	0.71	<0.0001
5	-2.62	5.7	0.59	<0.0001
6	-3.07	6.6	0.52	<0.0001
7	-3.60	7.7	0.51	<0.0001
8	-4.82	10	0.50	<0.0001
9	-5.85	12	0.54	<0.0001
10	-7.73	16	0.58	<0.0001
11	-8.95	18	0.64	<0.0001
12	-9.25	19	0.47	<0.0001
13	-10.51	22	0.43	<0.0001
14	-8.36	17	0.25	0.0040

Seasonal variation in temperature with depth demonstrated summer thermal stratification confined to the upper 100m both inside (Fig. 4.4a) and outside (Fig. 4.4b) the sGSL. Inside the sGSL, immature cod occupy warm surface waters (Fig. 4.4a) while mature cod are mainly found below the thermocline (Fig. 4.4b). Mean temperature inside the sGSL is significantly higher (Mann-Whitney; P<0.0001) for the depths occupied by immature cod (Shapiro-Wilks Test for Normality: P<0.0001; Median 3.6°C; Fig. 4.5a) than those occupied by the mature cod (Shapiro-Wilks Test for Normality: P<0.0001; Median 3.3°C; Fig. 4.5b). Mean temperature outside the sGSL is significantly lower (Mann-Whitney: P<0.0001) for the depths occupied by immature cod (Shapiro-Wilks Test for Normality: P<0.0001; Median 2.9°C; Fig. 4.5a) than those occupied by the mature cod (Shapiro-Wilks Test for Normality: P<0.0001; Median 5.2°C; Fig. 4.5b). Temperature associated with immature cod inside the sGSL showed a significant decline over the study period (Linear regression: $T_{in,i}^{immature} = -0.031Y + 0.65$; r^2=0.42; P<0.0001; Fig. 4.5a) while that for mature cod showed an increase, reduced in magnitude (i.e. lower r^2) but significant (Linear regression: $T_{in,i}^{mature} = 0.0062Y - 9.0$; r^2=0.08; P < 0.0001; Fig. 4.5b). Outside the sGSL, both immature and mature cod were restricted to depths below the seasonal warming. Temperature associated with immature cod outside the sGSL showed a slight increase over the study period (Linear regression: $T_{out,i}^{immature} = 0.0051Y - 7.2$; r^2=0.02; P < 0.0001; Fig. 4.5a) while the increase for the temperature associated with mature cod outside the sGSL was prominent (Linear regression: $T_{out,i}^{mature} = 0.017Time - 29$; r^2=0.39; P < 0.0001; Fig. 4.5b). The strongest trends remained after estimation of the stage-specific temperature series (T_i^{stage}) where the temperature estimates decreased over time for the waters occupied by the immature cod (Linear regression: $T_i^{immature} = -0.017Y + 37$; r^2=0.11; P < 0.0001; Fig. 4.5c) and increased over time for those of the mature cod (Linear regression: $T_i^{mature} = 0.016Time - 27$; r^2=0.05; P<0.0001).
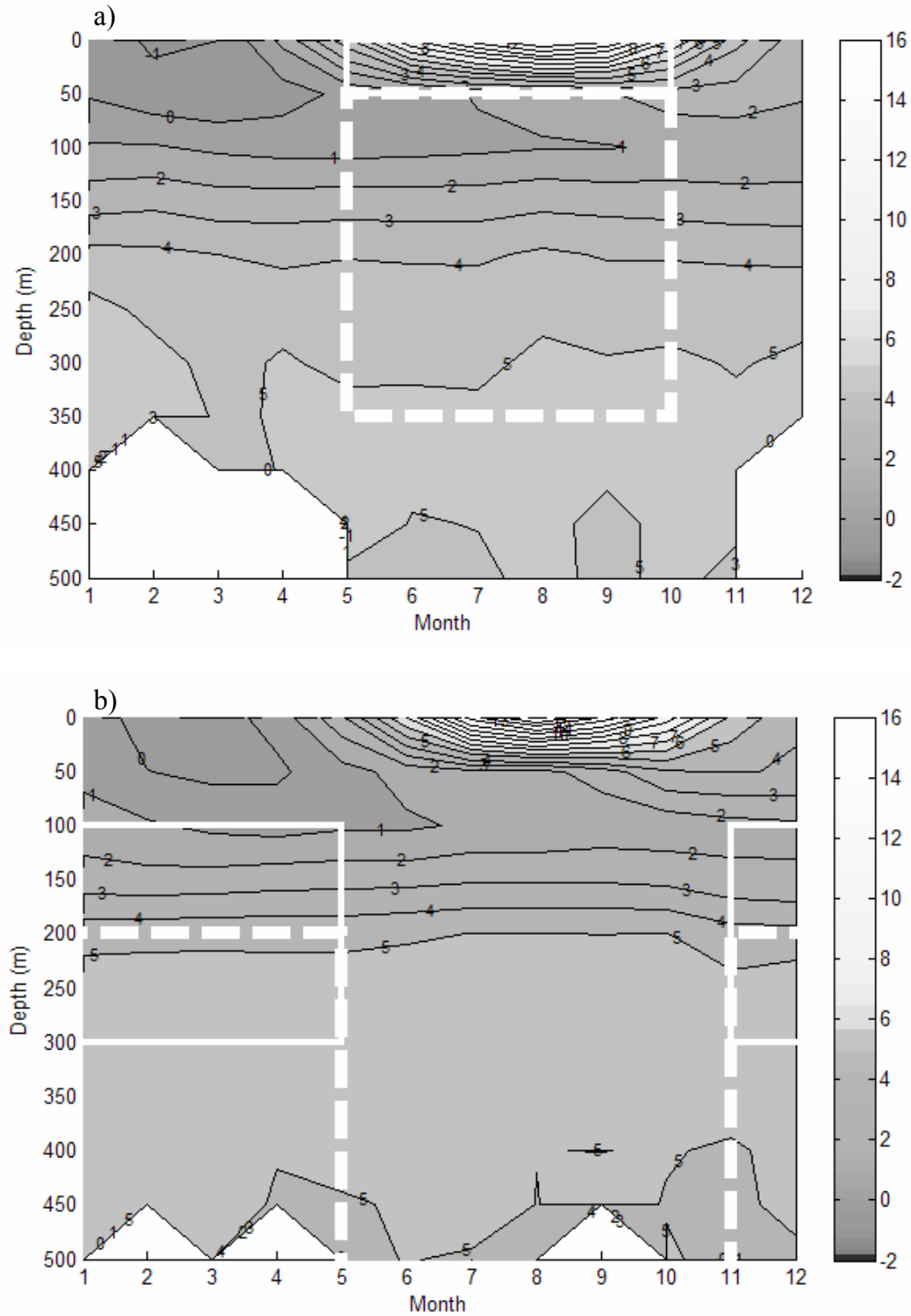
Figure 4.4: Seasonal variation in temperature with depth for a) inside (4T) and b) outside the sGSL. Depths occupied by immature (white solid line) and mature (white dashed line) are indicated. Missing values at depth (i.e. > 350m) are depicted in white.
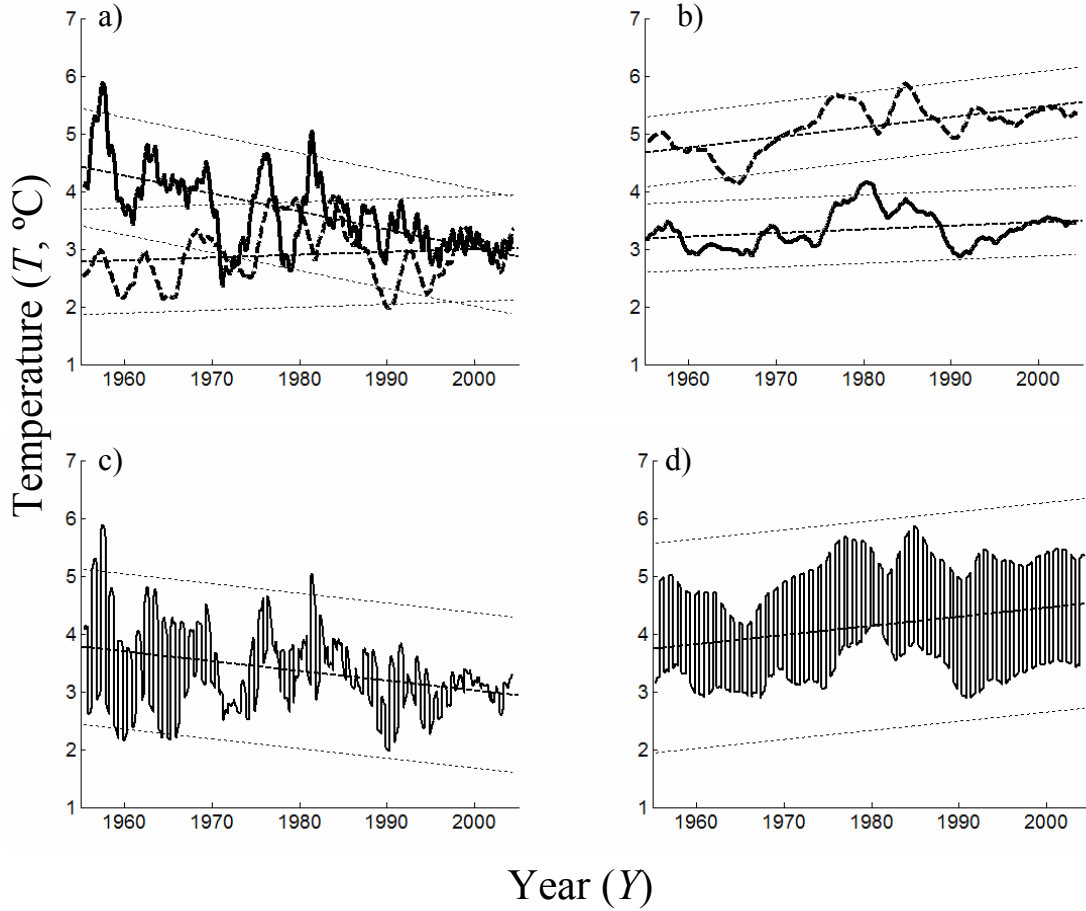
Figure 4.5: The 25-month smoothed temperature series ($T_{area,i}^{stage}$) interpolated at day (i) for areas inside ($T_{in,i}^{stage}$, solid lines, ab) and outside ($T_{out,i}^{stage}$, thick dashed lines, ab) the sGSL occupied by each stage: a) immature and b) mature cod. Linear regressions and 95% confidence intervals (thin dashed lines) are given for: a) immature cod inside (linear regression: $T_{in,i}^{immature} = -0.031Y + 0.65$; r^2=0.42; P<0.0001) and outside (linear regression: $T_{out,i}^{immature} = 0.0051Y - 7.2$; r^2=0.02; P<0.0001) the sGSL and b) mature cod inside (linear regression: $T_{in,i}^{mature} = 0.0062Y - 9.0$; r^2=0.08; P<0.0001) and outside (linear regression: $T_{out,i}^{mature} = 0.017Time - 29$; r^2=0.39; P<0.0001) the sGSL. Continuous stage-specific temperature series (T_i^{stage}) at day i determined for each stage c) immature (linear regression: $T_i^{immature} = -0.017Y + 37$; r^2=0.11; P<0.0001), d) mature (linear regression: $T_i^{mature} = 0.016Y - 27$; r^2=0.05; P<0.0001) from temperature time series in a) and b) respectively as well as migration timing (See Section 4.2).

Among the immature cod, the LaD-at-Time relations for the 1970 through 2000 year-classes were significantly different (Fig. 4.6a; ANCOVA, different slopes P=0.0084) with the slope of the relations declining with increasing year-class (Linear regression: $\beta' = -0.0014\,YearClass + 3.1$; r²=0.27; P=0.002; Fig. 4.7a) and no trend among the intercepts of the relations (Linear regression; P=0.11; Fig. 4.7c). While the LaD-at-GDD relations for the immature year-classes were also significantly different (Fig. 4.6b; ANCOVA, different slopes P=0.005) no trends were found among slopes (Linear regression: P=0.57; Fig. 4.7b) or intercepts of the relations (Linear regression; P=0.15; Fig. 4.7d).
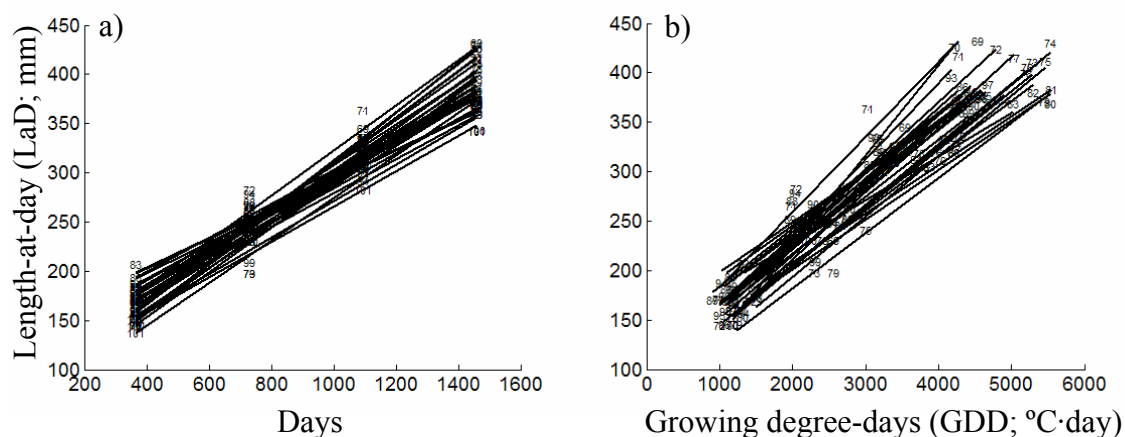
Figure 4.6: Length-at-day (mm) for immature sGSL cod haddock ages-1 to -4 as a function of a) calendar time (days, no significant relation among year classes, ANCOVA, different slopes P=0.0084); and as a function of b) GDD (ºC·day, no significant relation among year classes, ANCOVA, different slopes P=0.005). Numerals denoted year-class -1900.
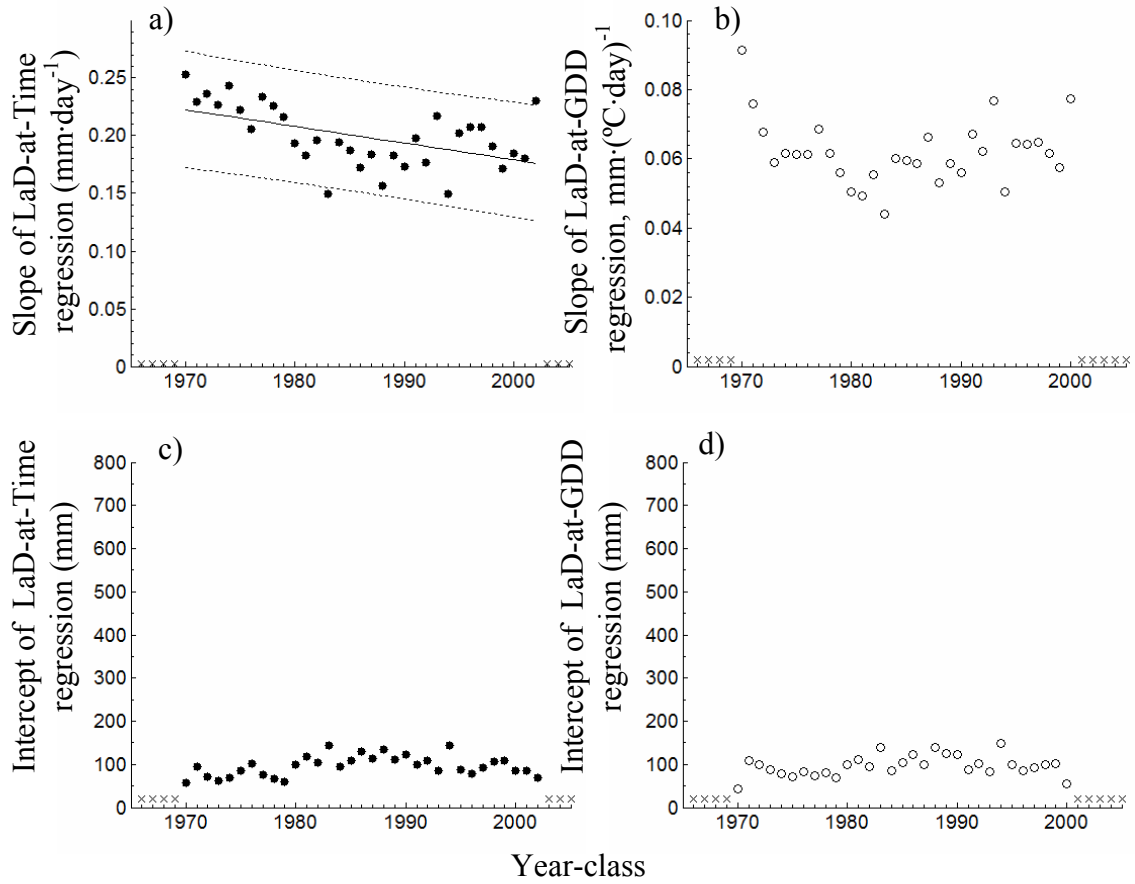
Figure 4.7: Parameters of the LaD-at-Time (a and c) and LaD-at-GDD (b and d) relations for immature cod (age-1-4) a) Slopes, mm·d^{-1}, of the LaD-at-*Time* relations demonstrate a statistic decline with increasing year-class Linear regression: $\beta' = -0.0014\,YearClass + 3.1$; r^2=0.27; P=0.002), b) Slopes, mm·(ºC·day)$^{-1}$, of the LaD-at-GDD relations show no significant trend (P=0.57), c) Intercepts, mm, of the LaD-at-*Time* relations show no significant trend (P=0.11), d) Intercepts, mm, of the LaD-at-GDD relations show no significant trend (P=0.15). Crosses denote year-classes with non-significant (P>0.05) relations (i.e. no change).

The LaD-at-Time relations for the 1966 through 1992 year-classes were significantly different for the mature cod (Fig. 4.8a; ANCOVA, different slopes P<0.0001) with the slope of the relations declining with increasing year-class (Linear regression: $\beta' = -0.0038\,YearClass + 7.5$; r^2=0.54; P<0.0001; Fig. 4.9a) and the intercepts of the relations increasing with increasing year-class (Linear regression: $\alpha' = 5.0\,YearClass - 9.7$; r^2=0.28; P=0.004; Fig. 4.9c). The LaD-at-GDD relations for the mature year-classes were also significantly different (Fig. 4.8b; ANCOVA, different slopes P<0.0001) with a similar though stronger (i.e. higher r^2) decline in slopes with year-class (Linear regression: $\beta = -0.00086\,YearClass - 1.7$; r^2=0.58; P<0.0001; Fig. 4.9b) than found using the LaD-at-Time relations. In contrast, the intercepts of the LaD-at-GDD relations declined with year-class (Linear regression: $\alpha = -3.2\,YearClass + 0.0069$; r^2=0.40; P=0.0003; Fig. 4.9d), a trend opposite to that of the LaD-at-Time relations. These trends in slope and intercept of the LaD-at-GDD relations among cod year-classes are similar to that observed among the haddock year-classes of **Chapter 3.** The 1969 year-class was an outlier due to an anomalously low length-at-age-14 (i.e. length-at-age-13 = 923mm, length-at-age-14 = 760mm).
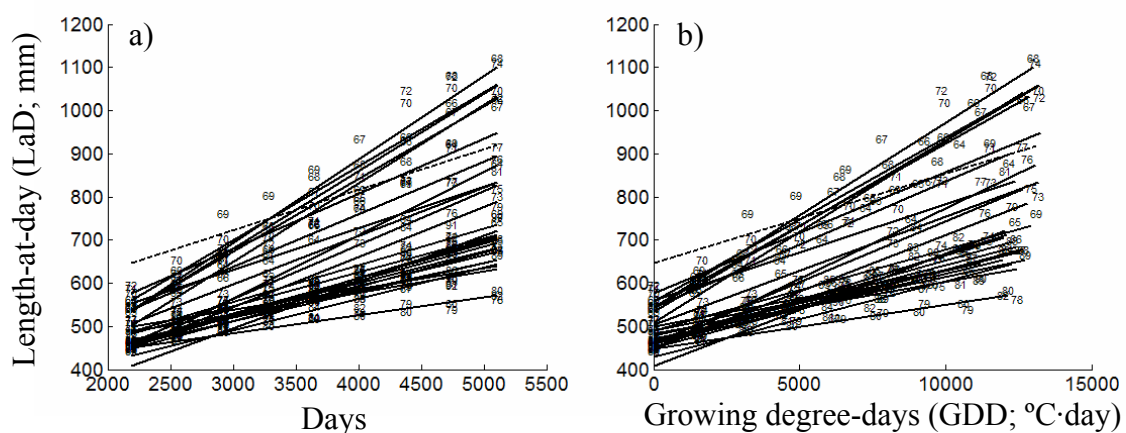
Figure 4.8: Length-at-day (mm) for mature sGSL cod ages-6 to -10 as a function of a) calendar time (days, no significant relation among year classes, ANCOVA, different slopes P<0.0001); and as a function of b) GDD (ºC·day, no significant relation among year classes, ANCOVA, different slopes P<0.0001). Numerals denote year-class - 1900. The 1969 year-class (dashed line) was an outlier (see Fig. 4.9).
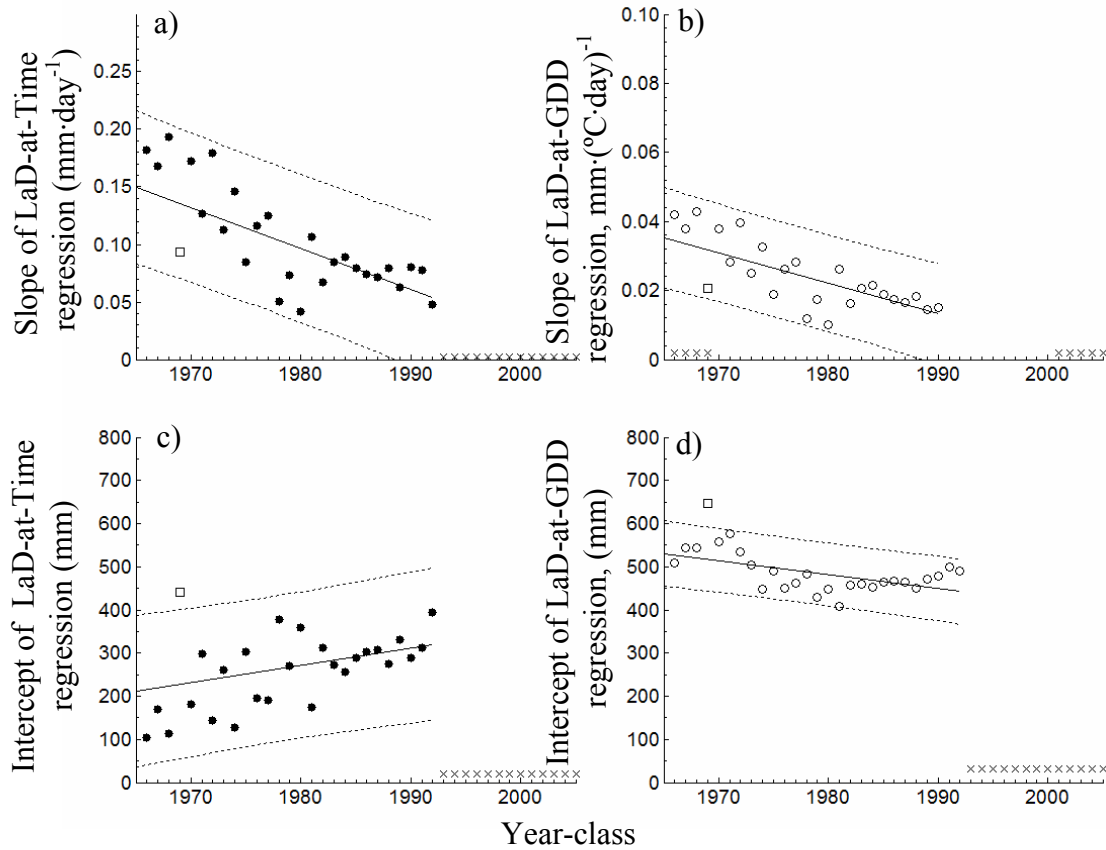
Figure 4.9: Parameters of the LaD-at-Time (a and c) and LaD-at-GDD (b and d) relations for mature cod (age-6-10) a) Slopes, mm·d^{-1}, of the LaD-at-Time relations demonstrate a statistic decline with increasing year-class (Linear regression: $\beta' = -0.0038\,YearClass + 7.5$; r^2=0.54; P<0.0001), b) Slopes, mm·(°C·day)$^{-1}$, of the LaD-at-GDD relations show a significant decline with increasing year-class (Linear regression: $\beta = -0.00086\,YearClass - 1.7$; r^2=0.58; P<0.0001), c) Intercepts, mm, of the LaD-at-Time relations show a significant increase with increasing year-class (Linear regression: $\alpha' = 5.0\,YearClass - 9.7$; r^2=0.28; P=0.004), d) Intercepts, mm, of the LaD-at-GDD relations show a significant decrease with increasing year-class (Linear regression: $\alpha = -3.2\,YearClass + 0.0069$; r^2=0.40; P=0.0003). Crosses denote year-classes with non-significant (P>0.05) relations (i.e. no change). The 1969 year-class (square) was removed as an outlier.

4.4 Discussion

Immature and mature cod occupy waters that differ significantly in depth and temperature both in and out of the sGSL (Fig. 4.4, 4.5ab). The decline in temperature of waters occupied by immature cod ($T_i^{immature}$; Fig. 4.5c, also noted by Swain and Kramer 1995) predicts a corresponding decline in growth of the fish when examined in calendar time; a prediction verified by the decline in slopes of the LaD-at-Time relations (Fig. 4.7a). How much of this decline in slope (i.e. inferred growth rate) is dependent on temperature variation is estimated when the LaD are regressed with GDD. Here, GDD (i.e. thermal history) variation associated with the immature fish is sufficient in explaining the trend in LaD variation among year-classes and no significant trend among slopes of the LaD-at-GDD relations is found. Thus, I conclude that the decline in size-at-age of immature cod is explained by thermal history (GDD) variation among year-classes. I do note that there is variation about the mean for both the slopes (Fig. 4.7b) and intercepts (Fig. 4.7d) of the LaD-at-GDD relations among immature year-classes that may be explored with other factors affecting growth (e.g. food consumption, size-selective fishing, etc.).

An increase in the temperature of the waters occupied by the mature cod (T_i^{mature}; Fig. 4.5d) predicts a corresponding increase in growth of the fish when examined in calendar time. However, the slope of the LaD-at-Time relation declined with increasing year-class (Fig. 4.9a) and this trend is maintained and defined when the LaD is examined with GDD (Fig. 4.9b), a result exactly opposite of what would be expected if temperature variation was responsible for the observed variation in cod size-at-age. In addition, a concurrent decline in intercepts of the LaD-at-GDD relation among year-classes is found (Fig. 4.9d). Thus (and as found with the haddock examined in **Chapter 3**), there is a decline in LaD among year-classes that is unexplained by temperature variation even when examined on the physiological time scale of the GDD metric.

One explanation of the remaining variation in the LaD-at-GDD relation (slope and intercept – a proxy for growth) among mature year-classes may be that the temperature estimates used in the GDD metric are misrepresentative of the variation in thermal history among year-classes (i.e. temperature-dependent variation in LaD remains). However, as the waters occupied by mature cod both inside and outside the sGSL experienced

increasing temperatures over the study period (Fig. 4.5), it is unlikely that any adjustment in depths or migration timing would allow for the significant and systematic declines in temperature we would expect if the observed declines in size-at-age were temperature-dependent.

Other factors besides temperature may explain the persistent declines in slope and intercept of the LaD-at-GDD relations among mature cod year-classes. A systematic decline in food consumption may be contributing to the declining size-at-age in this stock and an analysis of variation in food consumption by sGSL cod is examined in **Chapters 5 and 6**. Alternatively the temperature-independent declines in size-at-age (i.e. slope and intercept of the LaD-at-GDD relations) among cod year-classes are similar to that observed among the haddock year-classes in **Chapter 3**, a pattern most parsimoniously explained by size-selective fishing effects; a possibility further explored for sGSL cod year-classes in **Chapter 7**.

In conclusion the GDD metric has proven strength in explaining variation in LaD within and among year-classes for a wide diversity of fish (**Chapter 2** and Neuheimer and Taggart 2007). One of the limitations of the GDD metric lies in the ability to estimate the relevant variation in thermal history of the fish. While this is relatively straightforward under laboratory or limnological conditions, acquiring relevant temperature estimates is challenging for fish in the open marine environment that may demonstrate age-specific vertical stratification and/or extensive migrations. While tagging studies allow for temperature estimates sufficiently local and frequent (e.g. Palsson and Thorsteinsson 2003), the use of tags is limited by the lack of concurrent LaD measures (**Chapter 2**). Until such times as tags may allow for equally frequent length measures (**Chapter 2**) care must be taken to localize temperature estimates as much as possible. When this is done the GDD metric is able to identify that portion of variation in LaD that is a result of variation in thermal history among year-classes even in highly migratory species (e.g. immature year-classes above). The remaining variation in LaD among mature sGSL cod (i.e. declines in slope and intercept of LaD-at-GDD relation among year-classes) can be explored with variation in other factors affecting fish growth including food consumption and/or size-selective fishing mortality. As mentioned above, a quantitative analysis of variation in food consumption for sGSL cod is presented in

Chapters 5 and **6** while a discussion of remaining size-at-age variation and the potential implications of size-selective fishing are discussed in **Chapter 7**.

Chapter 5

Estimating Food Consumption in Fish: What Really Matters?

5.1 Introduction

5.1.1 Motivation

An important prerequisite for studies examining the trophic role of fishes is the acquisition of reliable information about fish food consumption and prey composition (Andersen 2001). Food consumption estimates are necessary in examining variation in growth rates and characterizing predator/prey dynamics (Trudel 1993). As a consequence, there has been a large increase in the scientific literature concerning many aspects of feeding-related physiology and ecology. However, clear and reliable relations between environmental influences and stock production including the relation between food consumption and population structure are rare (Dutil and Brander 2003). Gerking (1994) made it clear that if "*a reasonable estimate of food consumption can be made*, [then] *several aquatic ecological problems are simplified*" (e.g. fish production and growth of populations in different environments).

5.1.2 Estimating Food Consumption

As there are no direct methods of estimating food consumption in the field (Andersen 1998) efforts have turned to food consumption modelling through either bioenergetics or evacuation methods. Bioenergetic models involve estimating food consumption based on energy and/or nitrogen requirements and relations between food consumption and growth rate (Elliott and Persson 1978). These models typically rely on balanced equations using energy-based rate units (Kitchell et al. 1977; Hansson et al. 1996) requiring substantial information on individual growth rates of fish as a function of food ration and temperature. These models require numerous parameters (12-30+) that must be determined from empirical laboratory studies or "borrowed" from those of similar species in the literature (Hansen et al. 1993). As well, it is assumed that the

individually-based lab results can be approximated as population-based field estimates, ignoring individual and environmental variability (Boisclair and Leggett 1989; Hansen et al. 1993).

An alternative to the bioenergetics model is evacuation modelling which obtains population-based estimates of food consumption from estimates of evacuation rate and the average weight of food in the stomach over a sampling period. This is based on the following balance equation,

$$\frac{dS}{dt} = C(t) - G(t)$$, (1)

where *dS/dt* is the change in stomach contents over time, *C(t)* is the food consumption rate, and *G(t)* is the stomach evacuation rate, all with dimensions of MT^{-1}. For many species *G(t)* is proportional to the stomach contents raised to a power:

$$G(t) = p(S(t)^a)$$, (2)

where *S(t)* is the weight of food in the stomach at time *t* (M), and *p* ($M^{1-a}T^{-1}$) and *a* (dimensionless) are the rate and shape parameters respectively (Pennington 1985). The rate parameter (*p*) represents the entire set of factors that affect digestion (including temperature) and are assumed independent of the biomass in the stomach over time (MacPherson et al. 1989). Rearranging (1) and (2), the consumption rate can be given as,

$$C(t) = \frac{dS(t)}{dt} + p(S(t))^a$$, (3)

where *C(t)* is the consumption rate (MT^{-1}), *dS(t)/dt* is the change in stomach content weight over time (MT^{-1}), and *p* ($M^{1-a}T^{-1}$) and *a* (dimensionless) are the rate and shape parameters respectively.

5.1.3 The Pennington Method

Pennington (1985) used the above model (eqn. 3) to estimate the food consumption in fish by first describing the average consumption rate per hour (C_T) as:

$$C_T = \frac{1}{T}\int_0^T C(t)\,dt \qquad .$$ (4)

Substituting (4) into (3) above:

$$C_T = \frac{1}{T}\int_0^T \left(\frac{dS(t)}{dt} + p(S(t))^a\right) dt \qquad ,$$ (5)

$$C_T = \frac{1}{T}\int_0^T dS(t) + \frac{p}{T}\int_0^T (S(t))^a\,dt \qquad ,$$ (6)

$$C_T = \frac{(S(T) - S(0))}{T} + p \cdot \left(average\big[(S(t))^a\big]\right) \quad ,$$ (7)

where T is the sampling interval (i.e. from 0 to T hours in duration), $S(T)$ is the stomach content weight at the end of the interval (M), and $S(0)$ is the stomach content weight at the start of the interval (M). When T becomes large $(S(T)-S(0))/T = 0$ and,

$$C_T = p \cdot \left(average\big[(S(t))^a\big]\right) \qquad .$$ (8)

This was found to be a valid assumption for perch even when $S(T)$ and $S(0)$ differ by a factor of 2 (Boisclair and Leggett 1988). Pennington's model assumes: 1) the rate of evacuation is proportional to stomach content weight raised to a power, and 2) the parameters p and a are constant over the chosen period for all fish in the population Attempts have been made to further simplify this method by testing the assumption that,

$$average\big[(S(t))^a\big] = (average\big[(S(t))\big])^a \qquad ,$$ (9)

thereby allowing for field samples aggregated (i.e. pooled) by sampling time and/or predator size (Andersen 2001).

The shape parameter (a)

There is much debate surrounding the value of the shape parameter, *a*, resulting in the shape of the stomach evacuation rate (eqn. 2) ranging from linear ($a = 0$) to non-linear ($a \neq 0$). The linear model ($a = 0$, Fig. 5.1) was first introduced by Bajkov (1935) and regained attention for larval and juvenile fish (Bochdansky and Deibel 2001). The argument for a linear evacuation rate comes from the assumption that the majority of food (90%) will be digested rapidly (e.g. soft tissue) and can be approximated by a linear function followed by a phase of slower evacuation for residual food such as invertebrate exoskeletons (Olsen and Mullen 1986).

Non-linear models of the stomach evacuation rate include the square-root (volume-dependent), surface area and exponential models. The square-root model ($a = 0.5$, Fig. 5.1) is based on the premise that, if the stomach maintains a constant length, then the circumferential tension developed is proportional to the radius (Tyler 1970). As the radius of a cylinder varies with the square root of its volume, the tension developed will be proportional to the square root of the volume of food in the stomach. The square-root model has been used to describe stomach evacuation rate in three predatory gadoids; whiting, *Merlangius merlangus*, saithe, *Pollachius virens*, and cod, *Gadus morhua* (Andersen 2001). The surface-area model ($a = 0.67$, Fig. 5.1) assumes the stomach evacuation rate is determined by the amount of surface-area exposed to the action of stomach enzymes (Elliott and Persson 1978, Fänge and Grove 1979). As the weight of the particle decreases as a cubic function with digestion, the linearization of the change is proportional to the cube root of the weight of the food particle (Tyler 1970). If the surface of the particle decreases as the square of the weight, the rate of change of the particles weight is proportional to $(S^{1/3})^2$ or $S^{2/3}$. This leads to a stomach evacuation model with approximately $a = 0.67$. The exponential model ($a = 1$, Fig. 5.1) assumes that the stomach evacuation rate is dominated by the rate of associated enzyme reactions which are often exponential processes (Elliott and Persson 1978).
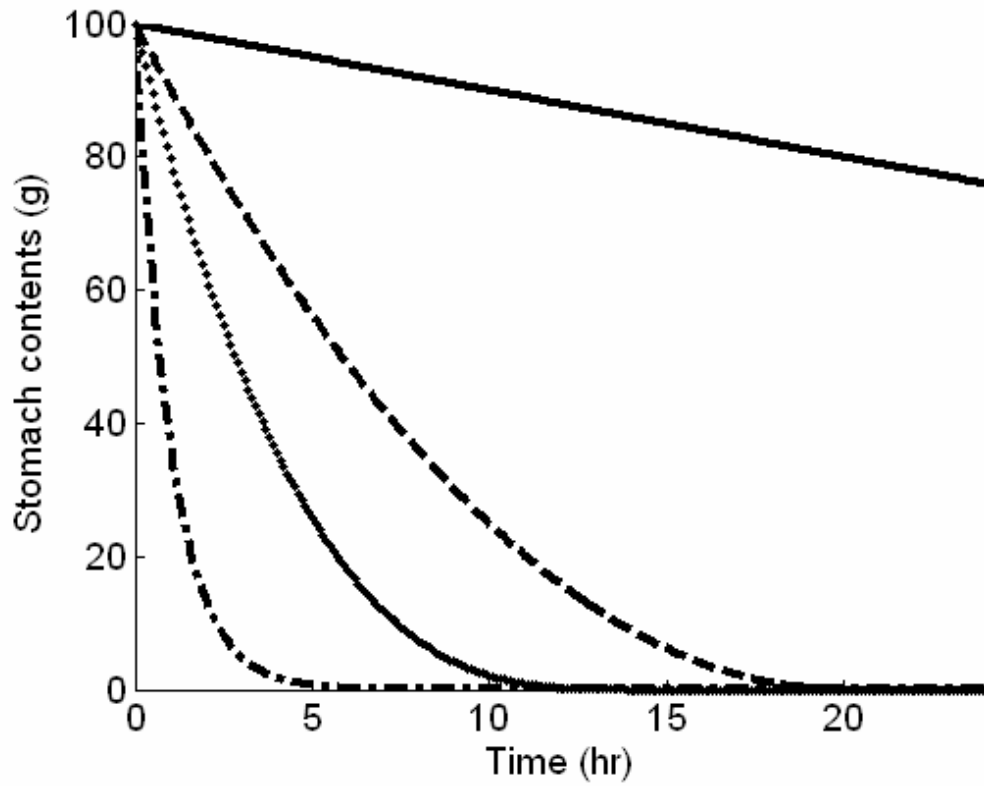
Figure 5.1: Change in stomach contents (g) over time (hr) during a period of non-feeding represented as $\dfrac{dS}{dt} = -pS^a$ with $a = 0$ (solid), $a = 0.5$ (dashed), $a = 0.67$ (dotted) or $a = 1$ (dash-dotted).

While many studies have attempted to characterize stomach evacuation rate, there is no consensus regarding the appropriate mathematical descriptor, the shape parameter, a (Temming and Herrmann 2003). Many have chosen models based on a least-squares fit, selected arbitrarily or by inspection (Bochdansky and Deibel 2001). This suggests that the mathematical relationships thus far provide little information concerning the biological and physical processes involved in stomach evacuation rate (Jobling 1986). As well, while it has been shown that some models (e.g. exponential, $a = 1$, and square-root, $a = 0.5$, evacuation) are quantitatively similar, investigators have yet to compare estimates of food consumption calculated with these models (Ruggerone 1989).

The rate parameter (p)

Traditionally the rate parameter (p) has been obtained under laboratory conditions where a group of fish is fed a finite meal and then held without food while stomach content weight is sampled periodically to determine the decline in stomach content weight over time (i.e. stomach evacuation rate) at specific conditions of temperature, food type, predator size, etc. Such laboratory methods are criticized as being incapable of representing the entire range of environmental variables that may influence the stomach evacuation rate. A number of studies describe *in situ* estimates of food consumption for periodic feeders (e.g. diel) using field estimates of weight of stomach contents measured over time (e.g. Sainsbury 1986; Arrhenius and Hansson 1994; Pedersen 2000). The evacuation rate is estimated from a (sometimes) apparent rate of decline in the weight of stomach contents within the 24 h period. This method has been used for estimating stomach evacuation rate in brown trout, tuna (Sainsbury 1986), herring (Arrhenius and Hansson 1994) and whiting (Pedersen 2000). One study found the estimate of food ration derived from this method had the same accuracy as that from the laboratory-based Elliott and Persson (1978) method for some species (Sainsbury 1986).

Studies have examined variation in the rate parameter with variation in factors such as temperature, predator size, and food energy-density (Andersen 1999, 2001). Temperature acts on the feeding physiology through five processes: 1) feeding rate, 2) hydrolytic activity of digestive enzymes, 3) stomach and intestinal motility, 4) secretory rate of digestive juice and 5) rate of intestinal absorption (Smit 1967; Kapoor et al. 1975).

Cod have been shown to experience an exponential increase in stomach evacuation rate to a maximum after which stomach evacuation rate decreases with an increase in temperature (Fig. 5.2; Persson 1979).
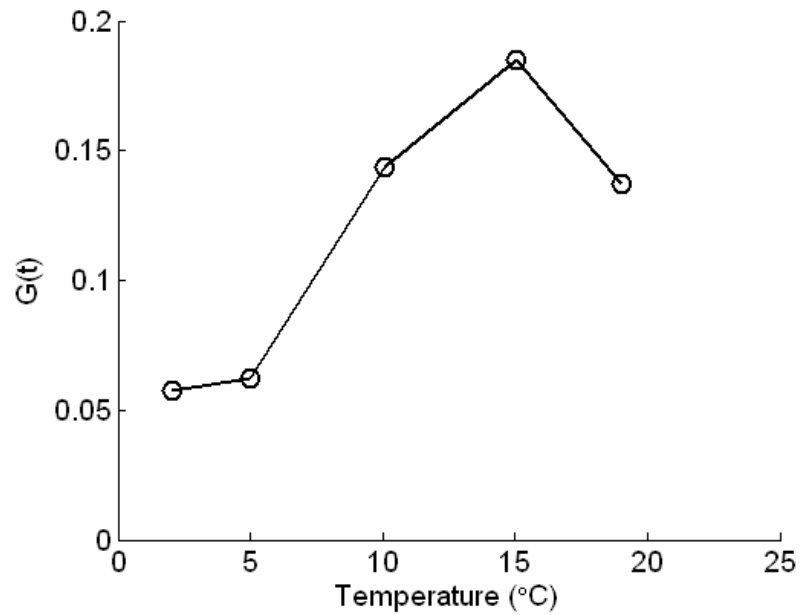
Figure 5.2: Instantaneous rate of evacuation from the stomach ($G(t)$, mg·hr^{-1}) as a function of temperature (T, ºC) for cod (Tyler 1970) as in Persson (1979).

As with most physiological rates (see **Chapter 2**) the response of evacuation rate to temperature variation is near-linear over a mid-range in temperatures (e.g. 5-15ºC in Fig. 5.2). This allows for characterization of the evacuation rate over the physiological time-scale represented by the growing-degree day or growing degree-hour (GDH), $g \cdot \left({}^{\circ}C \cdot h \right)^{-1}$, (**Chapter 2**; Neuheimer and Taggart 2007) rather than calendar time, $g \cdot h^{-1}$. While conventional formulations of evacuation rate can represent evacuation at constant temperatures (e.g. fish held at 6ºC for 4 h), representing evacuation rate in physiological time allows for constant (as above, e.g. fish held at 6ºC for 4 h = 24ºC·h), and variable (e.g. fish held at 6ºC for 2 h, then 4ºC for 4 h, then 8ºC for 4 h = 60ºC·h) temperatures. Thus, physiological time (GDD) has the potential to simplify and generalize many of the evacuation rate formulations (as shown in **Chapter 2**). For the purposes of this chapter I rely on empirical relationships from the published literature that have been exclusively developed on calendar time and are complicated by effects of other factors (e.g. predator size, see below). Thus the utility of the GDD metric in elucidating evacuation rates is left to future work.

A number of studies have found that stomach evacuation rate increases with increasing predator size (Hop and Tonn 1998; Andersen 1999, 2001; Temming and Herrmann 2003). In a study on North Sea cod (*Gadus morhua*), stomach evacuation rate increased with predator weight and was related to the allometric scaling of consumption with body weight (Temming and Herrmann 2003).

Much of the focus on describing the relation between stomach evacuation rate and food type has centered on food energy-density where evacuation rate decreases with increasing food energy-density (Jobling 1980; Durbin et al. 1983; Andersen 2001). For example, the stomach evacuation rate of cod feeding on high-energy fish food is only 10% of the stomach evacuation rate for low-energy crustacean food (Tyler 1970). While most food types are found to have evacuation times that are a simple function of their energy-density, there are some exceptions attributed to the physiology of the prey. For example, the stomach evacuation rate for cod feeding on brown shrimp (*Penaeus aztecus*) is anomalously low, despite the low energy content of the shrimp, due to the presence of an exoskeleton which could slow digestion (Temming and Herrmann 2003).

5.1.4 Chapter Objectives

In this chapter I evaluate the ability of the Pennington method (eqn. 7) to estimate fish food consumption in two ways. First, food consumption estimated from the Pennington method is compared to food consumption calculated from a model of the diurnal changes in fish stomach weight. In addition the parameters, (e.g. shape parameter, *a*), variables (e.g. weight, temperature, food energy-density), and model structure (e.g. consumption rate function) responsible for the majority of variation in the modelled food consumption are determined. Second, I compare food consumption estimated with the Pennington method to that estimated for laboratory-held fish in the published literature.

5.2 Methods

5.2.1 Stomach Contents Model

The diel changes in fish stomach content weight were modelled following eqn. 1 above. This requires an estimate of the food consumption, *C(t)*, and stomach evacuation, *G(t)*, rates at time *t*. The factors that explain the variation in observed food consumption rates include temperature, predator size, food energy-density, prey concentration, feeding period, level of food in the stomach and spatial distribution of prey (Swenson and Smith 1973, Durbin et al. 1983, Jensen 1998, Andersen 1999, 2001). Despite the finding that food material distributed more evenly in space will be consumed at a lower rate (Ivlev 1961) spatial distribution of prey was excluded for model simplicity. The resulting model can be summarized as follows,

$$\frac{dS}{dt} \approx \overbrace{\left(f\left(weight\right) \cdot f\left(temperature\right) \cdot f\left(prey\right) \cdot f\left(S(t-\Delta t)\right) \cdot f\left(light\right) \right)}^{C(t)} - \overbrace{\left(p\left(S(t-\Delta t)^{a}\right) \right)}^{G(t)}, \quad (10)$$

where the change in stomach content weight over time (*dS/dt*) is some function of predator size, *f(weight)*, ambient temperature, *f(temperature)*, prey concentration, *f(prey)*, weight of food in the stomach $f\left(S(t-\Delta t)\right)$ where Δt is the time-step, feeding period

f(light) and stomach evacuation rate $p\left(S(t-\Delta t)^a\right)$, which will be shown below to include variation due to food energy-density. Whenever possible relationships are fitted with results from studies on Atlantic cod (*Gadus morhua*).

Food consumption rate has been found to increase with temperature and predator size (Jones and Hislop 1978; Peters 1983; Arrhenius 1998). The combined effect of temperature and predator size (weight) on the maximum consumption rate has been described by two models. The first, developed by Jobling (1988) in a review of Atlantic cod energetics, is

$$C(t) \propto W^{0.80} e^{(0.10T - 0.00011T^3 - 1.5)} \qquad , \qquad\qquad (11)$$

hereafter called the Jobling function, where *C(t)* is the consumption rate, kJ·day^{-1}, *W* is the predator weight, g, and *T* is the temperature, ºC, (n = 50, r^2 = 0.91). The second model was used by Andersen and Riis-Vestergaard (2003) for investigating food conversion efficiency in two gadids (saithe and whiting),

$$C(t) \propto uW^v e^{dT} \qquad , \qquad\qquad (12)$$

hereafter called the Andersen and Riis-Vestergaard function, where *C(t)* is the consumption rate (kJ day^{-1}), *W* is predator weight (g), *T* is temperature (ºC), and *u, v* and *d* are parameter values estimated by curve fitting. A graphical representation of the two models is given in Fig. 5.3. The model in this study was initially developed using the Jobling function (eqn. 11) as it was developed specifically for cod. The sensitivity of model output to this function is examined by comparing model output using the Andersen and Riis-Vestergaard function (eqn. 12). Both functions provide food consumption in kJ·day^{-1}. The results were converted to g·h^{-1} using average energy-density for cod food (4.47 kJ·g^{-1}, Daan 1975).
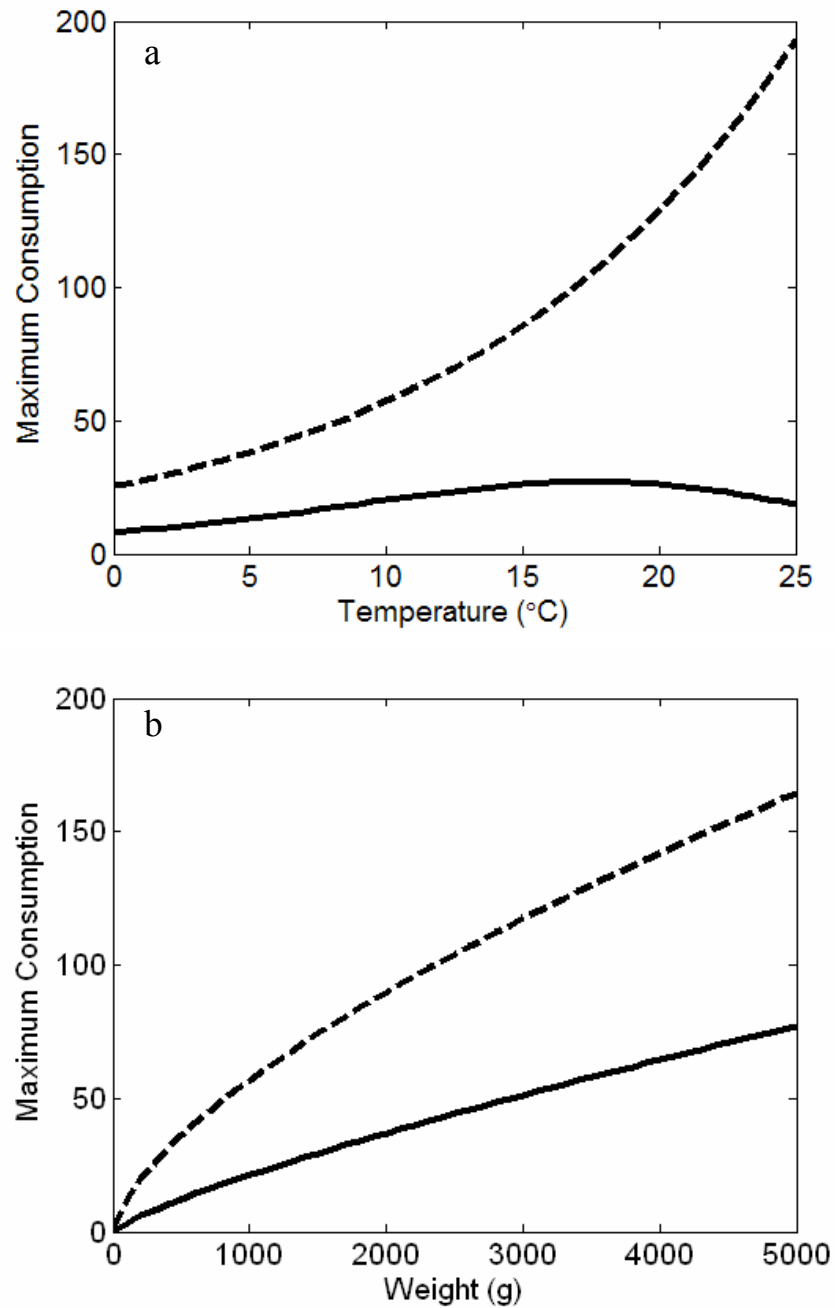
Figure 5.3: A graphical representation of the effects of (a) temperature (ºC) and (b) predator size (weight, g) on the maximum consumption rate (g·h^{-1}) for the Jobling (1988), solid lines and eqn. 11, and Andersen and Riis-Vestergaard (2003), dashed lines and eqn. 12, models. Parameter values are given in Table 5.1.

Consumption rate increases with increasing prey concentration (Swenson and Smith 1973, Jensen 1998). However, for many fish, the ration of food eaten will tend to approach a maximum under favorable feeding conditions (Ivlev 1961). Two functional responses were explored to describe the effect of prey concentration on the consumption rate. The first is the Ivlev (1961) functional response (similar in shape to Holling Type 2; Holling 1959),

$$C(t) \propto (1 - e^{-\varepsilon P}) \qquad , \tag{13}$$

where $C(t)$ is the consumption rate (g·h^{-1}), ε is the proportionality constant (m^2·mg^{-1}) and P is the prey concentration (mg·m^{-2}), as used by Jensen 1998 for walleye. The model was also examined using the Holling Type 3 functional response (Holling 1959) as described for vendace (*Coregonus albula*) in Heikinheimo (2001):

$$C(t) \propto \left(\frac{P^2}{P^2 + D^2} \right) \qquad , \tag{14}$$

where $C(t)$ is the consumption rate (g·h^{-1}), D is the half-saturation constant or the concentration (mg·m^{-2}) when the consumption is half maximum and P is the prey concentration (mg·m^{-2}). The two functional responses are presented in Fig. 5.4.
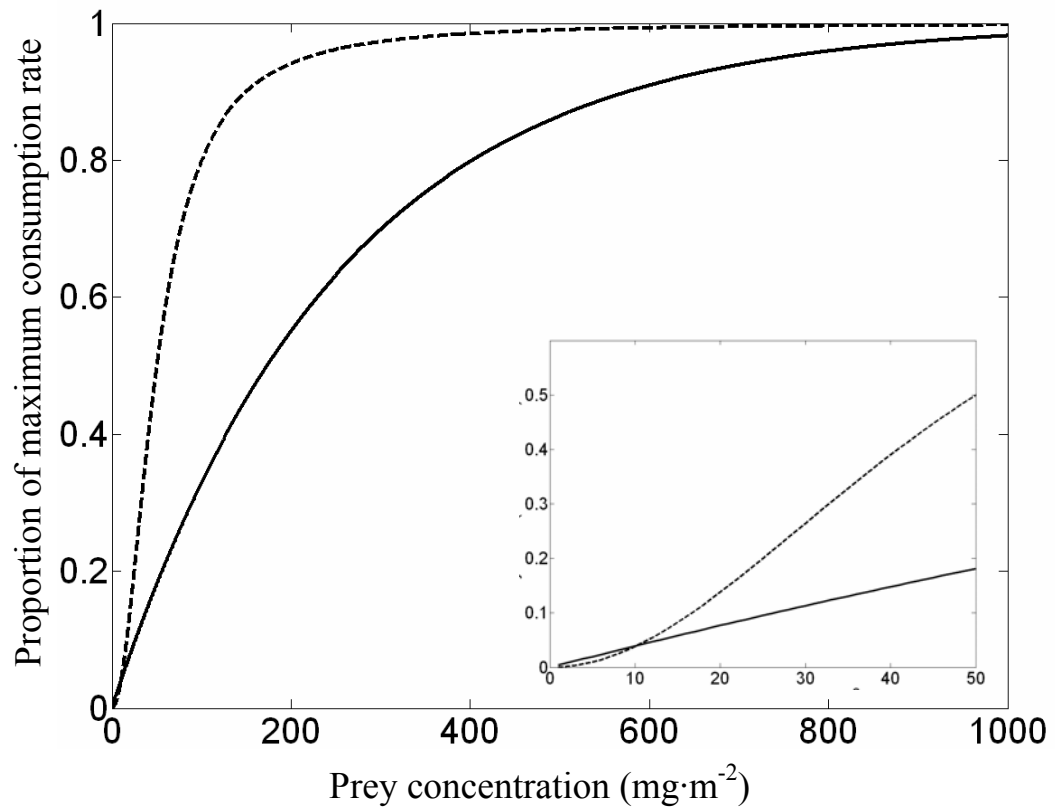
Figure 5.4: The effect of prey concentration (mg·m^{-2}) on the proportion of maximum consumption (dimensionless) given by the Ivlev (solid line, eqn. 13) and Holling Type 3 (dashed line, eqn. 14) functional responses. Parameter values are given in Table 5.1. Inset illustrates consumption rate at low prey concentrations.

There is conflicting information as to the effect of stomach content weight at time t on the consumption rate at the next time step ($t + \Delta t$); i.e. decreasing appetite with increasing stomach content weight. Some (Gwyther and Grove 1981; Jarre et al. 1991) have found consumption declined with increasing stomach content weight while Andersen (1999) found estimates were not improved with the inclusion of this appetite effect. I tested my model with both the presence and absence of an appetite effect. I modelled a decline in consumption with increasing stomach content weight as,

$$C(t) \propto \left(1 - \frac{S(t)}{S_{max}} \right) \quad \text{with } S_{max} = H \cdot W , \tag{15}$$

where $C(t)$ is the consumption rate (g·h^{-1}), $S(t)$ is the stomach content weight at time t (g), S_{max} is the stomach content weight at which ingestion becomes zero (g), W is the cod (predator) whole body weight (g), and H is the maximum stomach contents parameter (Fig. 5.5). The value for S_{max} was estimated from the stomach content weight in the DFO Cod Stomach Database to be approximately 1% of the cod (predator) weight (i.e. $H = 0.01$). This is probably a low estimate as many of the fish sampled will not be at maximum stomach content weight. Therefore, I also tested a S_{max} of 5% predator weight ($H = 0.05$) in the model (Jarre et al. 1991).
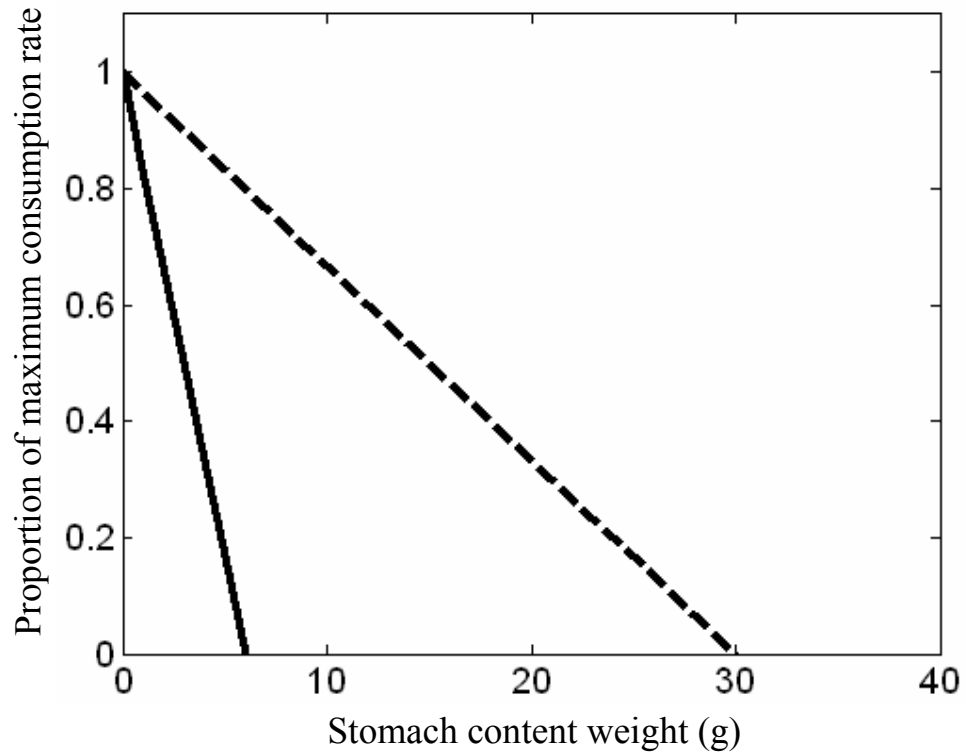
Figure 5.5: The proportion of maximum consumption rate S_{max} as a function of stomach content weight for a $W = 600$g fish with $H = 0.01$ (solid line) and $H = 0.05$ (dashed line) as in eqn. 15 (i.e. the appetite function). Parameter values are given in Table 5.1.

An estimate of the feeding periodicity of the fish improves the estimation of the consumption rate (Arrhenius 1998). As juvenile cod prey-capture increases with increasing light intensity (Tilseth and Ellertsen 1984), I modelled the feeding period of cod as a function of light intensity through a simple sine function,

$$Light = \sin\left(\tau - \frac{\pi}{2}\right) \quad , \tag{16}$$

where *Light* is the proportion of maximum light intensity (dimensionless) with maximum consumption (i.e. *Light* = 1) at 12:00, and τ is the time-of-day in radians (Fig. 5.6). As a first approach, no feeding occurs at night (Arrhenius 1998),

$$C(t) \propto \max(light, 0) \quad . \tag{17}$$

However, there is some evidence that cod feed at night (see **Chapter 6**) and the influence of night feeding on the modelled consumption rate is tested by including 25% night-time feeding as

$$C(t) \propto \max(light, 0.25) \tag{18}.$$
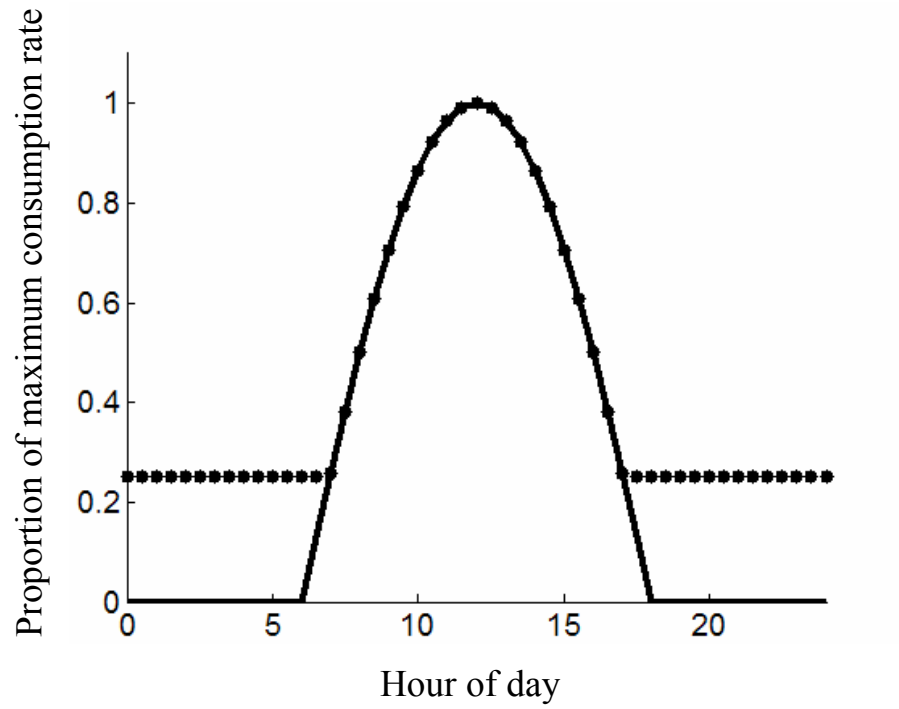
Figure 5.6: Proportion of maximum consumption rate as a function of hour of the day due to light intensity as described in (eqn. 16) with no night feeding (solid line) and 25% feeding at night (dotted line).

Modelling the stomach evacuation rate began with the general form of the power function (eqn. 2) which requires an estimate of the rate parameter (p). As above, the factors that explain the variation in p include temperature, predator size, and food energy-density (Andersen 1999, 2001). Andersen (1999) examined the variation in the p due to predator (cod) size, temperature, and food energy-density using the following relationship,

$$p = p_{wte}W^{\gamma}e^{\delta T}E^{-\mu} \quad ,$$
(19)

where p_{wte} is the rate constant as a function of weight, temperature and food energy-density, $g^{1-a-\gamma}\cdot(kJ\cdot g^{-1})^{\mu}\cdot hr^{-1}$, W is the predator weight (g), T is the temperature (°C), E is the food energy-density (kJ·g^{-1}), γ is the dimensionless predator weight parameter, δ is the temperature parameter (°C^{-1}) and μ is the dimensionless food energy-density parameter (Fig. 5.7ab). Andersen (1999) estimated the parameters (γ, δ, μ) by using the shape parameter, a, as a free parameter. I used this formulation (denoted hereafter as "Andersen 1") in the original model structure. I tested the sensitivity of the model to the choice of p formulation with three alternate p functions (Fig. 5.7):

i) "Andersen 2",

$$p = p_{wt}W^{\gamma}e^{\delta T} \qquad \text{(Andersen 2001)},$$
(20)

where p_{wt} is the rate constant as a function of weight and temperature $\left(g^{1-a-\gamma}\cdot hr^{-1}\right)$;

ii) "Durbin general",

$$p=0.0406(e^{0.111T}) \qquad \text{(Durbin et al. 1983)};$$
(21)

and iii) "Durbin fish food",

$$p=0.00406(e^{0.111T}) \qquad \text{(Durbin et al. 1983)},$$
(22)

with parameters as in eqn (19) above.
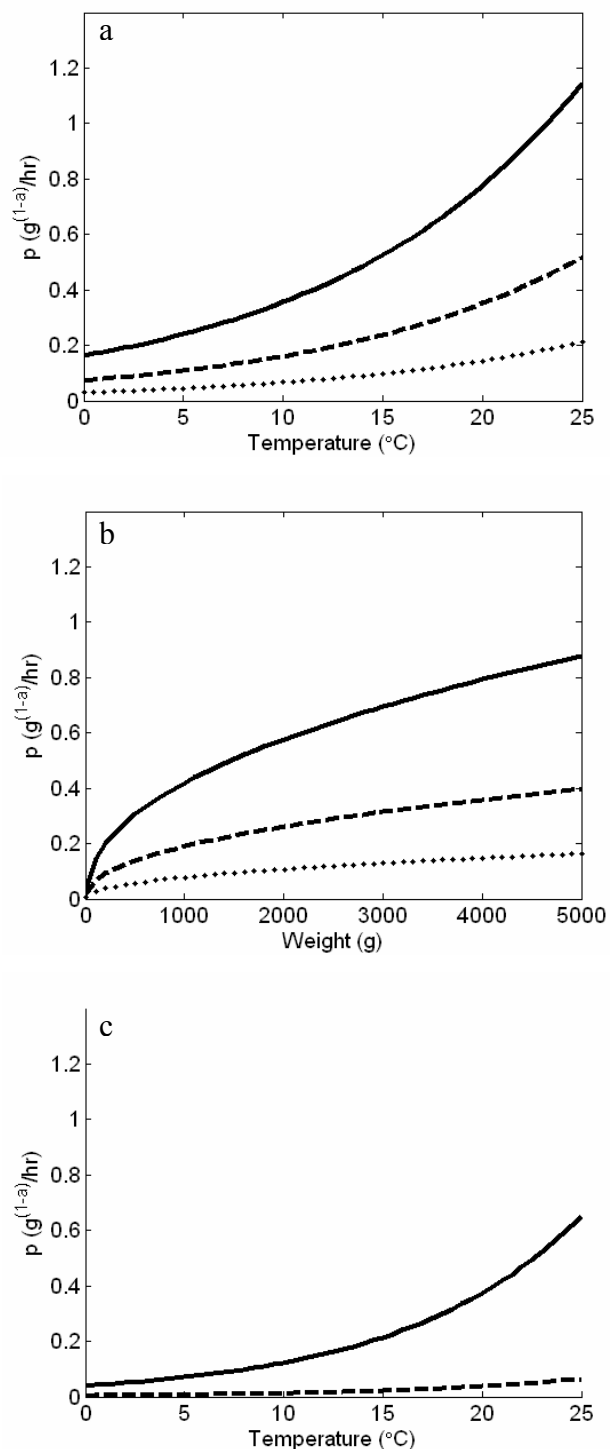
Figure 5.7: The Andersen 1 and Andersen 2 rate parameters (*p*) as a function of a) temperature (°C) and b) predator weight (g) with Andersen 1 (eqn. 19) at low food energy-density (2.27 kJ·g^{-1}, solid line) and high food energy-density, (5.70 kJ·g^{-1}, dashed line) and Andersen 2 (dotted line, eqn. 20). Also shown is (c) is the Durbin general (solid line, eqn. 21) and Durbin fish food (dashed line, eqn. 22) rate parameters as a function of temperature (°C). Parameter values are provided in Table 5.1.

The resulting model (eqn. 10) was solved with *a=0, a=0.5, a=0.67* and *a=1* using the Forward Euler approximation method (Burden and Faires 1989) which integrates using the first two terms of the Taylor expansion. A time step (Δt) of 10^{-3} h was determined as small enough to ensure stable limit cycles in the model without imposing long computation times. Smaller time steps of 10^{-4} h and 10^{-5} h demonstrated no significant differences in model output relative to using $\Delta t = 10^{-3}$ h. To avoid any influence from the stomach content weight initial condition, all model comparisons were performed when the model reached stable limit cycles between hours 59 and 86. Initial conditions, parameter estimates and relevant sources for the model are provided in Table 5.1.

Table 5.1: Model structure, initial conditions and parameter estimates for my model. Functional forms and associated parameters used in the original model structure are given in bold.

Description	Parameter	Symbol	Range	Initial condition	Source
Consumption - temperature and weight effects					
Jobling (1988)	**predator (cod) weight (g)**	**W**	**2, 7000**	**700**	**DFO Stomach Database**
	Ambient temperature (ºC)	**T**	**2, 22**	**7**	**Jobling (1988)**
	food energy-density (kJg^{-1})	**E**	**2.27, 5.70**	**4.47**	**Daan (1975)**
Andersen and Riis-Vestergaard (2003)	Parameter values (dimensionless)	u	n/a	36.2	Andersen and Riis-Vestergaard (2003)
		v	n/a	0.66	Andersen and Riis-Vestergaard (2003)
		d	n/a	0.081	Andersen and Riis-Vestergaard (2003)
Functional response					
Prey concentration (mgm^{-2})		**P**	**10^3, 2×10^4**	**10^4**	**Chénard (2004)**
Ivlev Functional Response	**Constant of proportionality (m^{2}mg^{-1})**	**ε**	**n/a**	**0.004**	**Jensen (1998)**
Holling Type 3 Functional Response	half-saturation constant (mgm^{-2})	D	n/a	50	Heikinheimo (2001)

Table 5.1. cont.

Description	Parameter	Symbol	Range	Initial condition	Source
Appetite effect					
$H = 0.01$ (eqn. 15)	$S_{max} = 0.01 \cdot W$	**n/a**	**n/a**	**DFO Stomach Database**
$H = 0.05$ (eqn. 15)	$S_{max} = 0.05 \cdot W$	n/a	n/a	Jarre et al. 1991
no appetite effect	n/a	n/a	n/a	this study
Light effect					
no feeding at night		**n/a**	**n/a**	this study
25% feeding at night		n/a	n/a	this study
Stomach evacuation rate					
Andersen 1 (2001)	**rate constant** $g^{1-a-\gamma} \cdot (kJ \cdot g^{-1})^{u} \cdot hr^{-1}$	p_{wte}	**n/a**	**0.0162**	**Andersen (2001)**
	predator size exponent (dimensionless)	γ	**±0.06**	**0.46**	**Andersen (2001)**
	temperature coefficient (ºC^{-1})	δ	**±0.017**	**0.078**	**Andersen (2001)**
	energy density coefficient (dimensionless)	μ	**±0.04**	**0.86**	**Andersen (2001)**
Andersen 2 (2001)	rate constant $\left(g^{1-a-\gamma} \cdot hr^{-1} \right)$	p_{wt}	n/a	0.0054	Andersen (2001)
	predator size exponent (dimensionless)	γ	±0.06	0.46	Andersen (2001)
	temperature coefficient (ºC^{-1})	δ	±0.017	0.078	Andersen (2001)
Durbin general $\left(g^{1-a} \cdot hr^{-1} \right)$		$p=0.0406(e^{0.111T})$		n/a	Durbin et al. (1983)
Durbin fish food $\left(g^{1-a} \cdot hr^{-1} \right)$		$p=0.00406(e^{0.111T})$		n/a	Durbin et al. (1983)

Sensitivity to shape parameter (a)

I compared mean modelled daily ration ($\overline{DR_{model}}$, g·day^{-1}), a measure of consumption over 24 hr, as estimated using the shape parameters $a = 0, 0.5, 0.67,$ and 1 using one-way ANOVA and Tukey-Kramer multiple comparison tests for sample sizes of $n = 10, 20, 30, 40, 50,$ and 100 fish randomly selected from a normal distribution of predator (cod) weight based on statistics from predator weights found in the DFO stomach-contents database (Shapiro-Wilks normality test, P = 0.94, **Chapter 6**). The normality of all samples and associated DR estimates were determined using the Shapiro-Wilks test (significance level = 0.05).

Sensitivity to variables

Normalized sensitivity was used to determine the variation in DR_{model} due to variation in model variables (weight, temperature and food energy-density). Normalized sensitivity is defined as the percentage change in DR_{model} from a percentage change in a variable e.g. predator weight, g (Fasham et al. 1990):

$$Sensitivity = \frac{\left(\dfrac{DR_{model,max} - DR_{model,min}}{DR_{model,max}} \right)}{\left(\dfrac{V_{max} - V_{min}}{V_{max}} \right)} \quad , \tag{23}$$

where *Sensitivity* is the normalized sensitivity (dimensionless), $DR_{model,max}$ is the maximum DR_{model} over the variable (weight, temperature, or food energy-density) range, $DR_{model,min}$ is the minimum DR_{model} over the variable range, V_{max} is the variable value resulting in $DR_{model,max}$ and V_{min} is the variable value resulting in $DR_{model,min}$.

5.2.2 Evaluating the Pennington Method with Modelled Consumption

As described above, DR can be estimated using Pennington's method (DR_P) that makes no presumptions regarding the value of the shape parameter (a):

$$DR_P = \left(\frac{24}{T}\right) \cdot C_T = \left(\frac{24}{T}\right) \cdot \left(\frac{(S(T) - S(0))}{T} + p \cdot (average\left[(S(t))^a\right])\right) \ , \tag{24}$$

where DR_P is the daily ration (g·day^{-1}), C_T is the consumption rate (g·hr^{-1}), T is the sampling interval (hr), $S(T)$ is the stomach content weight (g) at the end of the interval, $S(0)$ is the stomach content weight (g) at the start of the interval, p is the rate parameter (g^{1-a}·hr^{-1}), and a is the dimensionless shape parameter. For the Pennington method to be applicable for use with field data the $\frac{(S(T) - S(0))}{T}$ term in eqn. 24 is explicitly assumed to be negligible as this information is not available in the field.   This results in a simplified Pennington method (DR_P'),

$$DR_P' = \left(\frac{24}{T}\right) C_T = \left(\frac{24}{T}\right)(p(average\left[S(t)^a\right])) \ , \tag{25}$$

with the variables as in eqn. 24. The average Pennington DR was estimated with ($\overline{DR_P'}$, eqn. 25) and without ($\overline{DR_P}$, eqn. 24) the simplification were compared with a Wilcoxon Rank Sum test. In addition $\overline{DR_P'}$ was compared with $\overline{DR_{model}}$ using a Wilcoxon Rank Sum test to evaluate the accuracy of the Pennington method in estimating DR from variation in modelled stomach contents.

Another simplification (the averaging assumption of eqn. 9) allows for aggregated samples to be used when calculating DR (Andersen 2001).   The accuracy of the Pennington method in estimating DR with stomach contents samples aggregated over time was evaluated by comparing $\overline{DR_P'}$ predictions (now averaging $S(t)$ samples in time as shown in eqn. 9) with associated $\overline{DR_{model}}$ using a Wilcoxon Rank Sum test.

5.2.3 Sensitivity to Model Structure

Variation among results that may be due to model structure was investigated for each model variant (see Section 5.2.1) in three ways. First, differences in $\overline{DR_{model}}$ due to

model structure was estimated using Kruskal-Wallis analysis of variance and multiple comparison tests where necessary (Shapiro-Wilks, P < 0.05) . Second, the quantification of variation in $\overline{DR_{model}}$ due to variation in the shape parameter (*a*) was examined using one-way ANOVA with Tukey Kramer multiple comparison testing when necessary (Shapiro-Wilks test for normality P ≥ 0.05) for each model variant. Third, variations in the accuracy of the Pennington method (see Section 5.2.2) in predicting $\overline{DR_{model}}$ due to variations in model structure was determined using a two-sample t-test (Shapiro-Wilks test for normality, P ≥ 0.05) or Wilcoxon Rank Sum test (Shapiro-Wilks test for normality, P < 0.05) where appropriate.

5.2.4 Evaluating the Pennington Method with Consumption in the Published Literature

As no comparable Atlantic cod data were available, the stomach contents model was adjusted for the temperature (7.1°C), feeding periodicity and weight of trout used in Elliott and Persson's (1978) study to allow for comparisons between the Pennington method estimates of DR_P' and the empirical estimates of DR_{actual}. The food energy-density of the food (*Gammarus pulex*) was not provided by Elliott and Persson (1978) and therefore was estimated as 3.39 kJ·g^{-1} using the Jonsson (2003) study on the same animal.

5.3 Results

5.3.1 Stomach Contents Model

Sensitivity to shape parameter (a)

Use of the four shape parameters (a = 0, 0.5, 0.67, 1) resulted in different $\overline{DR_{model}}$ estimates for linear (i.e. a = 0) vs. non-linear (i.e. a = 0.5, 0.67, 1) stomach evacuation rates (Fig. 5.8; Shapiro-Wilks $0.10 \leq P \leq 0.88$; One-way ANOVA, P = 0.005). There was no difference in $\overline{DR_{model}}$ among the non-linear forms of a (Shapiro-Wilks $0.87 \leq P \leq 0.88$; One-way ANOVA, P = 0.87). This result was tested over sample sizes of n = 10, 20, 30, 40, 50, 100, and 200 and was consistent at sample sizes greater than n = 30 fish (Fig. 5.9). At sample sizes $10 < n < 30$, there were no differences among $\overline{DR_{model}}$ estimates based on any of the four forms of a (i.e. even differences due to linear vs. non-linear forms were absent). Expanding the study to examine intermediate forms of the shape parameter demonstrates the $\overline{DR_{model}}$ with a = 0 becomes different from that of the non-linear formulations ($a \neq 0$) at a shape parameter of a = 0.2 (Fig. 5.10).
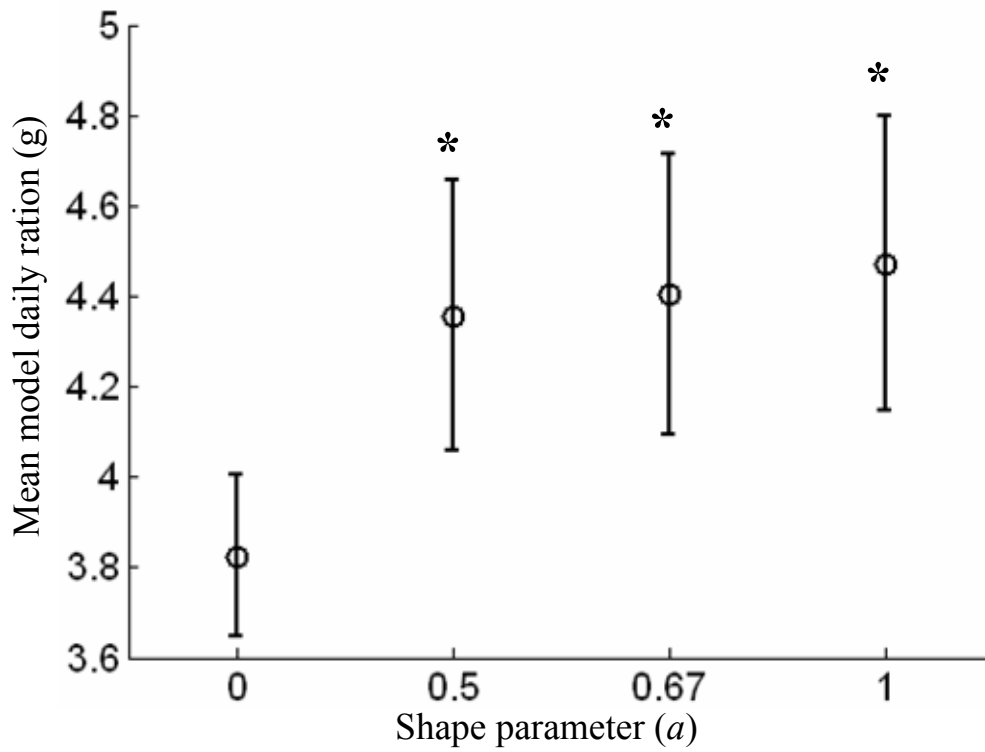
Figure 5.8: A comparison of $\overline{DR_{model}}$ and 95% confidence intervals around the mean using a shape parameter (a) of 0, 0.5, 0.67, or 1 (Shapiro-Wilks $0.10 \leq P \leq 0.88$; One-way ANOVA, P = 0.005).   Data marked with similar symbols (*) are similar (Tukey-Kramer, P = 0.87).
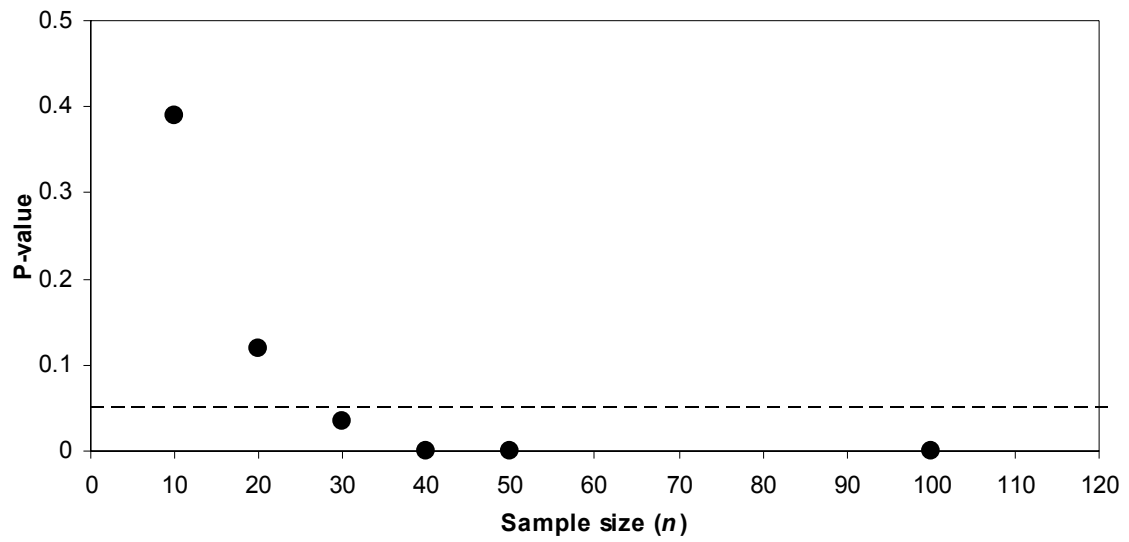
Figure 5.9: A comparison of one-way ANOVA P-values (all samples normal, Shapiro-Wilks $0.11 \le P \le 0.95$) comparing $\overline{DR_{model}}$ for $a = 0, 0.5, 0.67$ and 1 at sample sizes of $n = 10, 20, 30, 40, 50,$ and 100. Below a sample size of $n = 30$ fish, there is no difference between linear and non-linear forms of the model.
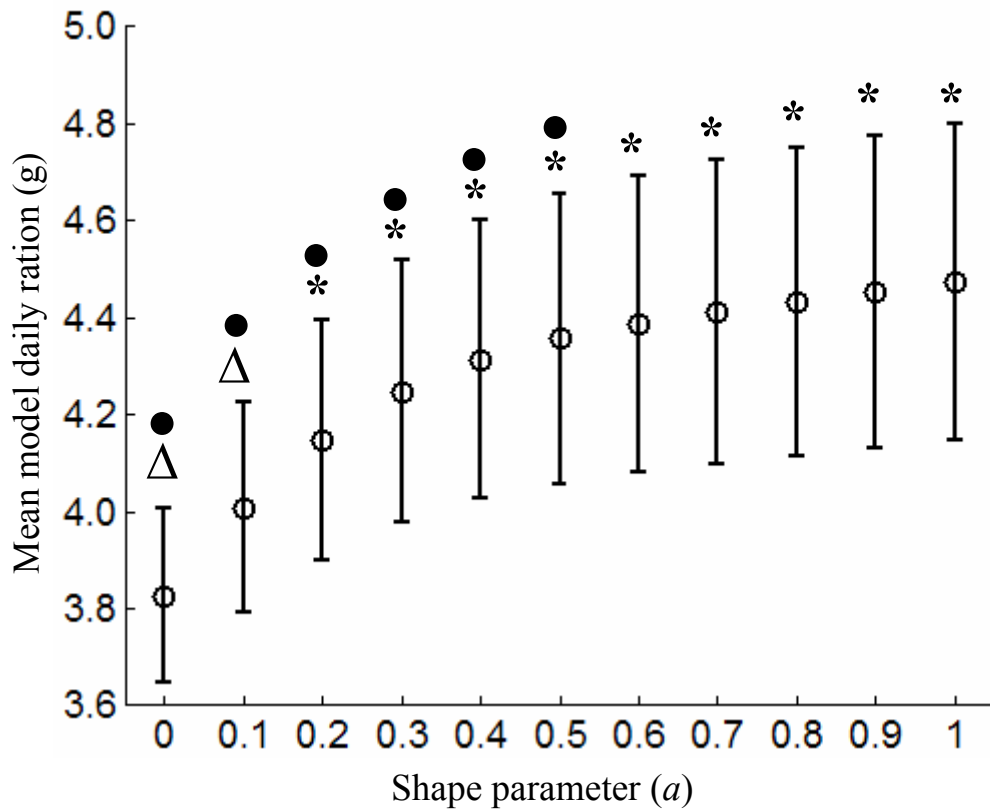
Figure 5.10: A comparison of $\overline{DR_{model}}$ and 95% confidence intervals using a shape parameter (*a*) of 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 or 1 assessed with ANOVA and Tukey-Kramer multiple comparison tests (P = 0.021).   Data marked with similar symbols (* or Δ or ●) are statistically similar. All DR_{model} samples are normally distributed (Shapiro-Wilks $0.10 \leq P \leq 0.89$).

Sensitivity to variables

To determine the variables contributing to the majority of the variation in DR_{model}, the model was run over a range in predator weight (g), temperature (ºC) and food energy-density (kJ·g^{-1}) values (Table 5.1, Fig. 5.11). Normalized sensitivity was used to quantify the relative effects of each of the three variables (eqn. 23, Table 5.2). The DR_{model} was most (and positively) sensitive to variation in predator weight (g, sensitivity = 0.99) and temperature (ºC, sensitivity = 0.67) and less (and negatively) sensitive to food energy-density (kJ g^{-1}, sensitivity = -0.12).
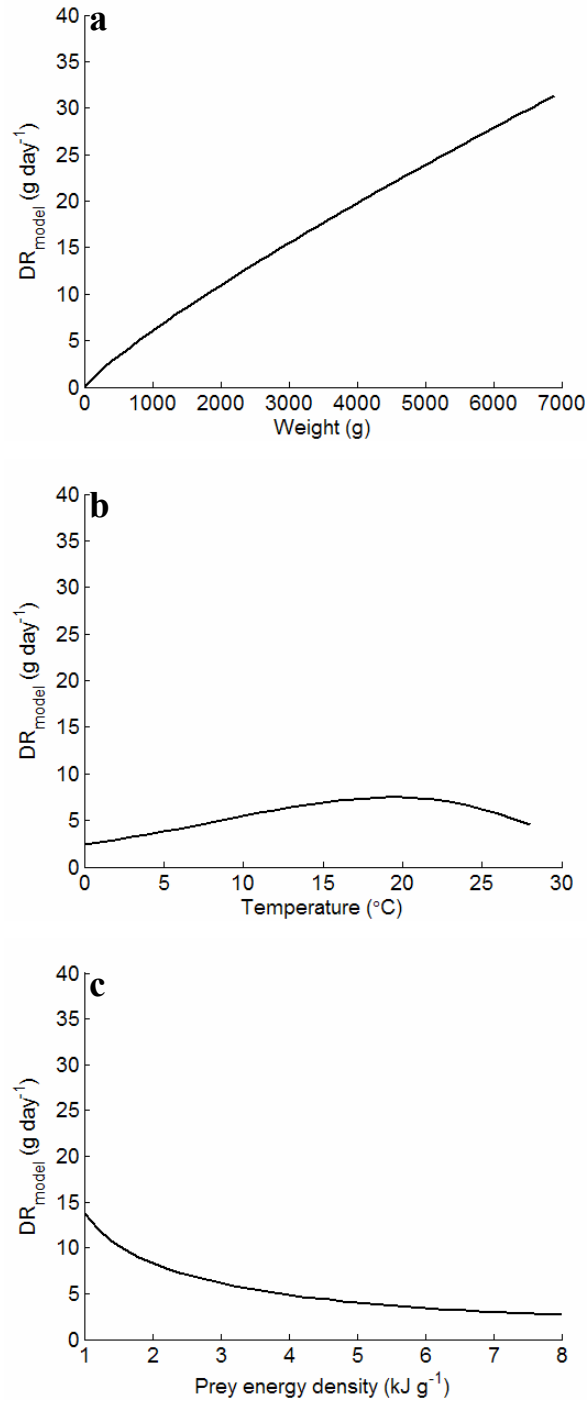
Figure 5.11: The DR_{model} (g·day^{-1}) over the variable range examined in this study: a) weight (g); b) temperature (°C); and c) food energy-density (kJ·g^{-1}). While one variable was examined, all others were held at the initial levels provided in Table 5.1.

Table 5.2: Range and results of normalized sensitivity analyses for the effect of changes in weight (g), temperature (°C), and food energy-density (kJ·g^{-1}) variables on DR_{model} as in eqn. 23.

Parameter	Range	Source	Normalized Sensitivity of DR_{model}
Weight (g)	2, 7000	DFO Stomach Database	0.99
Temperature (°C)	1, 28	Jobling (1988)	0.67
Food energy-density (kJ·g^{-1})	2.67, 5.67	Daan (1975)	-0.12

5.3.2. Evaluating the Pennington Method with Modelled Consumption

Average DR estimates derived from the simplified Pennington method ($\overline{DR_P}'$,eqn. 25) and those from the original formulation ($\overline{DR_P}$, eqn. 24) were statistically similar (Shapiro-Wilks $0.020 \leq P \leq 0.040$; Wilcoxon Rank Sum, P = 0.55). DR_P estimates based on modelled stomach-content weight aggregated over time (eqn. 9) were similar to those based on disaggregated stomach-content weight (Shapiro-Wilks $0.020 \leq P \leq 0.033$; Wilcoxon Rank Sum P = 0.30). As well the simplified Pennington method was able to predict mean modelled DR as $\overline{DR_P}'$ did not differ significantly from $\overline{DR_{model}}$ (Shapiro-Wilks $0.020 \leq P \leq 0.035$; Wilcoxon Rank Sum, P = 0.23). Linear regression of DR_P' against DR_{model} (Fig. 5.12) provides a near 1:1 relation (i.e. slope $\approx$ 1, intercept $\approx$ 0 and $DR_P' \approx DR_{model}$) when estimated among the non-linear forms of stomach evacuation rate (a = 0.5, 0.67 and 1); a = 0.5 being the most predictive (i.e. slope closest to 1, intercept closest to 0, Table 5.3).
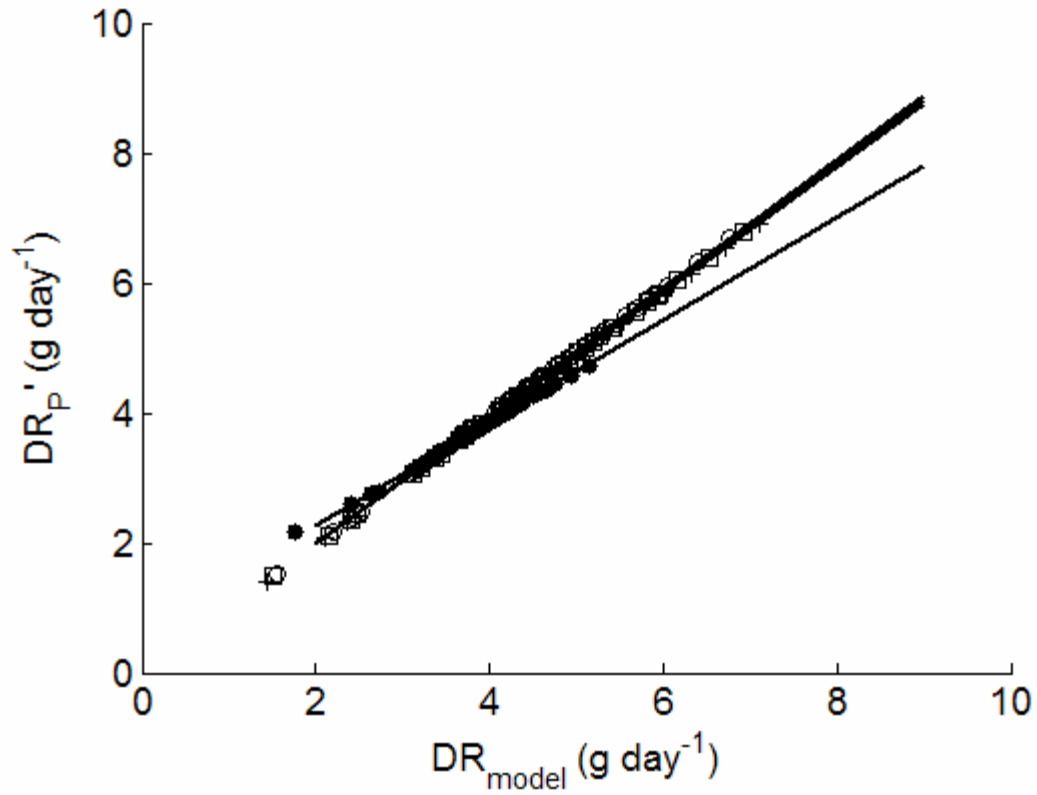
Figure 5.12: A comparison of DR_{model} and $DR_P{'}$ with $a = 0$ (filled circle), $a = 0.5$ (open circle), $a = 0.67$ (square), and $a = 1$ (+) with associated linear regressions (Table 4).

Table 5.3: Slopes, intercepts and associated linear regression parameters for $DR_p{'}$ as a function of DR_{model} using shape parameters $a = 0$, 0.5, 0.67, or 1 as in Fig. 5.12.

Shape parameter (a)	Slope	Intercept (g day^{-1})	r^2	P
0	0.79	0.67	0.99	< 0.0001
0.5	0.98	0.0048	0.99	< 0.0001
0.67	0.98	0.0229	0.99	< 0.0001
1	0.97	0.033	0.99	< 0.0001

5.3.3 Sensitivity to Model Structure

The effects of model structure on the results in this study were examined using three methods (Table 5.4).

First, $\overline{DR_{model}}$ estimates among model variants were compared to that of the original model structure using Kruskal-Wallis nonparametric analysis of variance with multiple comparison tests when necessary (Shapiro-Wilks test for normality P < 0.05). $\overline{DR_{model}}$ estimates were significantly lower relative to the original model structure using the Andersen and Riis-Vestergaard consumption function (P < 0.0001; 4.4 g vs. 3.0 g), Durbin's general rate parameter (P < 0.0001; 4.4 g vs. 3.5 g), and Durbin's fish rate parameter (P < 0.0001; 4.4 g vs. 1.1 g) variants. $\overline{DR_{model}}$ estimates were higher when compared to the original model structure using no stomach effect (P = 0.0006; 4.4 g vs. 6.0 g), stomach effect with 5% maximum stomach contents (P = 0.0006; 4.4 g vs. 5.5 g), night-time feeding at 25% of maximum (P < 0.0001; 4.4 g vs. 5.8 g), and Andersen 2 rate parameter (P < 0.0001; 4.4 g vs. 4.6 g) variants. $\overline{DR_{model}}$ estimates were similar when based on the Ivlev (Type 2) and Type 3 prey consumption variants (P = 0.96). However, the consumption rate based on the Type 3 functional response is consistently higher than that based on the Ivlev except at very low prey concentrations (Fig. 5.4). Thus, variation in $\overline{DR_{model}}$ due to the functional response variation explored here is more likely due to higher vs. lower consumption rates than it is to the effects of functional response shape. For all modelled components other than the choice of functional response, variation in model structure results in significant variation among $\overline{DR_{model}}$ estimates.

Second, $\overline{DR_{model}}$ estimates based on the four shape parameters ($a = 0, 0.5, 0.67$, and 1) were compared using one-way ANOVA and Tukey Kramer multiple comparison testing when necessary (Shapiro-Wilks test for normality P $\geq$ 0.05) for each model variant. Unlike the original model structure, non-linear ($a \neq 0$) and linear ($a = 0$) stomach evacuation rate forms demonstrated similar $\overline{DR_{model}}$ when based on the Andersen and Riis-Vestergaard consumption function (P = 0.63), appetite function (no effect of appetite: P = 0.99; $H = 0.05$: P = 0.10), and Andersen 2 rate parameter (P = 0.88) variants. All other model variants produced significant differences in $\overline{DR_{model}}$ when using non-

linear vs. linear forms of a (Table 5.4). In addition Durbin's rate parameter variants produced additional differences among non-linear forms of a (Table 3, P < 0.0001). Thus, the majority of model variants demonstrate that significant variation in $\overline{DR_{model}}$ only occurs between the linear ($a = 0$) and non-linear ($a = 0.5$, 0.67 and 1) forms of the stomach evacuation rate, if at all.

Third, the effect of model structure on the accuracy of the Pennington method to predict DR_{model} was examined by comparing $\overline{DR_p}'$ to $\overline{DR_{model}}$ for each structure variant using a two-sample t-test (Shapiro-Wilks test for normality, P ≥ 0.05) or Wilcoxon Rank Sum test (Shapiro-Wilks test for normality, P < 0.05) where appropriate (Table 5.4). The accuracy of the $\overline{DR_p}'$ estimates was maintained among all model variants (i.e. $\overline{DR_p}'$ and $\overline{DR_{model}}$ are significantly similar, $0.077 \leq P \leq 0.23$) except when the appetite function variants (no appetite effect, $H = 0.05$) or Durbin's fish food rate parameters are employed (i.e. $\overline{DR_p}'$ and $\overline{DR_{model}}$ are significantly different; P < 0.0017). Thus, the Pennington method is able to approximate the $\overline{DR_{model}}$ for almost all model variants.

Table 5.4: Table of model structure analytical results. Effect of model structure was tested through 1) comparison of $\overline{DR_{model}}$ with $a =$ 0.5 among model variants using Kruskal-Wallis nonparametric analysis of variance with multiple comparison testing when necessary (Shapiro-Wilks test for normality P < 0.05), 2) analysis of the effect of shape parameter (a) on the $\overline{DR_{model}}$ for each model variant using one-way ANOVA with Tukey Kramer multiple comparison testing when necessary (Shapiro-Wilks test for normality P ≥ 0.05), and 3) accuracy of $\overline{DR_p}$' when compared to $\overline{DR_{model}}$ using a two-sample t-test (Shapiro-Wilks test for normality, P ≥ 0.05) or Wilcoxon Rank Sum test (Shapiro-Wilks test for normality, P < 0.05) where appropriate. Model function variants used in the original model structure are shaded in grey.

Function	Variants	1) Estimate of daily ration *indicates statistically similar $\overline{DR_{model}}$	2) Analyze effect of a *indicates statistically similar $\overline{DR_{model}}$	3) Accuracy of DR_P' P-value for test comparing $\overline{DR_p}$' and $\overline{DR_{model}}$
consumption (temperature and weight effects)	Jobling (1988) $C_{max} = e^{((0.104T - 0.000112T^3 - 1.500) + 0.802 \ln W)}$	P < 0.0001	P = 0.005 a=0 a=0.5 * a=0.67 * a=1 *	Wilcoxon Rank Sum P = 0.23
	Andersen and Riis-Vestergaard (2003) $C_{max} = uW^v e^{dT}$		P = 0.63	Wilcoxon Rank Sum P = 0.16

Table 5.4 cont.

Function	Variants	1) Estimate of daily ration *indicates statistically similar $\overline{DR_{model}}$	2) Analyze effect of a *indicates statistically similar $\overline{DR_{model}}$	3) Accuracy of DR_P' P-value for test comparing $\overline{DR_p'}$ and $\overline{DR_{model}}$
Prey	Ivlev (Type 2)	P = 0.96	P = 0.005	Wilcoxon Rank Sum P = 0.23
			a=0	
			a=0.5 *	
			a=0.67 *	
			a=1 *	
	Type 3		P = 0.0052	Wilcoxon Rank Sum P = 0.23
			a=0	
			a=0.5 *	
			a=0.67 *	
			a=1 *	

Table 5.4 cont.

Function	Variants	1) Estimate of daily ration *indicates statistically similar $\overline{DR_{model}}$	2) Analyze effect of a *indicates statistically similar $\overline{DR_{model}}$	3) Accuracy of DR_P' P-value for test comparing $\overline{DR_p'}$ and $\overline{DR_{model}}$
Appetite effect	$H = 0.01$		P = 0.005 a=0 a=0.5 * a=0.67 * a=1 *	Wilcoxon Rank Sum P = 0.23
	no appetite effect	P = 0.0006	P = 0.99	Wilcoxon Rank Sum P < 0.0001
	$H = 0.05$		P = 0.10	Wilcoxon Rank Sum P = 0.0017

Table 5.4 cont.

Function	Variants	1) Estimate of daily ration *indicates statistically similar $\overline{DR_{model}}$	2) Analyze effect of *a* *indicates statistically similar $\overline{DR_{model}}$		3) Accuracy of DR_P' P-value for test comparing $\overline{DR_p}$' and $\overline{DR_{model}}$
Light effect	No night feeding	P < 0.0001	P = 0.005		Wilcoxon Rank Sum P = 0.23
			a=0		
			a=0.5	*	
			a=0.67	*	
			a=1	*	
	Night feeding at 25% of maximum		P < 0.0001		Two-sample t-test P = 0.19
			a=0		
			a=0.5	*	
			a=0.67	*	
			a=1	*	

Table 5.4 cont.

Parameter	Variation(s)	1) Estimate of daily ration *indicates statistically similar $\overline{DR_{model}}$	2) Analyze effect of a *indicates statistically similar $\overline{DR_{model}}$		3) Accuracy of DR_P' P-value for test comparing $\overline{DR_p}$' and $\overline{DR_{model}}$
Evacuation rate parameter (p)	Andersen 1 $\left(g^{1-a} \cdot hr^{-1}\right)$		P = 0.005	*	Wilcoxon Rank Sum P = 0.23
			a=0		
			a=0.5	*	
			a=0.67	*	
			a=1	*	
	Andersen 2 $\left(g^{1-a} \cdot hr^{-1}\right)$		P = 0.88	*	Wilcoxon Rank Sum P = 0.38
	Durbin general $\left(g^{1-a} \cdot hr^{-1}\right)$	P < 0.0001	P < 0.0001		Wilcoxon Rank Sum P = 0.077
			a=0		
			a=0.5	*	
			a=0.67	*/**	
			a=1	**	
	Durbin fish food $\left(g^{1-a} \cdot hr^{-1}\right)$		P < 0.0001		Wilcoxon Rank Sum P < 0.0001
			a=0		
			a=0.5	*	
			a=0.67	*	
			a=1		

5.3.4 Evaluating the Pennington Method with Consumption in the Published Literature

Average Pennington DR estimates, $\overline{DR_P}'$, lie within one standard deviation of empirical estimates of DR ($\overline{DR_{actual}}$) for trout in the laboratory (Figure 5.13).
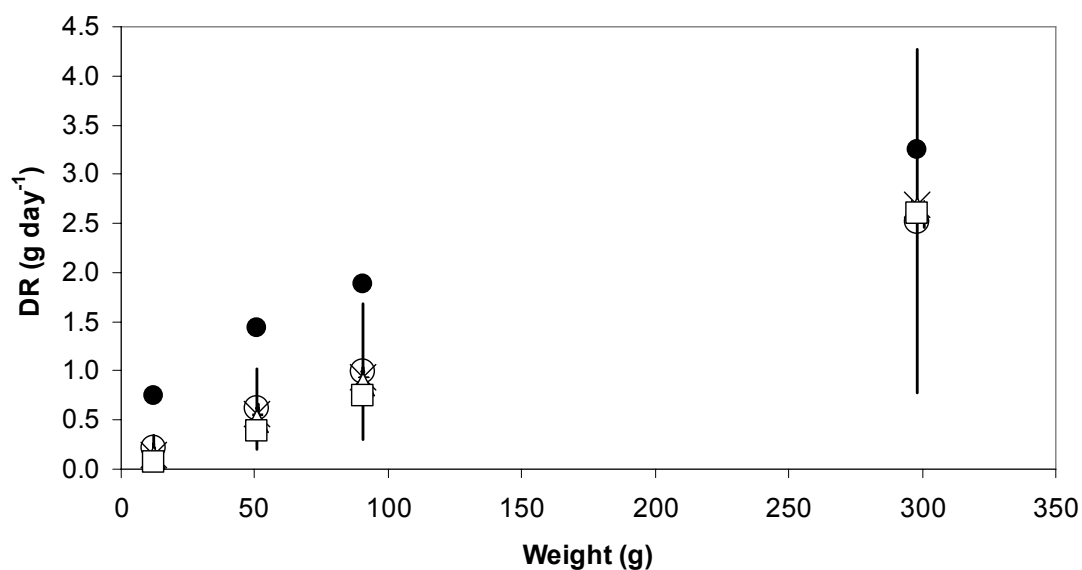
Figure 5.13: A comparison of DR estimates for trout (Elliott and Persson 1978). Shown are the average empirical consumption rates and standard deviations ($\overline{DR_{actual}}$, open circle, g day^{-1}, Elliott and Persson 1978) and average Pennington DR ($\overline{DR_P}'$, g·day^{-1}) estimated with a = 0 (filled circle), 0.5 (cross), 0.67 (triangle), and 1 (square).

5.4 Discussion

Comparisons of stomach evacuation rates among studies are thought to be hindered by differences among evacuation models (shape parameter), food size and type (energy-density), predator size and temperature effects and/or experimental methods (Ruggerone 1989). Despite the debate surrounding the exact value of the shape parameter (a) in the stomach evacuation function, to estimate mean DR ($\overline{DR_{model}}$) for a sample size of 50 fish, the only important differences result from using the linear ($a = 0$) vs. non-linear ($a = 0.5, 0.67, 1$) stomach evacuation rate forms and there is no significant difference among the non-linear forms (Fig. 5.8). Moreover, while absolute values of $\overline{DR_{model}}$ varied with model structure, the influence of the different shape parameter values (a) was the same (Section 5.3.3, Table 5.4). This result agrees with that of Andersen (1998) who found a non-linear stomach evacuation model resulted in a shape parameter (a) that varied from 0.36 to 0.77. In addition, Temming and Andersen (1994) found that for cod the stomach evacuation rate was non-linear ($a \neq 0$) and with the value of a dependent on food type (e.g. $a = 0.27$ for prawn, $a = 0.43$ for herring). For sample sizes $\leq$ 30 fish, no difference was found between non-linear and linear forms (P > 0.05). It is possible then, for small samples, that the form of the stomach evacuation rate function (shape parameter) may be selected arbitrarily without hindering the estimation of the mean DR. So what does matter in estimating daily ration?

Modelled DR (DR_{model}) was highly and positively sensitive to predator size (weight) and temperature and less sensitive to increases in food energy-density which negatively affected DR_{model} (Table 5.2). These results reflect a common hierarchy of factors found to influence rates in fishes. As with most physiological rates (Peters 1983), DR scales strongly with body size, a result found in a number of other studies (e.g. Dunbrack 1988; Andersen and Riis-Vestergaard 2003). Temperature had the second strongest effect on DR with increases in temperature leading to increases in DR over a mid-range of temperatures (Fig. 5.11b). As shown in **Chapter 2** (and in Neuheimer and Taggart 2007) temperature is a controlling factor for ectotherms because it governs cellular rates (Fry 1971) that results in a scaling of growth and associated rates with physiological time. While DR_{model} was less sensitive to food energy-density, the effect is

not negligible (Sensitivity = -0.12, Fig. 5.11c). A significant effect of food energy-density on DR is reported in earlier studies (MacDonald et al. 1982; Olson and Boggs 1986) where the slope and shape of the evacuation rate is partially controlled by the fat content of the food; i.e. energy density. Rindorf and Lewy (2004) reported that ignoring individual prey type resulted in a bias in the consumption estimate by as much as 150% in whiting. Pedersen (2000) used Andersen's (1999) model to estimate DR for whiting and reported DR was significantly different among years and groups of whiting and was dependent on the energy-density of the stomach contents. As such, it is possible that there is feedback between the amount of energy contained in the digestive chime and the mechanisms controlling the secretion of stomach acid, enzymes and gut hormones in some fish (Jobling 1986). Thus, it appears predictive DR_{model} estimates require an accurate representation of weight and temperature while improved estimates are obtained when food energy-density information is also available.

Two simplifications of the Pennington method were examined in this study. It was found that disregarding the $\frac{(S(T) - S(0))}{T}$ term in eqn. 24 did not result in significantly different $\overline{DR_P}$ estimates. These results agree with those of Boisclair and Leggett (1988) who found consumption estimates in yellow perch (*Perca flavescens*) were accurate even when *S(T)* and *S(0)* differed by a factor of 2. This simplification is necessary for the application of the Pennington method to stomach content data from the field as *S(T)* and *S(0)* are not often available from field samples.

As information about stomach content data are usually aggregated (e.g. among sampling times or individuals), it is important to determine if the assumption given in eqn. 9 is valid (Andersen 2001). Mathematically, $average\big[(S(t))^a\big]$ and $(average\big[(S(t))\big])^a$ will differ unless all values of *S(t)* are equal (Ursin et al. 1985) and therefore, aggregated stomach content data will likely be biased by the frequency distribution of *S(t)* (Andersen 2001). For *S(t)* aggregated in time, this study demonstrated no significant difference between the DR_{model} when estimated using disaggregated or aggregated sampling times even though *S(t)* estimates were not all equal. However, my study did not include a large number of empty stomachs (i.e. *S(t)* = 0 g) which can result in large sampling bias (Ursin et al. 1985). Indeed, the bias in DR estimated from aggregated data can increase to

several hundred percent when empty stomachs are included in the calculation (Rindorf and Lewy 2004). Stomach contents may also be aggregated among individuals. As shown above, DR_{model} estimates are highly sensitive to predator size and it is likely that aggregating over a large range in predator weights could result in large uncertainties in the DR estimates. This was reported by Rindorf and Lewy (2004) in their study of whiting where consumption estimates demonstrated a 63% bias when made with stomach contents aggregated among individuals despite the fact that the fish were from a relatively small length-class (25-30 cm). The same authors demonstrated that bias due to aggregated data increased with an increase in stomach content variance and provided a correction factor for aggregated stomach contents based on the distribution of stomach contents over time.

Comparisons between $\overline{DR_P}'$ and $\overline{DR_{model}}$ demonstrated that the Pennington method is able to approximate the modelled DR. This result was maintained for almost all model variants (Section 5.3.3). As well, the Pennington method (parameterized with a = 0.5) sufficiently predicted mean consumption by trout in the lab ($\overline{DR_{actual}}$, Fig. 5.13) when predator size, temperature and food energy-density information were incorporated. The predictive power of the Pennington method was highest for modelled DR using the non-linear forms of a (Fig. 5.12, slope closer to one, intercept closer to zero) with those estimates made using a = 0.5 being the most predictive. Similarly, the majority of fish-feeding studies have shown the non-linear functions of the stomach evacuation to be the best descriptors of laboratory and field data (e.g. Elliott 1972; Jones 1974; Persson 1979; 1981; Basimi and Grove 1985; Grove et al. 1985; Brett and Higgs 1970; Ruggerone 1989; Mergadt and Temming 1997; Andersen 1998, 1999, 2001; Temming and Herrmann 2003).

To date, the modelling of stomach evacuation has been mainly limited to empirical 'fits' with "a consistent physiological model explaining the minimum forces governing evacuation patterns…yet to be established" (Andersen 1998). Based on the most probable factors that describe variation in stomach content weight, I have developed a simple model of change in stomach content weight over time that can be used to assess the influence of different factors (e.g. predator weight, temperature, food energy-density) on DR estimates. Demonstrating that the majority of variation in estimated DR occurs

when using the linear vs. non-linear shape parameters ($n > 30$), it is possible that estimating the (perhaps unattainable) near-exact value of the shape parameter (a) may provide little improvement in food consumption estimates. In this chapter the Pennington method (with $a = 0.5$) is shown to be a suitable method of estimating daily ration when parameterized with predator size, temperature and food energy-density. These results appear to satisfy the need for a reasonable estimate of consumption rate based on stomach content weight samples in the field that would allow for food-dependent variations in growth to be estimated. I explore this possibility in **Chapter 6** where I employ the Pennington method to estimate variation in food consumption of Atlantic cod in the southern Gulf of St. Lawrence and **Chapter 7** where I explore the food consumption variations with variations in size-at-age for this stock.

Chapter 6

Temporal Variation in Stomach Content and Food Consumption of Atlantic Cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence

6.1 Introduction

Quantitative estimates of food consumption by fish are necessary for ecosystem studies to allow for the estimation of the effects of environmental change on fish feeding and resulting impacts on other ecosystem components (e.g. prey species, nutrient pathways). In addition, food consumption estimates are essential for many aspects of fish ecology and physiology, including estimates of bioenergetic pathways for individuals, stock production and trophic relationships among species (Jobling 1981, Sainsbury 1986). In particular, fish size-at-age (i.e. growth) is directly affected by the amount and type of food consumed by the fish (Waiwood and Majkowski 1984). Thus, accurate estimates of temporal variation in food consumption are necessary to disentangle the various factors contributing to variation in fish size-at-age over time.

Food consumption among fishes varies in time (intra- and inter-annually) and location (feeding, spawning and over-wintering grounds) such that estimates of stomach contents (including weight and food type) and food consumption rate must be made sufficiently frequently and be specific to the stock or population in question (Hanson and Chouinard 2002). Atlantic cod (*Gadus morhua*) food consumption exhibits intra- and inter-annual variation in the type and amount (i.e. daily ration, DR, g·day^{-1}) of prey consumed (Hanson and Chouinard 1996). Cod are generalist feeders and eat a broad diet of invertebrate (e.g. shrimp, worms) and fish (e.g. herring, American plaice, capelin) food (DFO 2004, Chénard 2004). Cod diet varies through the life of the fish due to size-specific diet changes and variation in the prey field (Casas and Paz 1996, Hanson and Chouinard 1996). As cod size (e.g. length) increases, DR and the proportion of fish in the diet increases (Hanson and Chouinard 1996). As well, cod DR varies with intra- and

inter-annual variations in the prey field. There is a direct relation between prey in cod stomachs and prey availability in the feeding environment (Fahrig et al. 1993, DFO 2004). Thus, quantifying the influence of varying food consumption on cod size-at-age requires estimates of cod DR over a range of temporal scales.

In this chapter, I estimate inter- and intra-annual variation in food consumption of cod in the southern Gulf of St. Lawrence (sGSL) from 1987 through 2004 by examining variations in stomach content (e.g. stomach fullness, % empty stomachs, prey type) and the resulting DR (g·day^{-1}) estimates. While earlier estimates of food consumption have been determined for this stock, they are restricted to a limited range of sampling years (e.g. Waiwood and Majkowski 1984, Schwalme and Chouinard 1999) or seasons (e.g. Hanson and Chouinard 2002). The results of this chapter will provide estimates of the variation in DR for sGSL cod at a higher temporal resolution that may be used to examine the influence of changing food consumption on variation in size-at-age (**Chapter 7**).

6.2 Methods

6.2.1 Cod Stomach Sampling

The focus stock of this study is the southern Gulf of St. Lawrence (sGSL; Northwest Atlantic Fisheries Organization, NAFO, statistical division 4T, see **Chapter 4**) Atlantic cod (*Gadus morhua*) stock. Unpublished stomach content estimates and associated data were collected in 1987, 1990 through 1996, and 1999 through 2004 (*n* = 21344) as part of Fisheries and Oceans Canada (DFO) research surveys, sentinel surveys as well as trips of opportunity (Fig. 6.1). Cod stomachs were frozen and later dissected to quantify food at the Gulf Fisheries Centre (J.M. Hanson, Gulf Fisheries Centre, Moncton, NB, unpublished). The stomachs were thawed and food removed from mucus and water. The number of each food type items was recorded along with the blotted wet weight (g). Fish in stomachs were identified to species when possible or at a minimum, flatfish and roundfish were differentiated. Invertebrate food was identified to species when possible. Stomach content data include information on predator (cod) total length, round weight, stomach content weight, food type abundance and wet weight. I recoded all data to unique record format to simplify analysis and to designate food type (Table 6.1) to allow

disaggregated and aggregated quantification of diet variation over time and by fish size (length).
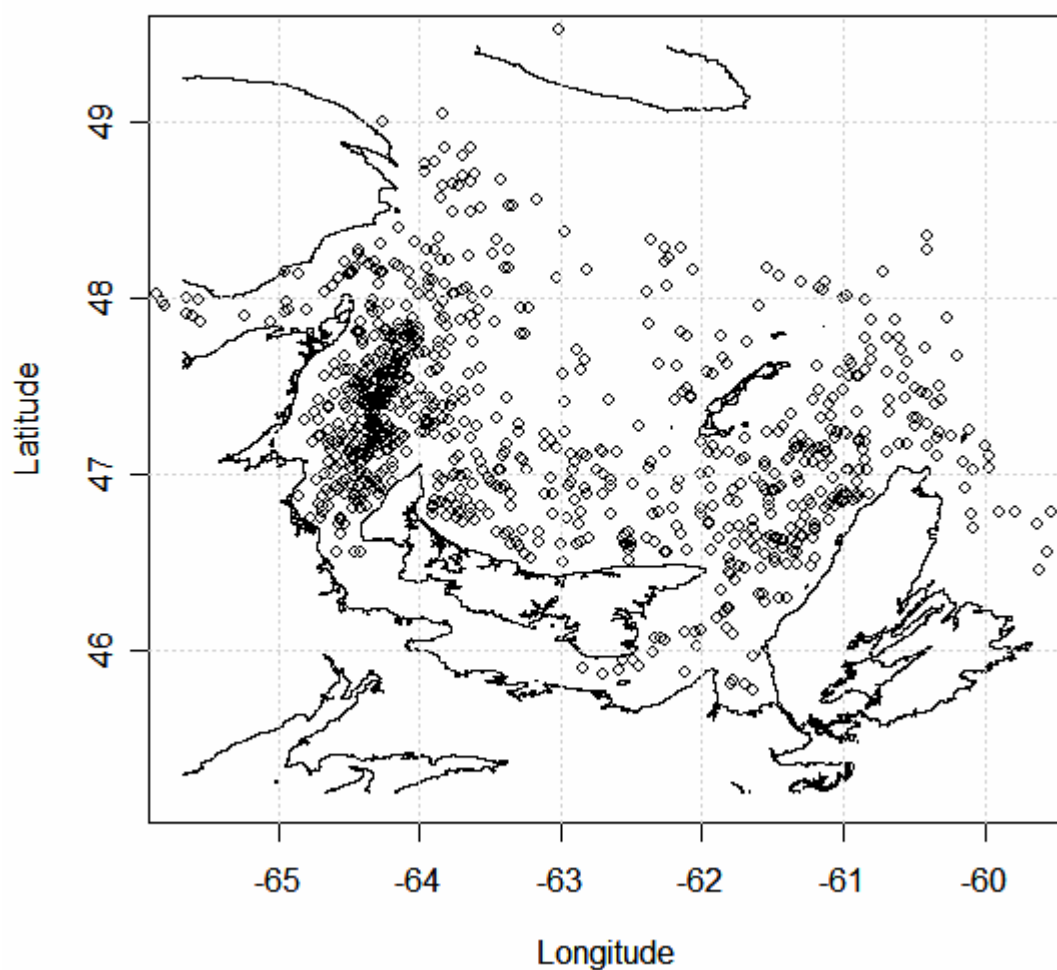
Figure 6.1: Chart of the southern Gulf of St. Lawrence (sGSL) indicating cod stomach sampling locations (open circle) for all years.

Table 6.1: Food types in southern Gulf of St. Lawrence cod stomachs.

Type Code	Group Name	Examples (species and/or common names)
A	Fish	herring (*Clupea harengus*)
B	Worm	acorn worm
C	Algae	red algae
D	Poriferan	sponge
E	Cnidarian	sea anemone
F	Mollusc	propeller clam (*Cyrtodaria siliqua*)
G	Echinoderm	sea cucumber
H	Bryozoan	bryozoan colony
I	Miscellaneous	fish eggs, skate egg case
J	Shrimp	Arctic argid (*Argis dentata)*
K	Amphipod	Caprellid amphipod
L	Copepod	*Calanus finmarchicus*
M	Crab	snow crab
N	Miscellaneous crustacean	unidentified crustacean remains
O	Euphausiid	Northern krill (*Meganyctiphanes Norvegica*)
P	Isopod	*Idotea* sp.
Q	Cumacean	*Eudorella* sp.
R	Mysid	*Mysis mixta*
S	Ctenophore	comb jelly

6.2.2 Estimating Stomach Content Variation

Variation in cod stomach samples was analyzed over time (year, month, hour) and length-class (length-class size = 5 cm) using three indices: 1) stomach fullness index (*SFI*, g·cm^{-3}),

$$SFI = \left(\left(\frac{W_{ST}}{(L_F)^3} \right) \cdot 1000 \right) \qquad , \qquad (1)$$

where W_{ST} is the total weight of food in the stomach, g, and L_F is the fish length, cm, (adapted from Pedersen 1994); 2) the proportion of empty stomachs (%*E*, dimensionless),

$$\%E = \frac{N_{\%E}}{N} \quad , \tag{2}$$

where $N_{\%E}$ is the abundance of empty stomachs over a given period (year, month, hour) and N is the abundance of stomachs over the same period; and 3) frequency of food-type occurrence in the stomachs; a first approximation of food type variation in the stomach. Food type variation was evaluated according to i) fish or invertebrate food and ii) food type (e.g. shrimp, amphipod, etc.; Table 6.1) aggregates.

6.2.3 Estimating Food Consumption (Daily Ration, DR)

Estimates of food consumed by fish in the field have been made using a wide range of models that combine stomach content estimates and evacuation rates (He and Wurtsbaugh 1993, Andersen 2001). I have shown that one such model, based on the Pennington method, provides realistic estimates of DR (**Chapter 5**, Pennington 1985) when based on stomach content weight and by including factors that explain variation in consumption (e.g. predator size, temperature and food energy-density). Average food consumption was evaluated as DR using the simplified Pennington method (DR_P', **Chapter 5**),

$$DR_P' = 24 \cdot \left[p_{LTE} \cdot L^{1.44} \cdot e^{0.078T} \cdot E^{-0.86} \cdot \overline{S(t)^a} \right] \quad , \tag{3}$$

where DR_P' is the daily ration (g·day^{-1}), p_{LTE} is the evacuation rate parameter (g^{1-a}· hr^{-1}) = 1.57 x 10^{-3} kJ$^{0.86}$ cm$^{-1.44}$ g$^{-1.36}$ hr^{-1}, L is predator (cod) length (cm), T is temperature (°C), E is the food energy-density (kJ·g^{-1} wet weight), $\overline{S(t)^a}$ is the mean weight of stomach contents (g, see below) and a is the shape parameter (dimensionless) as detailed in **Chapter 5**. Predator length (cm) was chosen as the estimate of predator size to allow for the analysis of DR estimates according to length-at-age (needed for **Chapter 7**). A shape parameter of $a = 0.5$ was used as this demonstrated improved accuracy when predicting modelled DR (**Chapter 5**) relative to other forms (e.g. $a = 0$). I also used bomb calorimetric estimates of food energy-density for cod feeding in the sGSL (Chénard 2004; BSc. Honours student whom I co-supervised). Food energy-density was estimated for

seven fish species (Atlantic mackerel, *Scomber sombrus*, Atlantic herring, *Clupea harengus*, sand lance, *Ammodytes* sp., capelin, *Mallotus villosus*, daubed shanny, *Leptoclinus maculates*, American plaice, *Hippoglossoides platessoides*, and snakeblenny, *Lumpenus lampretaeformis*) and nine invertebrate food types (sea star, whelk, sand dollar, shrimp, sea cucumber, hermit crab, scallop, sea urchin, and basket star) collected in the southern Gulf of St. Lawrence in 2003 (Chénard 2004). Average $S(t)^a$ ($\overline{S(t)^a}_{L,M,Y}$) was estimated for each cod fish length-class (cm, start length-class length L), month (M) and year (Y). $DR_P{'}_{L,M,Y,E}$ was estimated for each $\overline{S(t)^a}_{L,M,Y}$ using mean cod length (cm) and ambient temperature (ºC, **Chapter 4**) with 1) mean (E = *mean*, 4.38 kJ·g^{-1}) and 2) type-specific (E = *type*, proportional for weight of fish, 5.82 kJ g^{-1}, and invertebrate, 2.95 kJ g^{-1}, as food in the stomach) energy-density. The latter was chosen to allow for effects of food energy-density on the estimation of DR (**Chapter 5**). Ambient temperature (ºC) data for cod in the sGSL was obtained as described in **Chapter 4**. DR for fish with length < 40cm was estimated using mean ambient temperature for immature cod and that for fish ≥ 40cm with mean ambient temperature for mature cod (see **Chapter 4**).

6.3 Results

6.3.1 Variation in Cod Stomach Samples

Sampling intensity of cod varied over years with the majority of sampling occurring in 1992 through 1995 and 2001 and 2002 (Fig. 6.2a). The majority of cod stomachs (42%) were sampled during September surveys (Fig. 6.2b) with sampling of some years restricted to the summer/autumn months (i.e. August, September, e.g. 1990, 1991, Fig. 6.3). Due to this seasonal sampling bias, interannual variation in DR estimates was restricted to September sampling (see Section 6.3.3 below). Cod were sampled throughout the day (Fig. 6.2c) with most sampling conducted between 08:00 and 12:00.
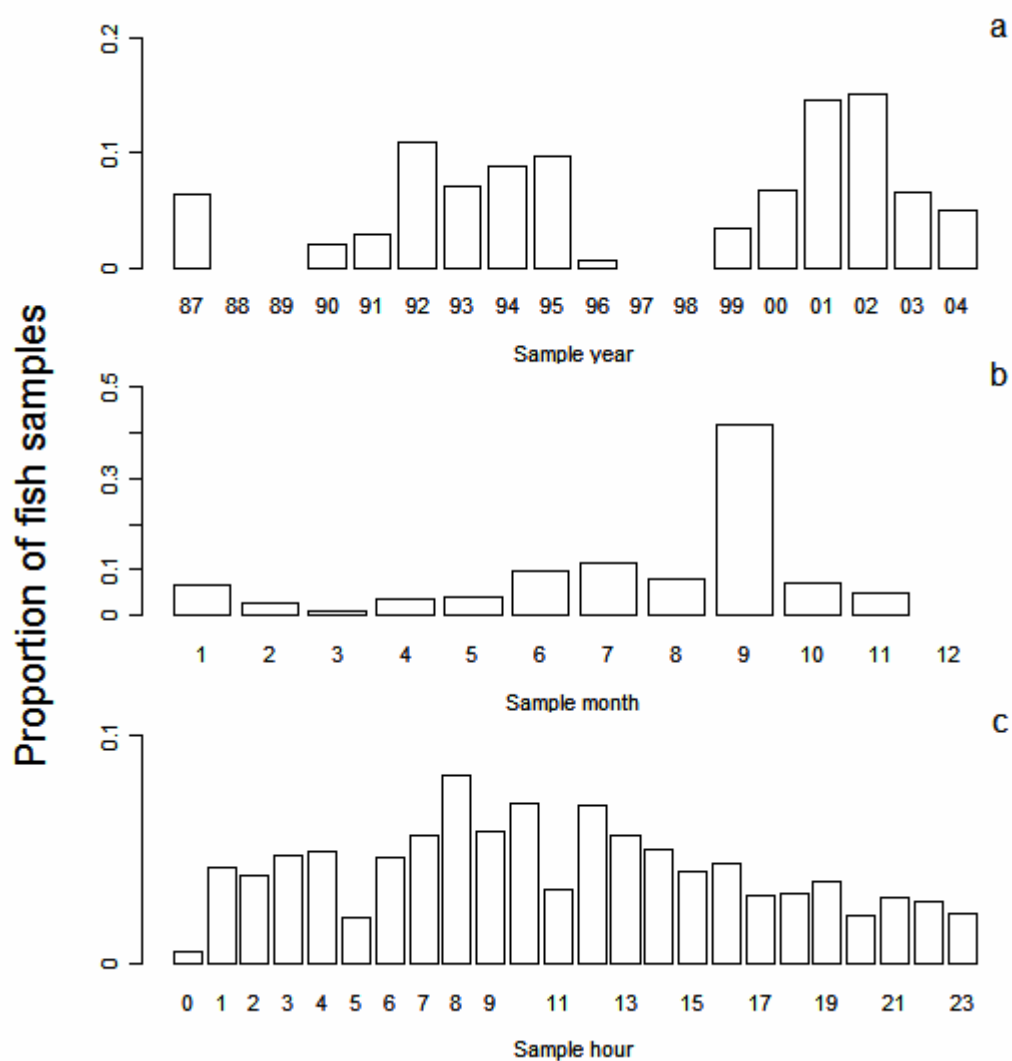
Figure 6.2: Proportion of cod stomach samples by (a) year, (b) month, and (c) hour.
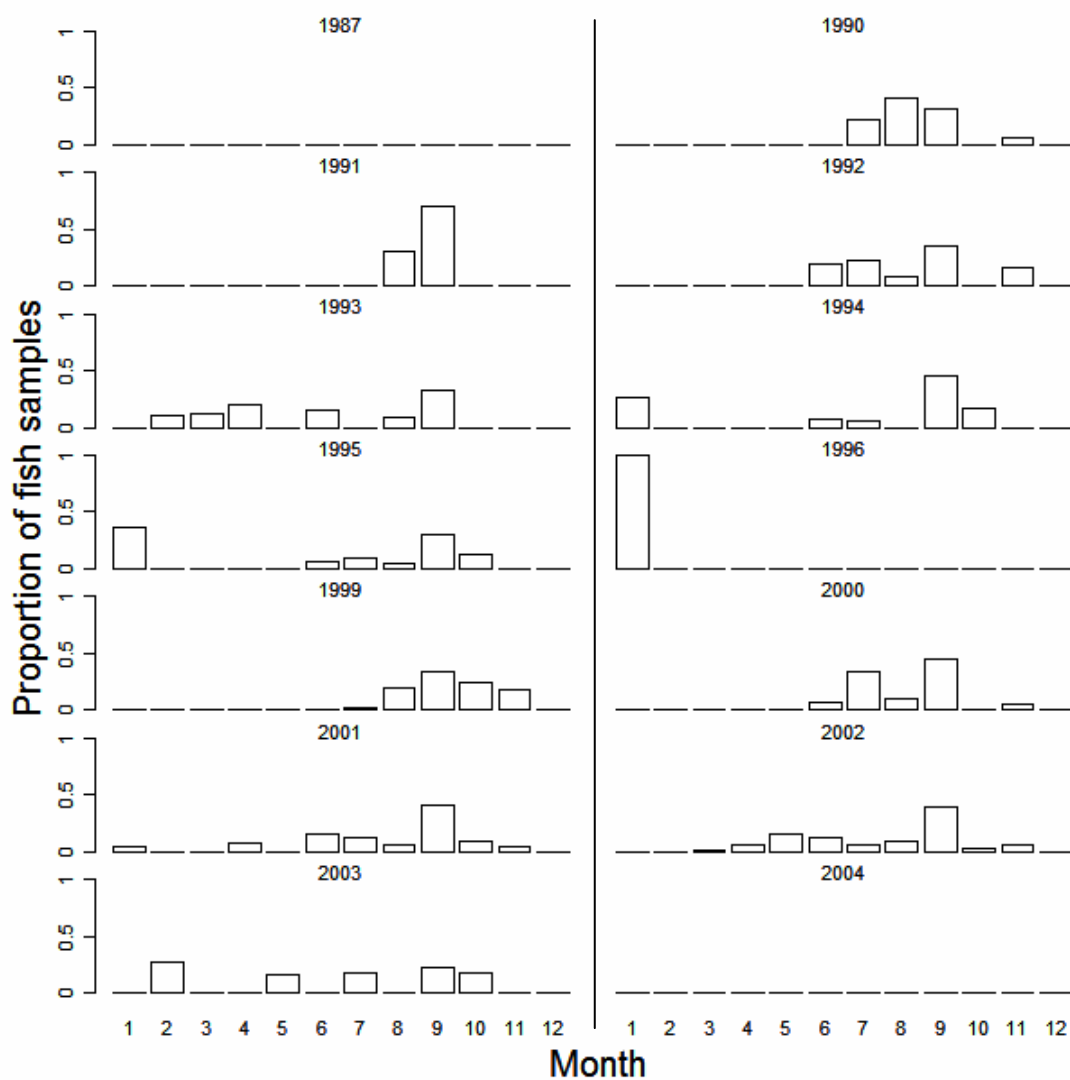
Figure 6.3: Monthly proportions for cod stomach sample collections by month-of-year. Sample months for 1987 stomachs were unavailable.

Sampled cod exhibited a median size of 686g and 42cm (Fig. 6.4) and a weight-at-length relation of $W = 0.007 \cdot L^{3.05}$ (Fig. 6.5), entirely consistent with the Atlantic cod weight-at-length relations shown in Fig. 2.2, **Chapter 2**.
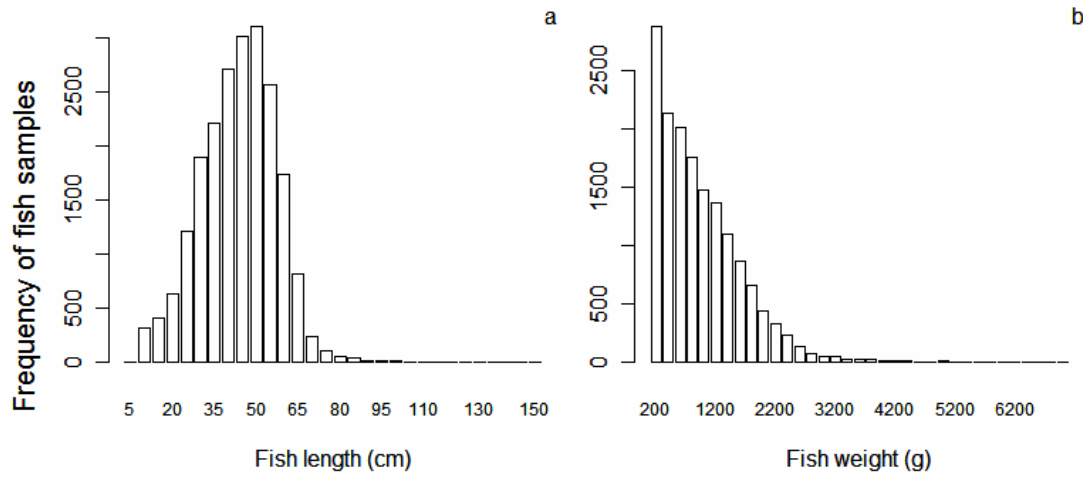
Figure 6.4: Frequency of cod (a) length, cm, and (b) weight, g, of cod providing stomach samples
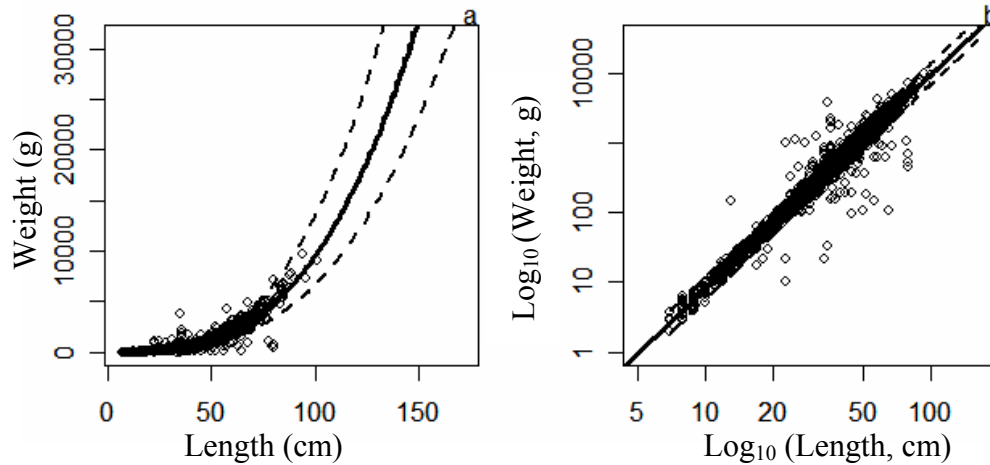
Figure 6.5: Cod weight-at-length relations as arithmetic (a, $W = 0.007 \cdot L^{3.05}$) and $\log_{10}$ (b, $\log_{10} W = -2.129 + 3.05 \cdot \log_{10} L$). Outliers may be due to bias in sampling season (Figure 6.2b) as fish weight varies significantly with season.

While the length frequency distribution of cod samples varied in time (Fig. 6.6) there was no significant trend in median length over years (Linear regression, P = 0.65). Median length (33 cm) was lower in February than other months (40 to 48 cm). There was no significant trend in median length with collection hour-of-day (Linear regression, P=0.48) though the median length at 01:00 (28 cm) and 19:00 (33 cm) was lower than other sampling hours (37 to 46 cm).
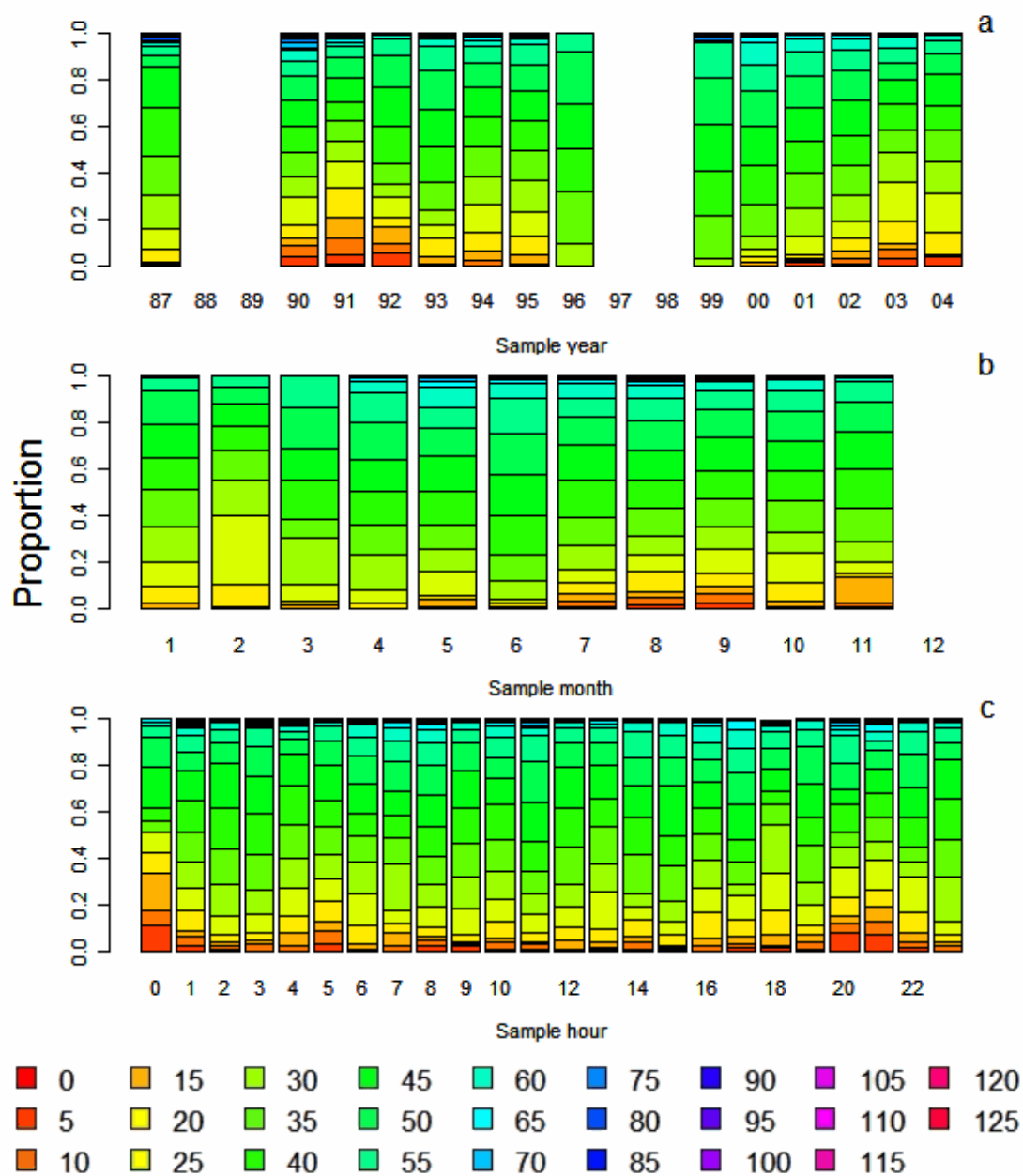
Figure 6.6: Proportion of length (colours, 5 cm length-class start length) by (a) year, (b) month, and (c) hour.

6.3.2 Variation in Stomach Contents

While stomach fullness varied among years (Kruskal Wallis, P < 0.0001) there was no trend in stomach fullness among years (Linear regression, P = 0.37; Fig. 6.7a). There was a seasonal trend in SFI within a year (Kruskal Wallis, P < 0.001, Fig. 6.7b) with highest SFI in the July stomach samples. Median stomach fullness (0.12 g·cm^{-3}) in summer (July) was an order of magnitude higher than winter (January: 0.011 g·cm^{-3}). Stomach fullness was different among hours (Kruskal-Wallis, P < 0.0001) with a slight decrease in SFI with hour-of-day collection (Linear Regression, r^2=0.29, P = 0.007; Fig. 6.7c). However, as this result would require fish feeding specifically from 23:00 to 0:00 it is more likely this decline is due to a artifact from non-uniform sampling (Figure 6.2c).
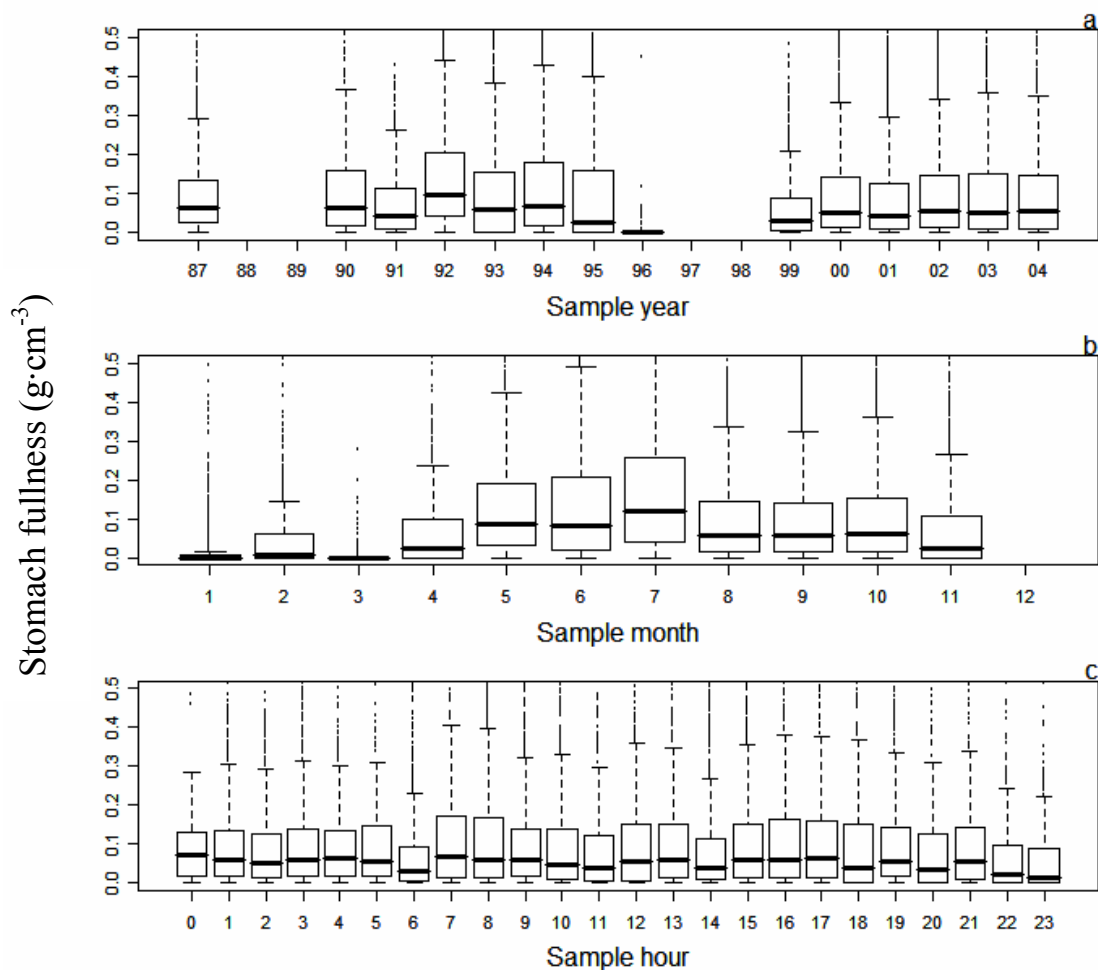
Figure 6.7: Box and whisker plots of stomach fullness (g·cm⁻³) over sample collection (a) year, (b) month, and (c) hour. Horizontal lines are lower quartile, median and upper quartile while whiskers denote extent of data with outliers as ".".

As might be expected, the variation in %E over time (year, month, hour, Fig. 6.8) was negatively correlated with SFI (Fig. 6.7). %E was higher in stomachs from 1993, 1995, and 1996 (Fig. 6.8a) as well as in winter samples (January, February, March, April and November; Fig. 6.8b). Also %E demonstrated a slight increased with hour-of-day collection (Linear regression, adjusted r^2=0.34, P = 0.002; Fig. 6.9c). However, and as above, this may be a sampling artifact.
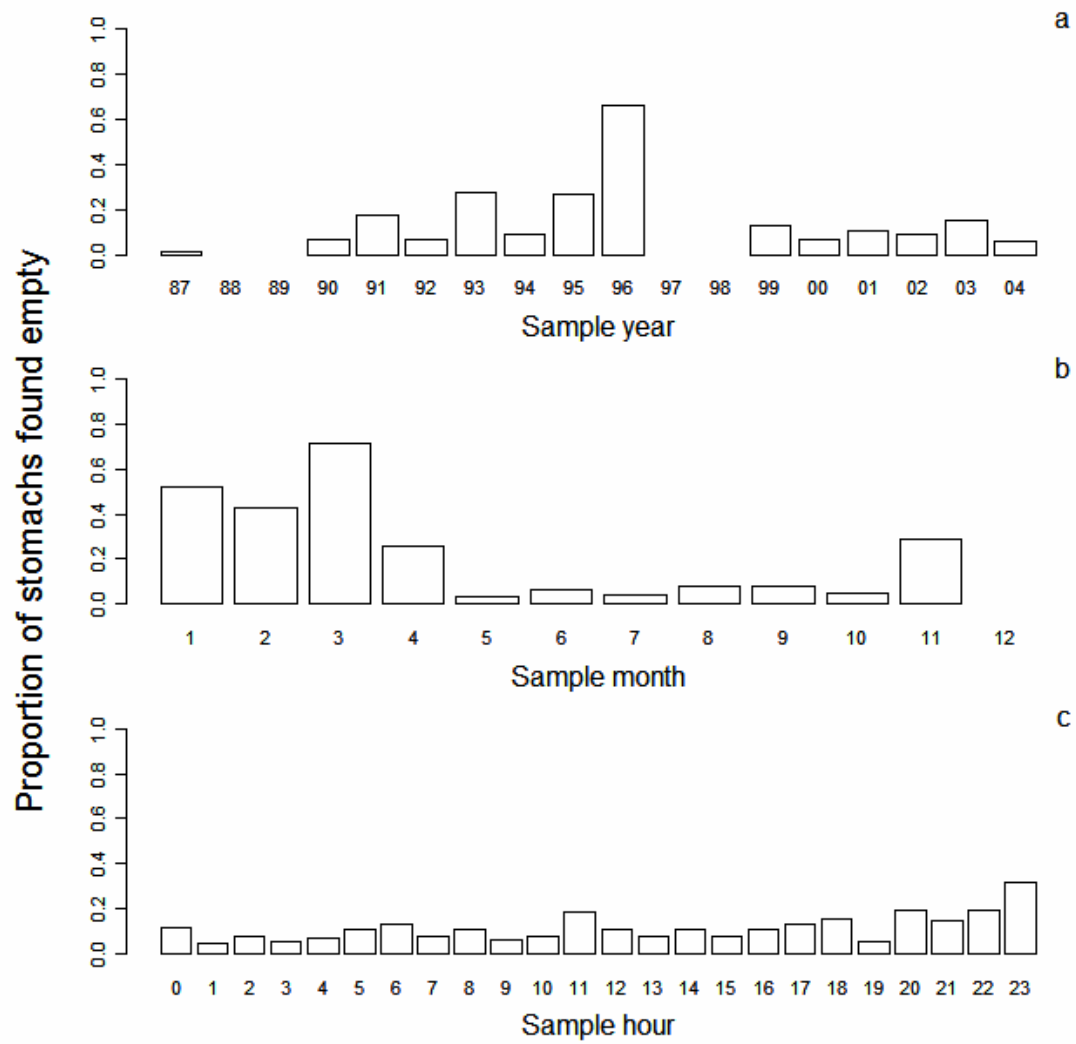
Figure 6.8: Proportion of empty stomachs (%E) over sample (a) year, (b) month, and (c) hour.

Invertebrate food occurred more frequently than fish food in the cod stomachs (86% vs. 14% occurrence respectively, Fig. 6.9). Food type occurrence throughout the study period was highest (representing 77% of total food type occurrence, Fig. 6.10) for shrimp (21%), amphipod (20%), fish (14%), mysid (13%), and worm (10%) food types. The remaining (23%) food type occurrence was made up of 14 other food types (see Fig. 6.10).
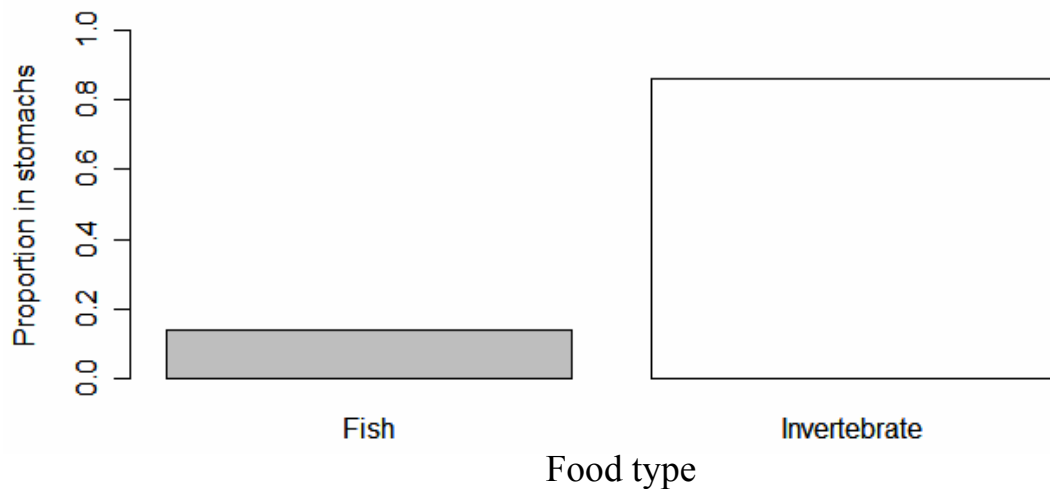
Figure 6.9: Proportion of fish (grey) and invertebrate (white) food in the cod stomach sample collections.
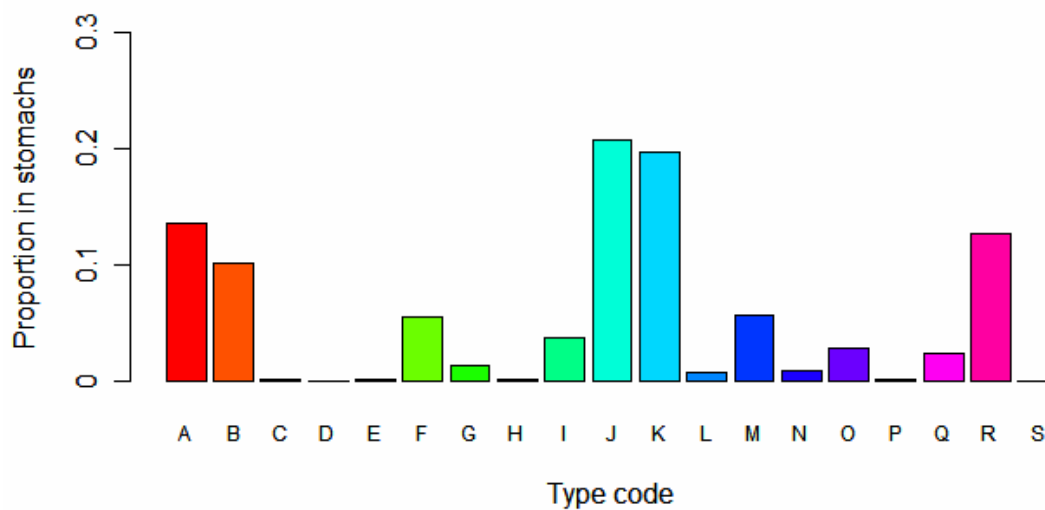
Figure 6.10: Proportion of food type in the cod stomach sample collections with (A) fish, (B) worm, (C) algae, (D) poriferan, (E) cnidarian, (F) mollusc, (G) echinoderm, (H) bryozoan, (I) miscellaneous, (J) shrimp, (K) amphipod, (L) copepod, (M) crab, (N) miscellaneous crustacean, (O) euphasiid, (P) isopod, (Q) cumacean, (R) mysid and (S) ctenophore (Table 6.1)

The type of food in the stomachs varied systematically with predator (cod) length (Fig. 6.11a). The proportional occurrence of fish increased with cod size (Logistic regression, $P_{fish} = \dfrac{1}{1+e^{(4.2-0.053 \cdot L)}}$, P < 0.0085; Fig. 6.11). There was a decrease in many of the invertebrate food types (i.e. worms, shrimp, amphipods, copepods, miscellaneous crustaceans, euphausiids, isopods, cumaceans, mysids) with increasing cod size (Fig. 6.12; Approximate linear regressions, $0.18 \geq r^2 \leq 0.75$, $0.033 \geq P \leq 0.001$; Table 6.2).
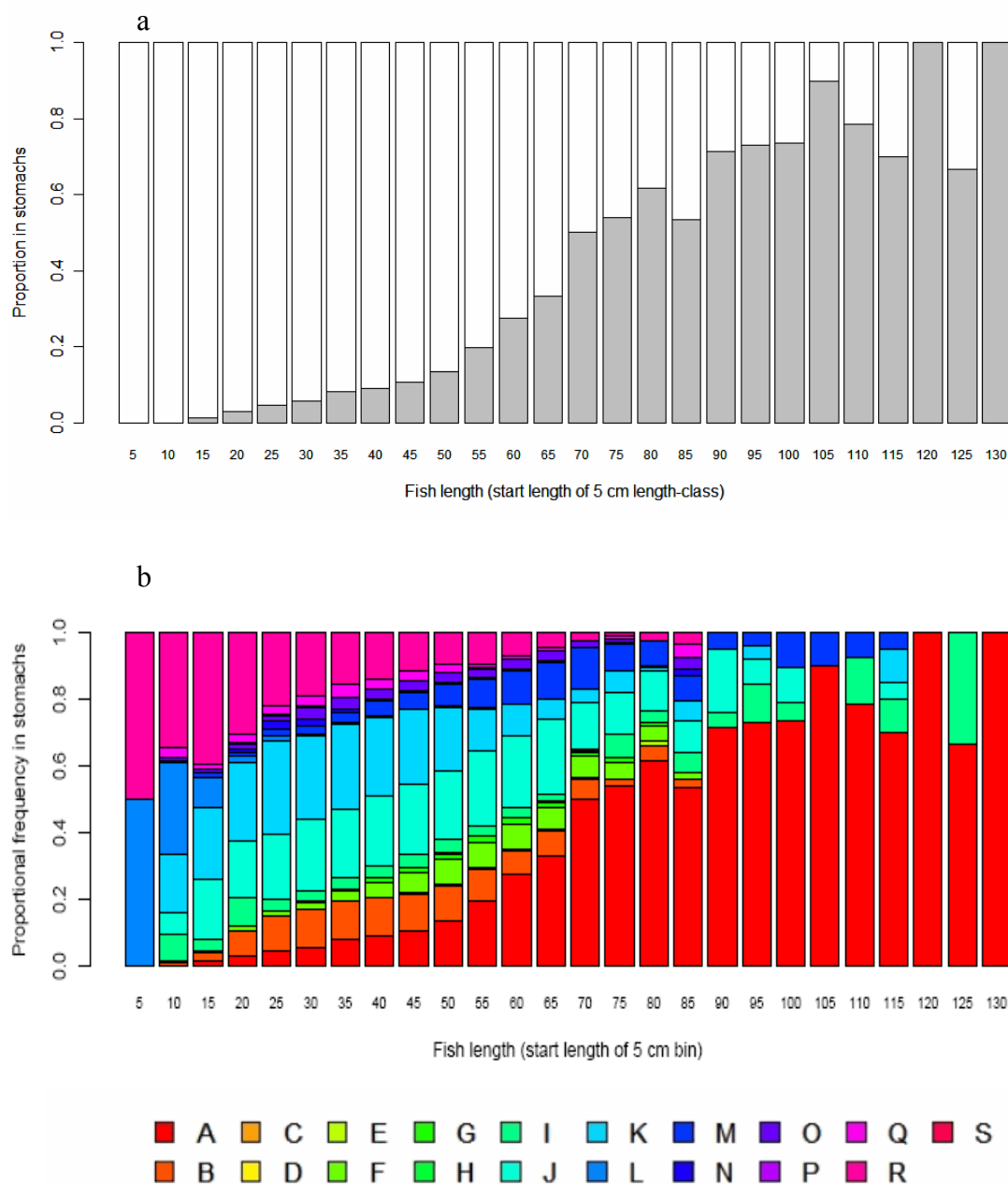
Figure 6.11: Variation in proportion of food types in cod stomachs as a function of cod length for a) fish (grey) and invertebrate (white) types and for b) food type: (A) fish, (B) worm, (C) algae, (D) poriferan, (E) cnidarian, (F) mollusc, (G) echinoderm, (H) bryozoan, (I) miscellaneous, (J) shrimp, (K) amphipod, (L) copepod, (M) crab, (N) miscellaneous crustacean, (O) euphasiid, (P) isopod, (Q) cumacean, (R) mysid and (S) ctenophore (Table 6.1).

Table 6.2: Parameters of linear regression approximation for variation in proportional occurrence of invertebrate food type among predator length classes. Parameters of non-significant regressions (P > 0.05) are excluded.

Type code	Food type	Linear regression parameters Proportional occurrence = β·Length-class start length + α			
		Slope (β, cm^{-1})	Intercept (α)	r^2	P-value
B	Worm	-0.00072	0.093	0.35	0.0014
C	Algae				0.28
D	Poriferan				0.23
E	Cnidarian				0.84
F	Mollusc				0.20
G	Echinoderm				0.28
H	Bryozoan				0.47
I	Miscellaneous				0.11
J	Shrimp	-0.0013	0.21	0.32	0.0023
K	Amphipod	-0.0020	0.24	0.54	<0.0001
L	Copepod	-0.0015	0.14	0.26	0.0073
M	Crab				0.29
N	Miscellaneous crustacean	-7.4×10^{-5}	0.010	0.18	0.033
O	Euphausiid	-0.00019	0.026	0.26	0.0079
P	Isopod	-2.9×10^{-5}	0.0030	0.45	0.00019
Q	Cumacean	-0.00022	0.027	0.40	0.00047
R	Mysid	-0.0032	0.32	0.75	<0.0001
S	Ctenophore				0.20

Among all stomach samples, food type occurrence exhibited systematic variation among years with an increase in the proportional frequency of fish-type food to a maximum of 19% in 2000 followed by a systematic decline (Fig. 6.12a). This pattern was maintained when examined within length-classes (e.g. 45 cm through 55 cm length-classes, Fig. 6.13) to avoid the influence of cod length on food-type occurrence (Table 6.2). Occurrence of invertebrate-type food types also varied among years (Fig. 6.12b) with mollusc, echinoderm, shrimp, crab and mysid food types increasing among years and miscellaneous, amphipod, miscellaneous crustacean and cumacean food types decreasing among years (Linear regression approximation, Table 6.3).

Figure 6.12: Variation in proportion of food type in cod stomach collections as a function of sample collection year for a) fish (grey) and invertebrate (white) types, and for b) food type with (A) fish, (B) worm, (C) algae, (D) poriferan, (E) cnidarian, (F) mollusc, (G) echinoderm, (H) bryozoan, (I) miscellaneous, (J) shrimp, (K) amphipod, (L) copepod, (M) crab, (N) miscellaneous crustacean, (O) euphasiid, (P) isopod, (Q) cumacean, (R) mysid and (S) ctenophore (Appendix 6.5).
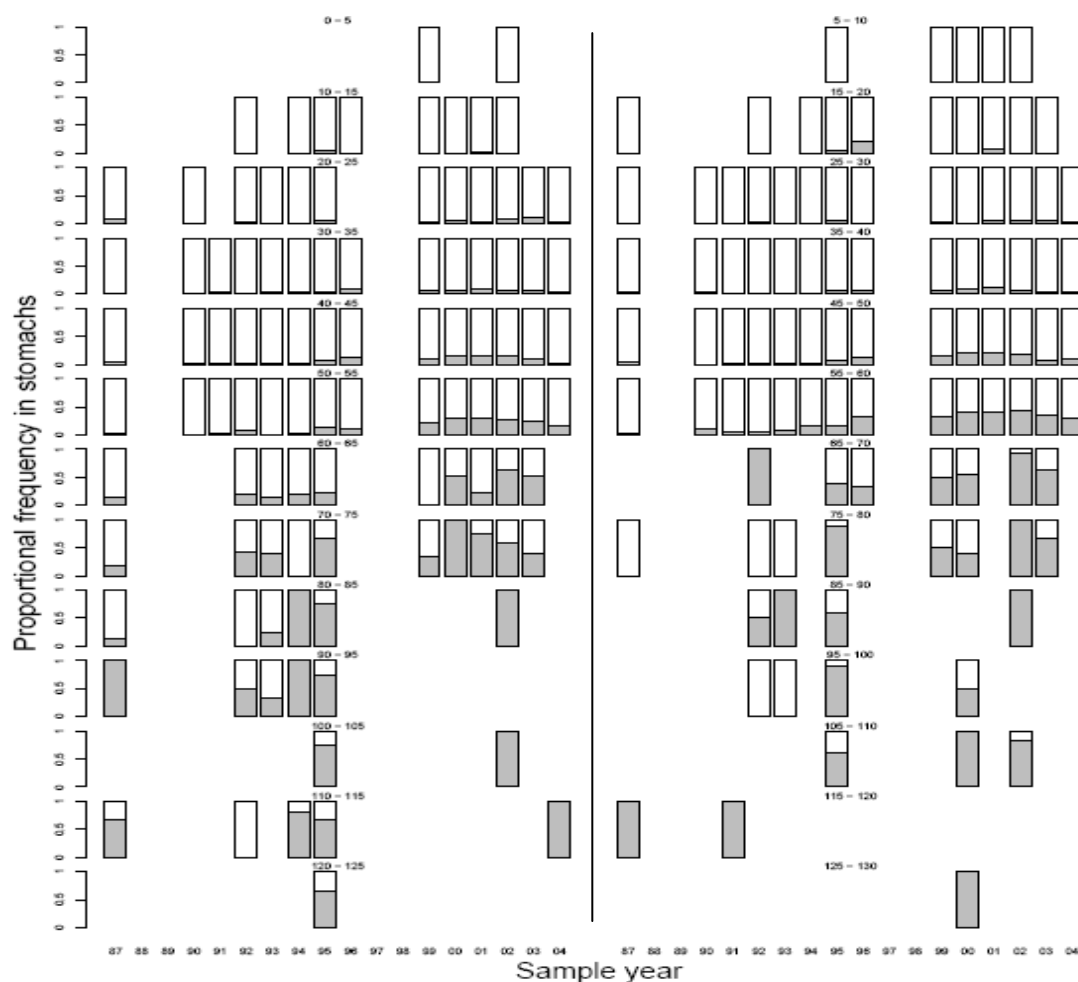
Figure 6.13: Variation in proportion of food type in cod stomach collections with sample year for fish (grey) and invertebrate (white) types within length-classes (5cm length-classes, labels are start length-class length).

Table 6.3: Parameters of linear regression approximation for variation in proportional occurrence of food type with sample collection year. Shading indicates regressions with positive slope. Parameters for non-significant regressions (P > 0.05) are excluded.

Type code	Food type	Linear regression parameters Proportional occurrence = β·year + α			
		Slope (β)	Intercept (α)	r^2	P-value
A	Fish	0.0085	-16	0.53	0.0031
B	Worm				0.39
C	Algae				0.53
D	Poriferan				0.67
E	Cnidarian				0.20
F	Mollusc	0.0053	-11	0.68	0.00028
G	Echinoderm	0.00070	-1.4	0.32	0.034
H	Bryozoan				0.33
I	Miscellaneous	-0.0054	11	0.69	0.00024
J	Shrimp	0.013	-26	0.54	0.0029
K	Amphipod	-0.026	52	0.80	<0.0001
L	Copepod				0.11
M	Crab	0.0018	-3.4	0.53	0.0032
N	Miscellaneous crustacean	-0.0010	2.1	0.49	0.0051
O	Euphausiid				0.14
P	Isopod				0.35
Q	Cumacean	-0.0049	9.9	0.45	0.0084
R	Mysid	0.0088	-17	0.57	0.0018
S	Ctenophore				n/a

Among all stomach samples, food-type occurrence exhibited variation among months with the highest proportional frequency of fish occurring in May (28%, Fig. 6.14a). However, limited evidence for this trend was found when stomach content within length-classes was examined with month (Fig. 6.15). Invertebrate food-types exhibited seasonality in frequency of occurrence in the stomachs (Fig. 6.14b). The month of May samples demonstrated minimum occurrence of amphipod and mysid food while month of March samples exhibited minimum occurrence of worm, mollusc and echinoderm food.
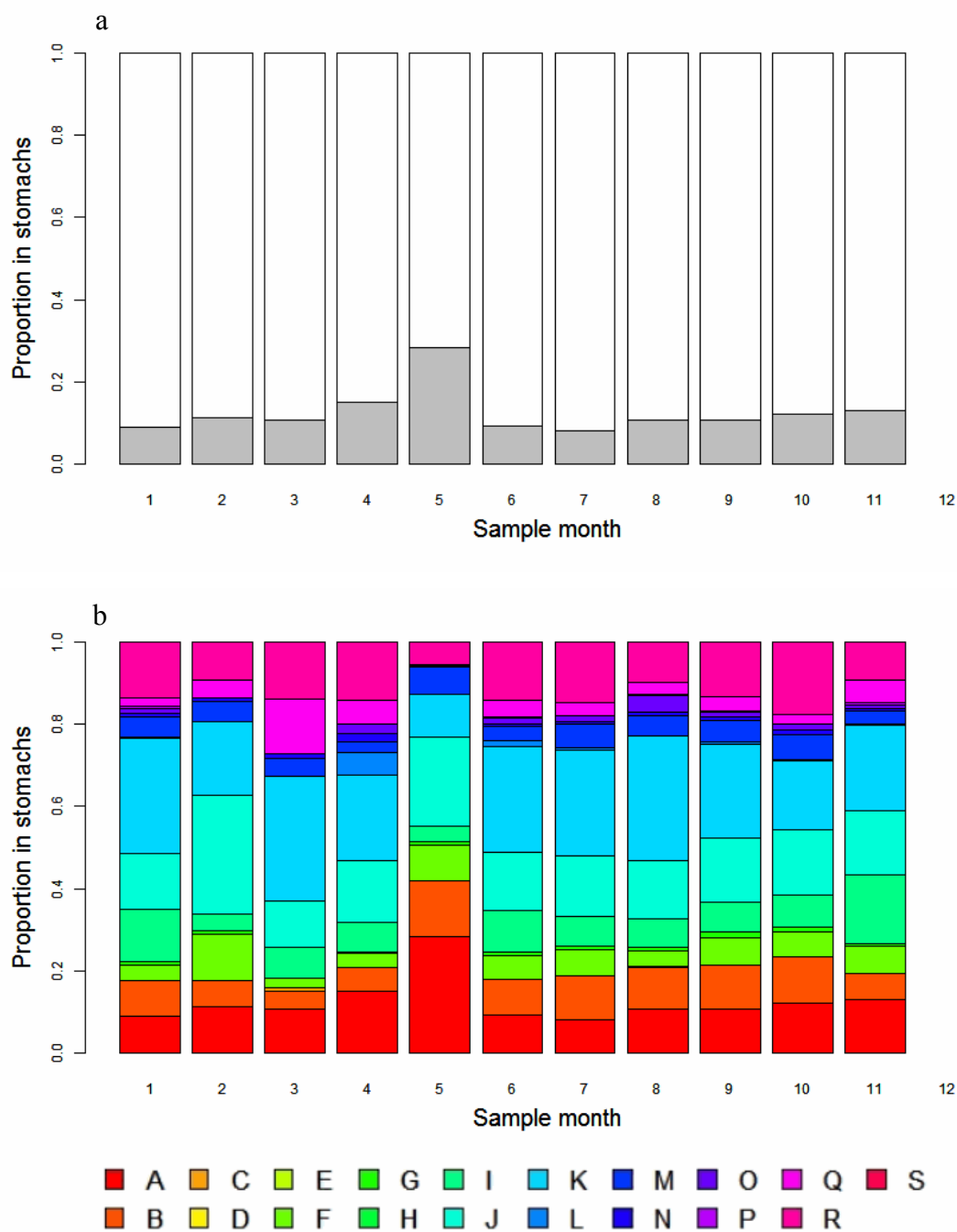
Figure 6.14: Variation in proportion of food type in cod stomachs as a function of sample collection month for a) fish (grey) and invertebrate (white) types, and for b) food type: with (A) fish, (B) worm, (C) algae, (D) poriferan, (E) cnidarian, (F) mollusc, (G) echinoderm, (H) bryozoan, (I) miscellaneous, (J) shrimp, (K) amphipod, (L) copepod, (M) crab, (N) miscellaneous crustacean, (O) euphasiid, (P) isopod, (Q) cumacean, (R) mysid and (S) ctenophore (Table 6.1).
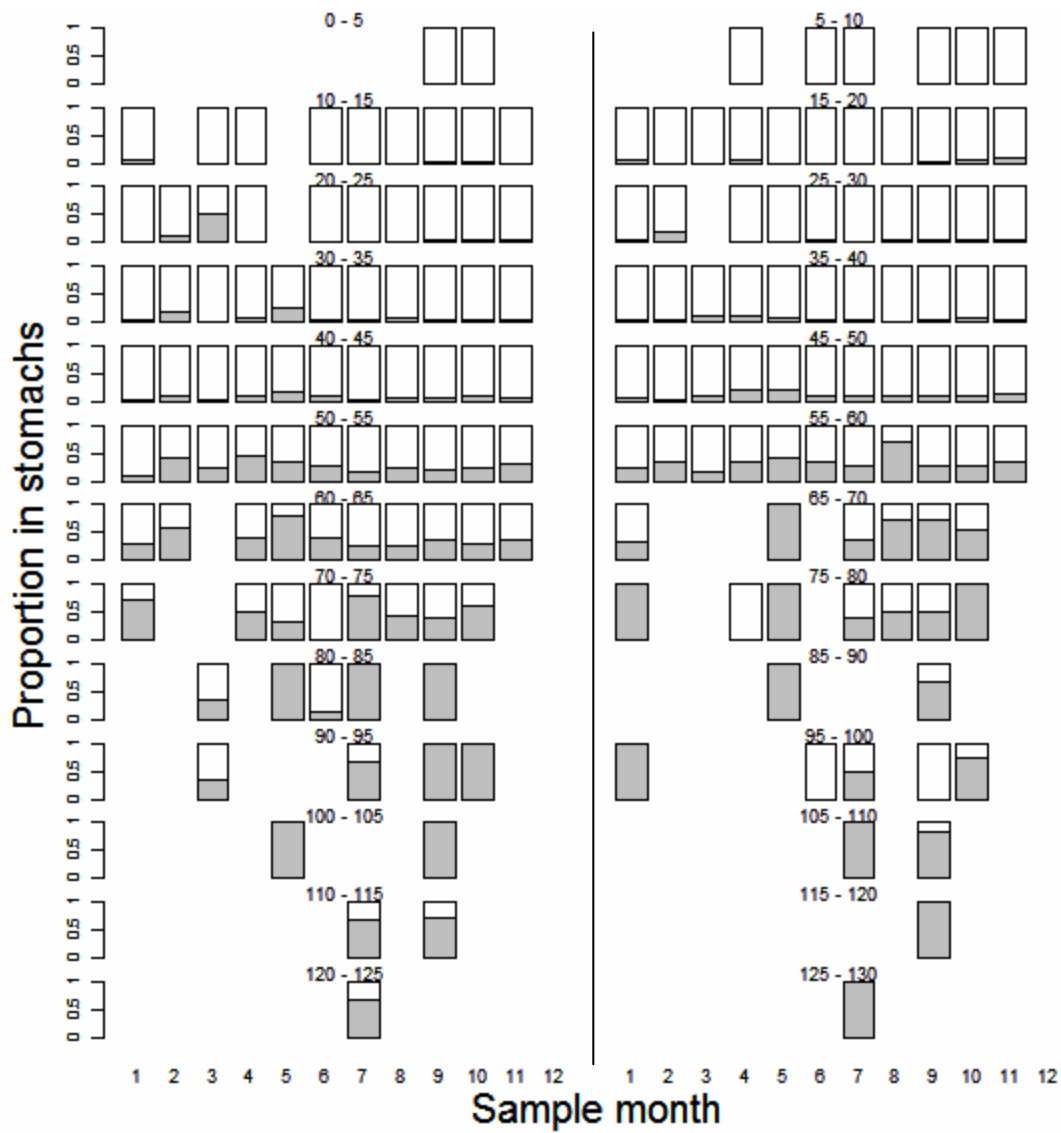
Figure 6.15: Variation in proportion of food type in cod stomachs with sample collection month for fish (grey) and for invertebrate (white) types within length-classes (5cm length-class, labels are start length of length-class, cm).

Food-type in the stomach samples exhibited variation with sample-collection hour for fish-type food (Fig. 6.16a) as well as for some invertebrate-type food (Fig. 6.16b) following two general patterns. Fish, mollusc, shrimp and mysid food types exhibited maximum occurrence in the stomachs during daylight (approximately 06:00 through 18:00) while amphipod, euphausiid, cumacean and miscellaneous crustacean food-types indicated maximum occurrence in the stomachs during night (approximately 23:00 through 05:00).
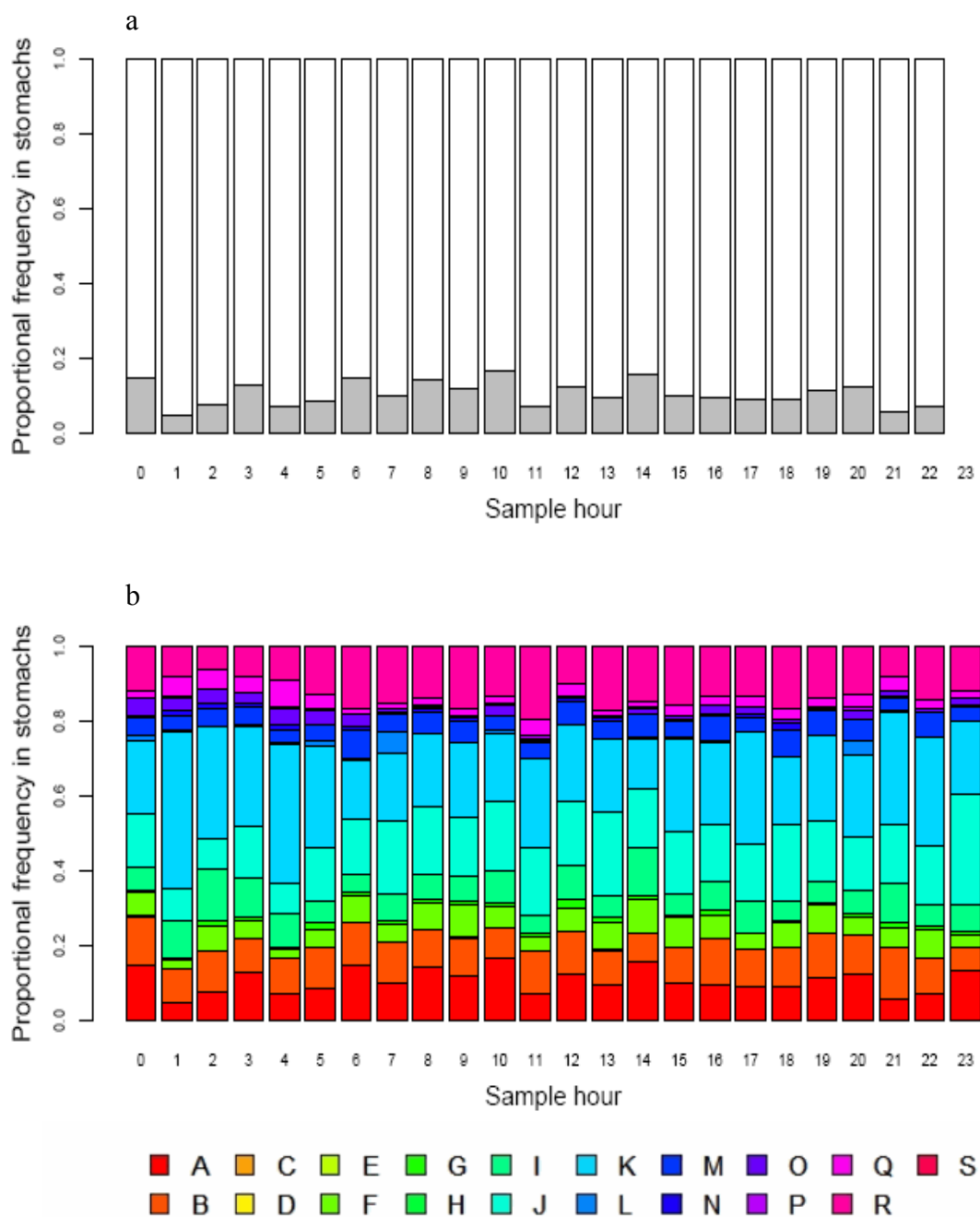
Figure 6.16: Variation in proportion of food type in cod stomachs as a function of sample collection hour for a) fish (grey) and invertebrate (white) food types, and for b) food types: (A) fish, (B) worm, (C) algae, (D) poriferan, (E) cnidarian, (F) mollusc, (G) echinoderm, (H) bryozoan, (I) miscellaneous, (J) shrimp, (K) amphipod, (L) copepod, (M) crab, (N) miscellaneous crustacean, (O) euphasiid, (P) isopod, (Q) cumacean, (R) mysid and (S) ctenophore (Table 6.1).

6.3.3. Variation in Daily Ration

Average monthly DR estimated using the simplified Pennington method (DR_P', g·day^{-1}, eqn. 3) varied seasonally (Fig. 6.17) with maximum consumption in mid-July (month = 7.5, Fig. 6.18). For predators (cod) < 40cm, DR estimates calculated using average food energy-density was lower than that estimated using the type-specific food energy-density estimates (Shapiro-Wilks P > 0.55, Paired t-test P < 0.0001). Conversely, for predators (cod) ≥ 40cm, DR estimates calculated using average food energy-density was higher than that estimated using the type-specific food-energy density estimates (Shapiro-Wilks P > 0.40, Paired t-test P = 0.0005).
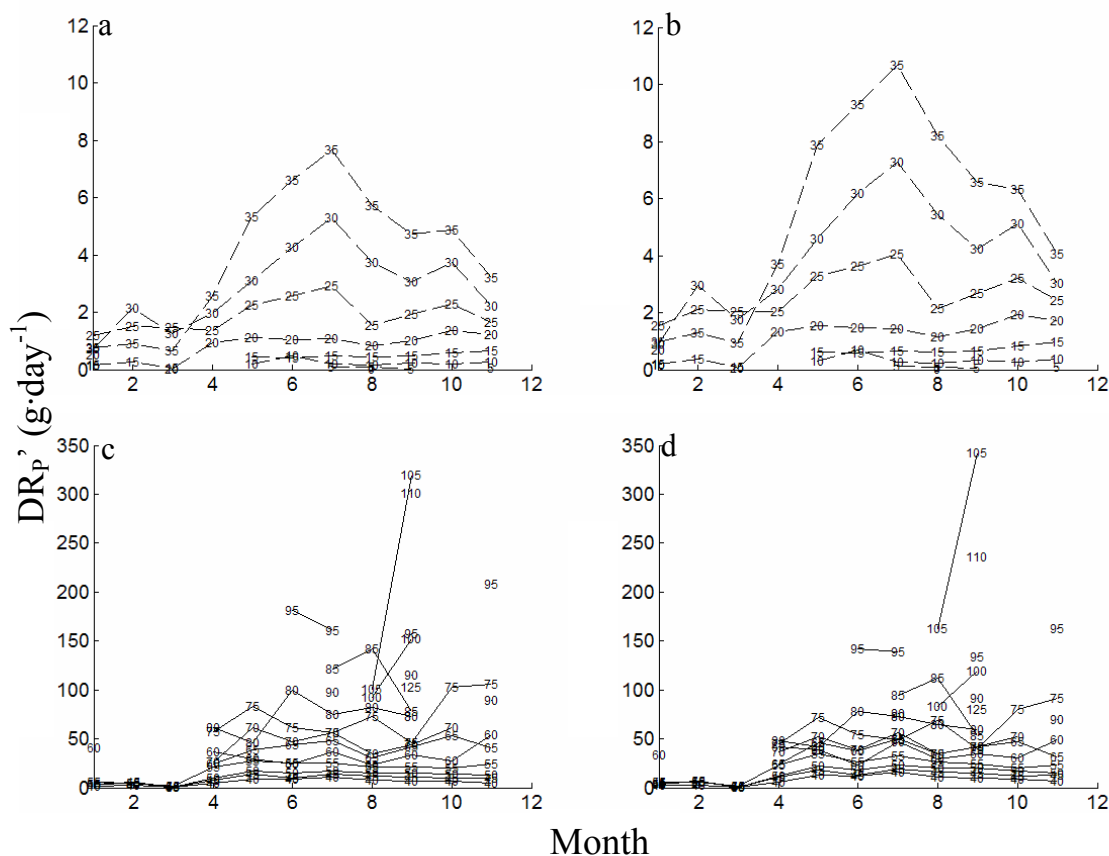
Figure 6.17: Monthly daily ration (DR$_P$'; g·day^{-1}) averaged over all years by cod length-class (5cm length-class, labels are length-class start length) using mean (a, length-class length < 40cm; c, length-class length ≥ 40cm) and type-specific food energy-densities (b, length-class length < 40cm; d, length-class length ≥ 40cm).
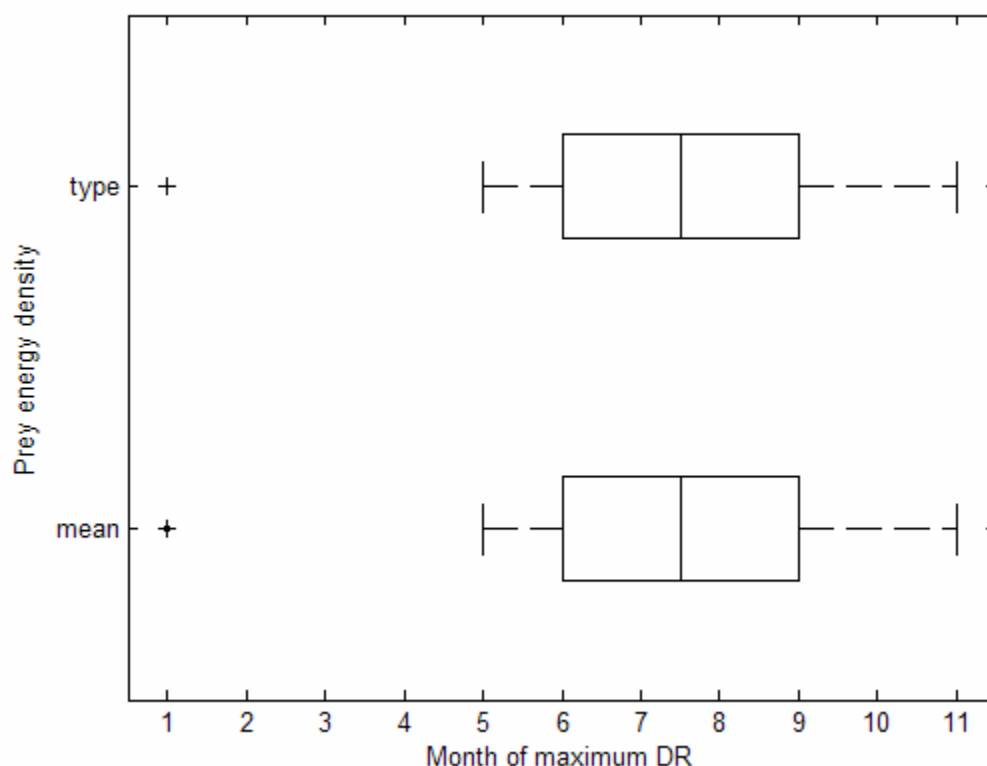
Figure 6.18: Box and whisker plots of timing (month) of maximum DR_P' (g·day^{-1}) among cod length-classes using average and type-specific food energy-densities. Vertical lines are lower quartile, median and upper quartile while whiskers denote extent of data with outliers as +.

Due to sampling-year constraints, an examination of inter-annual variation in September DR resulted in two time-series: early-1990s (1990 through 1995) and early-2000s (1999 through 2004, Fig. 6.19). September DR estimated with average food energy-density was similar between time periods for all length-classes (Fig. 6.19ac; Shapiro-Wilks $P < 0.0001$; Wilcoxon Rank Sum $P > 0.24$) except 35-40cm where September DR in the early-1990s was higher than that in the early-2000s (Shapiro-Wilks $P < 0.0001$; Wilcoxon Rank Sum $P = 0.0043$). During the early-1990s, cod 15-20cm and 40-50cm exhibited increasing September DR with year (Fig. 6.19ac; Linear regression, $0.69 \leq r^2 \leq 0.93$, $0.0018 \leq P \leq 0.039$). During the early-2000s there was no trend in

September DR over years within length-classes (Fig. 6.19ac; Linear regression, $0.09 \leq P \leq 0.97$). All results are similar for DR estimated with type-specific food energy-densities (Fig. 6.19bd).
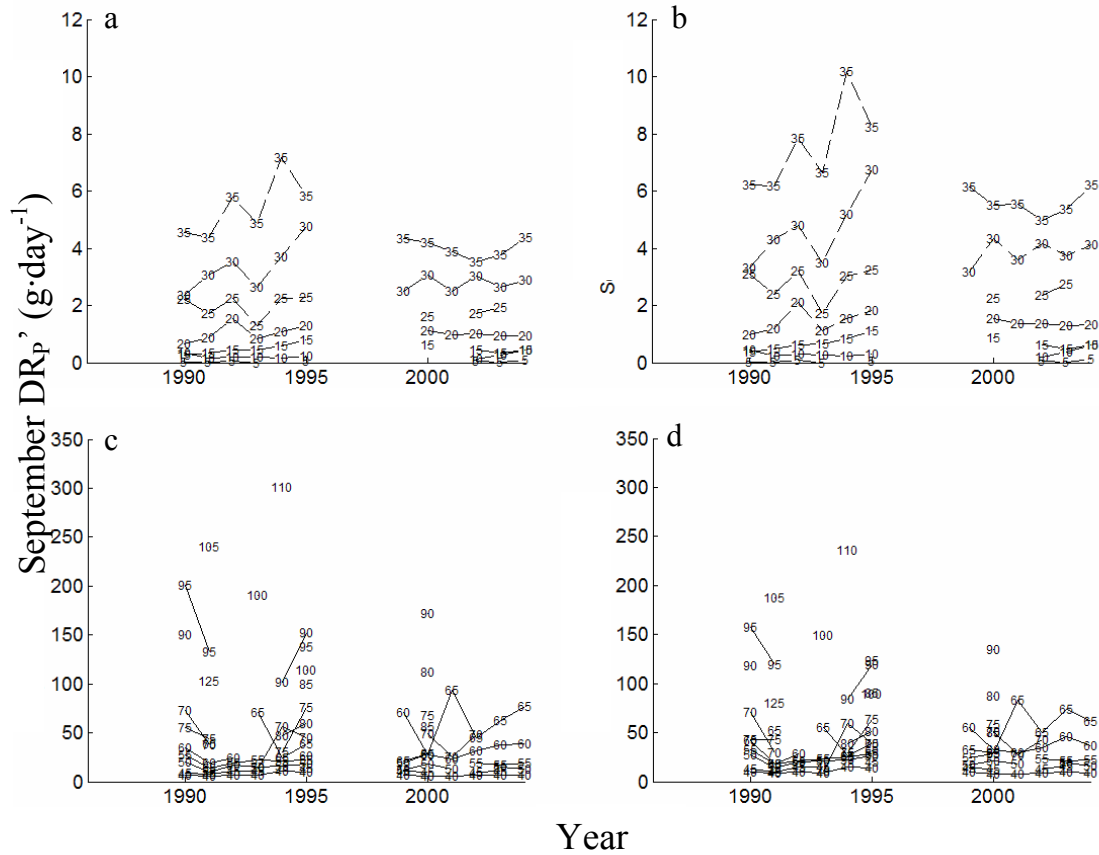
Figure 6.19: September DR (g·day^{-1}) by year and cod length-classes (5cm length-class, labels are length-class start length) using mean (a, length < 40cm; c, length ≥ 40cm) and type-specific food energy-densities (b, length < 40cm; d, length ≥ 40cm).

6.4 Discussion

Quantitative analysis of southern Gulf of St. Lawrence cod stomach contents demonstrated significant variations in diet and DR with cod size and at a number of temporal scales (year, month, and hour). Larger cod exhibited higher stomach content weight and proportion of fish food in the stomach as was found in previous diet studies on sGSL cod (Powles 1958, Waiwood and Majkowski 1984, Schwalme and Chouinard 1999) as well as on other cod stocks (e.g. Flemish Cap, Newfoundland, Casas and Paz 1996). In particular, Powles (1958) found small cod (11-30cm) exhibited a diet mainly of crustaceans (mysids, euphasiids and amphipods) with no fish as food found in stomachs of cod smaller than 19cm, as observed here (Fig. 6.11). Thus, I conclude food type occurrence and subsequent DR estimates must be adjusted for length frequency of cod in the stomach samples before inferences can be made about temporal variation in food consumption in relation to growth.

Previous studies have demonstrated inter-annual variation in stomach contents for sGSL cod. For example, a decrease in ambient ocean euphausiid abundance during 1990 to 2000 was correlated with a decrease in euphausiids in cod stomachs and increased feeding on mysids and shrimp (Hanson and Chouinard 2002). I found increases in fish, mollusc, echinoderm, shrimp, crab and mysid food types over the sampling years (1987 through 2004 excluding 1988, 1989, 1997 and 1998) while miscellaneous, amphipod, miscellaneous crustacean, and cumacean food types decreased. While this may be an indication of changes occurring in the prey field of the fish, it may also be the result of sampling limitations. The stomach sample collections used in this study are biased towards September collections with some sampling-years restricted to this month (e.g. 1990, 1991). While there was little evidence that this bias would result in a bias in median length of the cod collected (Fig. 6.6), variation in sample month among years may result in uncertainties in estimates of inter-annual variation in DR and food type consumed as estimates of stomach fullness, proportion of empty stomachs and occurrence of some food types varied with sample month (Fig. 6.7b, 6.8b, 6.14). For example, while there was much variation in %E among years (Fig. 6.8a), those years with the highest %E (e.g. 1993, 1995, 1996) were years dominated by winter sampling (Fig. 6.3). In addition, fish and invertebrate (amphipod, mysid, mollusc, echinoderm) food types

varied with season (6.14). Thus, I conclude that sampling limitations must be considered before variation in SFI, %E or food type in the diet can be legitimately considered as an indication of a changing prey field.

As mentioned above, intra-annual variation in SFI, %E and food-type occurrence was demonstrated in the cod stomach samples. SFI reached a maximum in July with little feeding during winter months (January to March) in accord with previous studies (Schwalme and Chouinard 1999). Accordingly, %E was highest during winter months (55% from January to March) in agreement with the published literature for cod in this region (64% from December to April in Schwalme and Chouinard 1999). Limited feeding in winter months may be the result of seasonal changes in the available prey field. Invertebrate prey availability follows the timing of productivity in the sGSL while benthic invertebrates are likely less available in the overwintering grounds outside the sGSL than within the sGSL in the summer (Waiwood and Majkowski 1984, Schwalme and Chouinard 1999). While it is likely that fish prey are present in the overwintering grounds, it is hypothesized that they may be occupying different depths than the overwintering cod (e.g. herring, Chouinard 1994). Thus, I suggest that seasonal variation in SFI, %E and resulting food type occurrence is due to variations in temporal and/or spatial overlap of cod with their prey field.

Cod stomachs exhibited some variation in food-type occurrence with collection hour. Fish, mollusc, shrimp and mysid food occurred more frequently in stomachs collected during daylight while amphipod, euphausiid, cumacean and miscellaneous crustacean food occurred more frequently in stomachs collected during the night. As cod length did not differ with collection hour (Fig. 6.6), this may be the result of variation in prey capture rates due to a combination of light intensity and prey swimming ability (i.e. fast swimmers such as fish prey are only catchable during high light intensities). Juvenile cod are visual feeders (Tilseth and Ellertsen 1984). In addition, prey capture potential has been shown to vary with light intensity for other fish predators (e.g. Atlantic salmon, *Salmo salar*, Fraser and Metcalfe 1997). Thus, I suggest that diel variation in diet may be the result of variations in prey capture probability among food types.

For cod < 40cm, DR estimates made using average food energy-density were lower than those made using type-specific food energy-densities as the type-specific food

energy densities allow for the effect of a low fish : invertebrate ratio in the diet of small cod (i.e. small cod eat more food but the food has lower energy-density). Accordingly, for cod ≥ 40cm, using type-specific food energy-densities results in DR estimates lower than those estimated using an average food energy-density as large cod are consuming a higher fish : invertebrate ratio (i.e. large cod eat less food but the food has higher energy-density). Thus, I conclude that including food energy-density information specific to the food types in the stomach results in significantly different (and potentially improved) DR estimates, even when using broad aggregate food-classes; e.g. fish vs. invertebrate food.

Following trends in SFI, DR varied seasonally with maximum consumption occurring in mid-July. September DR was examined among years as this was the most consistently sampled month. With few exceptions (e.g. 15-20 cm and 40-50 cm cod in the early-1990s) there was little variation in the September DR among sampling years for a standard predator (cod) length. Moreover, DR estimates for the early-2000s were constant for all length classes. As mentioned above, there is seasonality in DR and food type occurrence in the cod stomachs. Thus, estimates of yearly DR variation may differ from these September-only results when other sampling months are included.

This study presents the first detailed examination of the wealth of data available in the DFO cod stomach database at the Gulf Fisheries Centre. I have described intra- and inter-annual and length-specific trends in Atlantic cod consumption (food type and DR) that may prove essential for studies of the sGSL ecosystem. In particular, my description of length-specific variation in cod feeding can be combined with information on the length distribution of the stock to aid in the characterization of the ecological impacts of Atlantic cod feeding in the sGSL. By recoding the database in unique record format the data may now be mined for other investigations related to sGSL cod food consumption such as quantifications of spatial variations in stomach contents and species-specific prey consumption. In addition stomach contents may now be examined in relation to data on the prey field available to the cod to assess prey selectivity, predator – prey interactions (He and Wurtsbaugh 1993) as well as the use of predators as samplers of the prey environment (Fahrig et al. 1993). For the purposes of this thesis I have restricted my analysis to quantitative estimation of inter- and intra-annual variation in stomach contents

(e.g. fish vs. invertebrate food occurrence) and associated DR. The results of this chapter provide estimates of relative changes in food consumption by sGSL cod from 1987 to 2004 which can be explored in relation to changing cod size-at-age in an effort to identify food-dependent variation in growth for this stock (**Chapter 7**).

Chapter 7

Variation in Atlantic Cod (*Gadus morhua*) Size-at-Age: Disentangling Effects of Variation in Temperature (Growing Degree-Day) and Food Consumption

7.1 Introduction

Explaining variation in fish size-at-age is necessary for studies of fish physiology, population dynamics, energy pathways between trophic levels as well as the estimation of the influence of fishing pressure and associated management strategies. Observed variation in fish size-at-age may be the result of variation in many different factors. Of the factors influencing fish size-at-age, temperature governs much of the scope of growth for ectotherms (**Chapter 2**). The growth of fish is also strongly regulated by the quantity and type of food consumed with a positive relationship between food consumption and growth in many species (e.g. Elliott 1975). In addition, as most fishing gear is size-selective (Sinclair et al. 2002), fishing mortality may result in evolutionary changes in growth and maturation (Law 2000) that can confound explained variation in size-at-age. This leads me to four hypotheses that variation in fish growth (in this case sGSL cod size-at-age) is explained by variation in 1) temperature, 2) food consumption, 3) size-selective fishing, or 4) some combination of the above.

The extrication of the factors influencing fish size-at-age requires estimation of factor variation on a time-scale relevant to the fish. As the size-at-age measure is an integrative one, it follows that analyzing variation in size-at-age due to environmental factors must be examined on an integrative time-scale rather than a mean or instantaneous one. As temperature is one controlling factor governing reaction rates at the cellular level (Fry 1971) size-at-age variation due to varying thermal histories of the fish must be examined before other possible factors are explored. As demonstrated in **Chapters 2** and **3**, integrated temperature estimated as growing degree-day (GDD) allows the measurement of temperature variation on a physiological time-scale relevant to fish size-

at-age. The GDD metric is able to explain that fraction of variation in size-at-age that is the result of variation in temperature, whether that fraction represents the majority (e.g. among herring datasets, **Chapter 2**) or only a small amount (e.g. among haddock year-classes, **Chapter 3**) of the total variation in size-at-age.   In all cases, temperature variation must be examined foremost (Brander 1995), thereby allowing the residual variation in size-at-age to be explored.

The influence of temperature variation on Atlantic cod (*Gadus morhua*) length-at-age (i.e. length-at-day, LaD, converted to cm for this chapter) in the southern Gulf of St. Lawrence (sGSL) was quantified through the growing degree-day (GDD, $°C·day^{-1}$) metric in **Chapter 4**. While there were no significant trends in LaD-at-GDD relations among year-classes for immature cod, that for the mature fish demonstrated declines in both slope and intercept with increasing year-class (**Chapter 4**). In this chapter the remaining, temperature-independent variation in size-at-age among cod year-classes is explored using food consumption and size-selective (fishing) mortality indices. Here I explore the hypotheses that the decline in length-at-age for sGSL cod is a function of 1) food consumption variation, 2) size-selective fishing effects, or 3) a combination of the two.

7.2 Methods

7.2.1 Variation in Cod Length-at-Age

As shown in **Chapter 4**, sGSL cod demonstrate a significant decline in length-at-ages-4+ over the late-1970s and early 1980s with length-at-ages-4+ remaining low through the 1990s and 2000s. This decline in LaD remained after the cod were examined as year-classes and compared in physiological time (GDD) as LaD-at-GDD relations demonstrate declines in both slope, $cm(°C·yr)^{-1}$, and intercept, cm, with increasing year-classes (reproduced in Fig. 7.1).
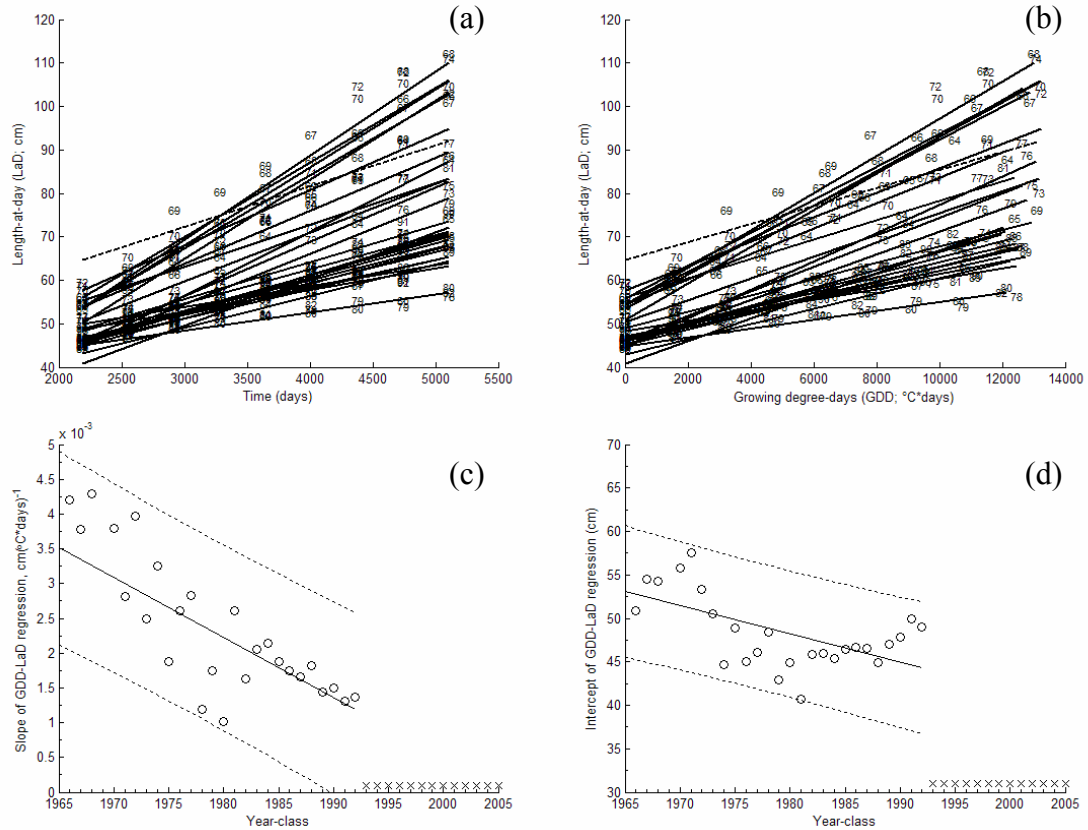
Figure 7.1: Length-at-day (cm) for mature sGSL cod ages-6 to -14 as a function of a) calendar time (days, no significant relation among year classes, ANCOVA, different slopes P<0.0001); and as a function of b) GDD (ºC·day, no significant relation among year classes, ANCOVA, different slopes P<0.0001). Data-labels denote year-class - 1900. The 1969 year-class (dashed line) was an outlier.   Also shown are parameters of the LaD-at-GDD relations for mature cod (age-6-14). c) Slopes, cm·(ºC·day)$^{-1}$, of the LaD-at-GDD relations show a significant decline with increasing year-class (Linear regression: $\beta = -8.6 \times 10^{-5}\, YearClass - 0.17$; r^2 = 0.58; P < 0.0001), b) Intercepts, cm, of the LaD-at-GDD relations show a significant decline with increasing year-class (Linear regression: $\alpha = -0.32\, YearClass + 6.9 x 10^2$; r^2=0.40; P=0.0003). Crosses denote year-classes with non-significant (P > 0.05) relations. The 1969 year-class (square) was removed as an outlier. (Reproduced from **Chapter 4**)

7.2.2 Estimating Food Consumption Variation

Variation in LaD (cm) due to variation in food consumption was examined using daily ration (DR, g·day^{-1}) estimates calculated for this stock in **Chapter 6**. Temporal variation in food consumption (as $DR_P'_{L,M,Y,E}$, g·day^{-1}, mean daily ration at month M, year Y and food energy-density E) was estimated for sGSL cod from 1990 through 2004 (excluding 1988, 1989, 1997 and 1998) using both mean ($E = mean$) and type-specific ($E = type$) food energy-densities.

To allow for the necessary temporal integration (series data), the mean monthly DR estimates ($DR_P'_{L,M,Y,E}$, **Chapter 6**) at length-class (length-class start length L), month (M), and year (Y) were linearly interpolated (month to month) where necessary and subsequently used to interpolate daily DR estimates ($DR_P'_{L,i,E}$ at day i). The interpolated DR estimates ($DR_P'_{L,i,E}$) were then smoothed using a 6-month (183 day) moving average, an extent chosen as the 6-month smoothing did not introduce new uncertainty into the time series (see Section 7.3). The variation in DR estimates for each year-class was integrated to allow for comparison with the integrative growth measure LaD as cumulative food consumption (CFC; g,). CFC$_E$ (g) at day n using food energy-density E is calculated as follows,

$$CFC_E(n) = \sum_{i=1}^{n}\left(DR_P'_{L,i,E} - DR_{Th}\right)\cdot\Delta d, \quad DR_{Th} \geq DR_P'_{L,i,E} \quad , \qquad (1)$$

where $DR_P'_{L,i,E}$ is the DR at day i for length-class L, DR_{Th} is a predetermined threshold daily ration, and Δd is a set time step (sampling frequency, i.e. 1 d). DR_{Th} was designated as 0 g·day^{-1}. Variation in LaD and CFC for mature cod in each year-class was compared by examining the variation in CFC$_E$ accumulated to age-10 (CFC$_E$-to-age-10) with the slope of the LaD-at-GDD relation (β'), cm(ºC·day)$^{-1}$. CFC$_E$-to-age-10 was chosen as DR estimates for lengths-at-ages-11+ were sparsely represented (**Chapter 6**).

7.2.3 Estimating Size-Selective Fishing Pressure

sGSL cod have been exploited commercially since the 16th century (DFO 2004) and were subjected to overexploitation during the 1960s and 1970s (Hanson and Chouinard 1992). The stock declined in the mid-1970s at which time (1974) catch limits were imposed (Hanson and Chouinard 1992). The stock recovered somewhat (late-1970s) before a sharp decline in stock biomass (along with most other cod stocks in the Northwest Atlantic) caused the introduction of a moratorium in the fishery in 1993 (Hanson and Chouinard 1992). The moratorium lasted from September 1993 through May 1998 (Chouinard et al. 2006) after which time the fishery was re-opened at low total allowable catch (TAC) limits. The fishery has remained at reduced TAC levels since 1998 with the exception of a year-long closure of the fishery in 2003 (DFO 2004). As a measure of temporal variation in size-selective fishing pressure, the annual length-at-maximum-fishing-mortality (cm) from 1971 through 1994 was estimated using annual fishing-mortality-at-age and length-at-age (Chouinard et al. 2006) estimates for this stock (as in **Chapter 3**).

7.3 Results

Due to the limited range of DR estimates (1990 through 2004, excluding 1988, 1989, 1997 and 1998) variation in cod LaD due to DR variation was restricted to the mature fish (ages-6 to 14) of the 1986 through 1992 year-classes (e.g. the 1992 year-class was age-6 in 1998). Interpolated DR estimates ($DR_P{'}_{L,i,type}$) varied over time (Fig. 7.2) and length-class resulting in variation in the CFC time series among year-classes (Fig. 7.3). Evidence for the missing sampling years (1997 and 1998, **Chapter 6**) is observed in the interpolated DR time-series shown in Fig. 7.2.
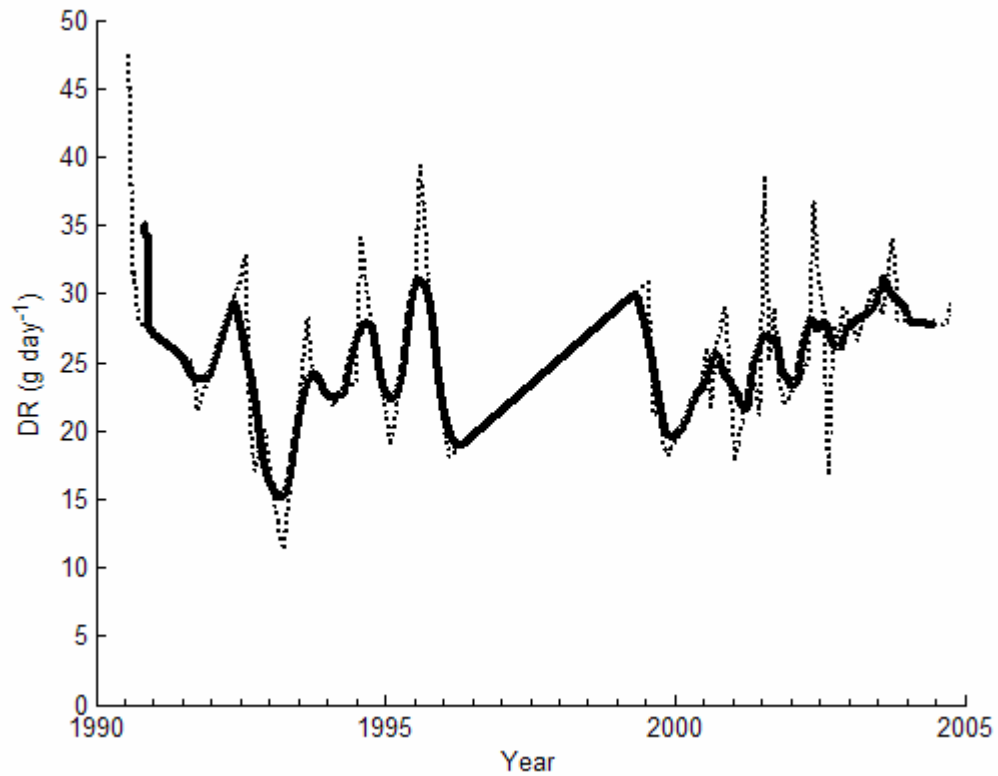
Figure 7.2:   Time series of $DR_P{'}_{L,i,type}$ interpolated at day i (dotted line, g day^{-1}) and subsequently smoothed (solid line) averaged over length-class (L) 40 – 70 cm. The $DR_P{'}_{L,i,type}$ estimates for 1997 and 1998 are missing due to lack of stomach sampling during these years (**Chapter 6**).
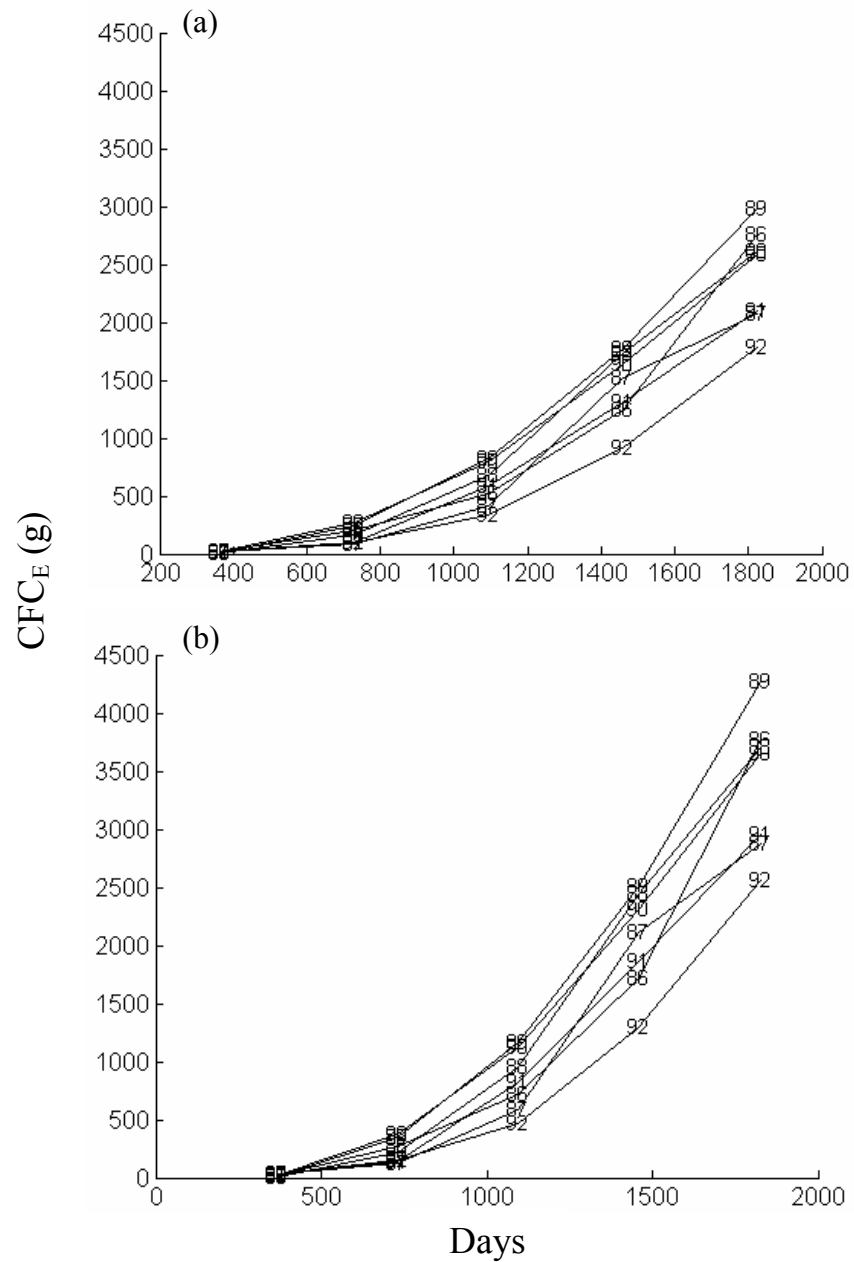
Figure 7.3: Time series of cumulative food consumption (CFC$_E$, g) at day for year-classes 1986 through 1992 and for ages-6 through -10 using a) mean food energy-density (CFC$_{mean}$) and b) type-specific food energy-densities (CFC$_{type}$).

CFC$_E$-to-age-10 (g) was used as an estimate of variation in food consumption among year-classes. While slope of the LaD-at-GDD relation (β), cm(ºC·day)$^{-1}$, declined with increasing year-class (Fig. 7.4a and **Chapter 4**), there was no correlation between β and CFC$_E$-to-age-10 using either the mean or type-specific food energy-densities (Fig. 7.4b). Therefore, declines in the size-at-age among year-classes (LaD-at-GDD relation) are not explained by differences in food consumption (CFC$_E$-to-age-10).
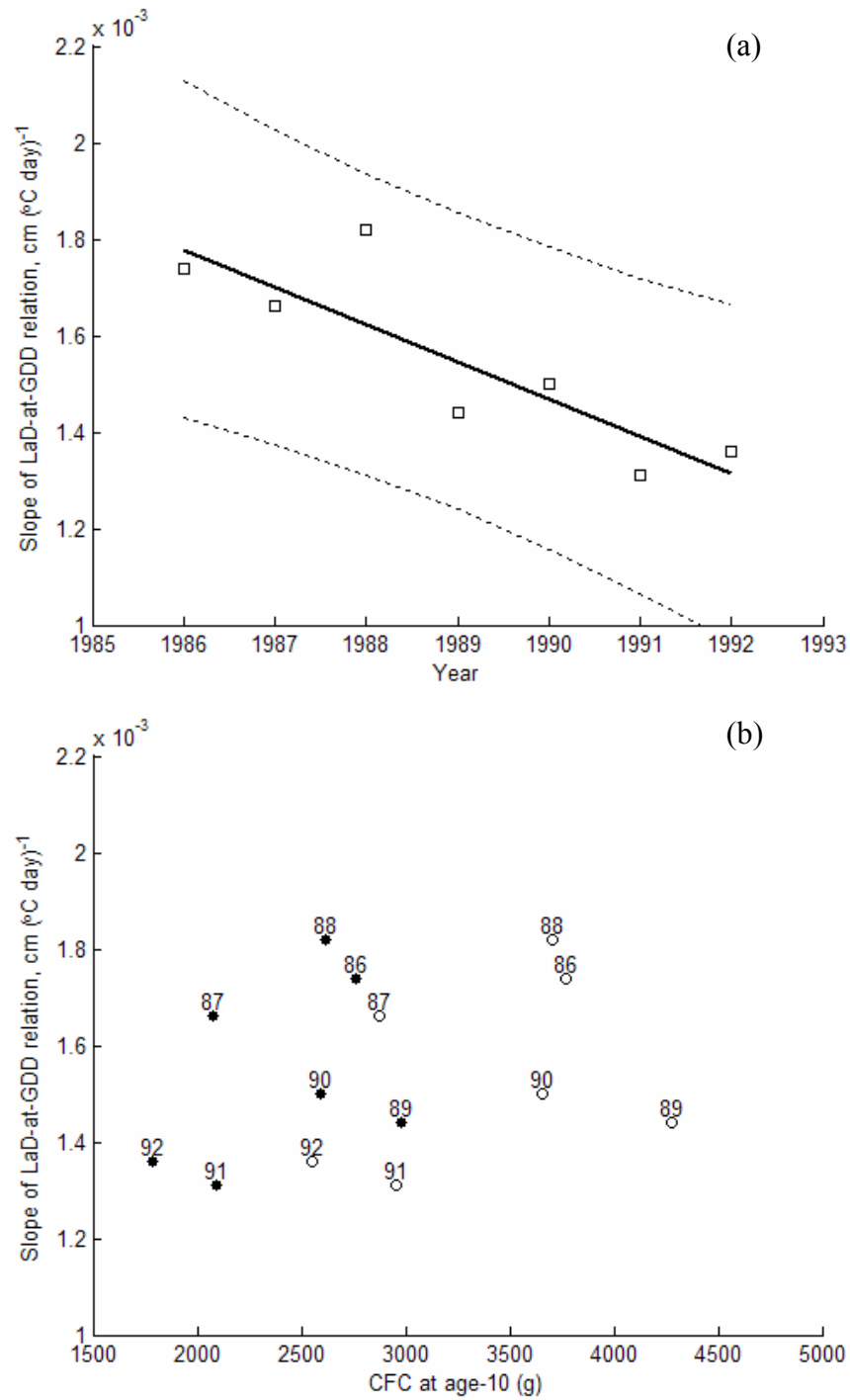
Figure 7.4: Slopes, cm($^{\circ}$C·day)$^{-1}$, of the LaD-at-GDD relations for the 1986 through 1992 year-classes as a function of a) year-class (Linear regression: $\beta = -7.7 \times 10^{-5} \, YearClass + 0.15; \ r^2 = 0.73; \ P = 0.015$) and b) CFC$_{E}$-to-age-10 (g) using mean (closed circles, no relation, Linear regression: P = 0.36) and type-specific (open circles, no relation , Linear regression: P = 0.44) food energy-densities. Data labels are year-class − 1900.

During the period of high exploitation (1970s and 1980s) fishing mortality was greatest for the larger fish in the population (Fig. 7.5a). Similar to that observed for the Scotian Shelf haddock (**Chapter 3**), there was a significant decline in length-at-maximum-fishing-mortality (cm) with year as the size at maximum fishing mortality followed the largest fish in the stock through time (Linear regression, length-at-maximum-fishing-mortality = -0.032·Year + 64, r^2 = 0.45, P < 0.0001; Fig. 7.5b).
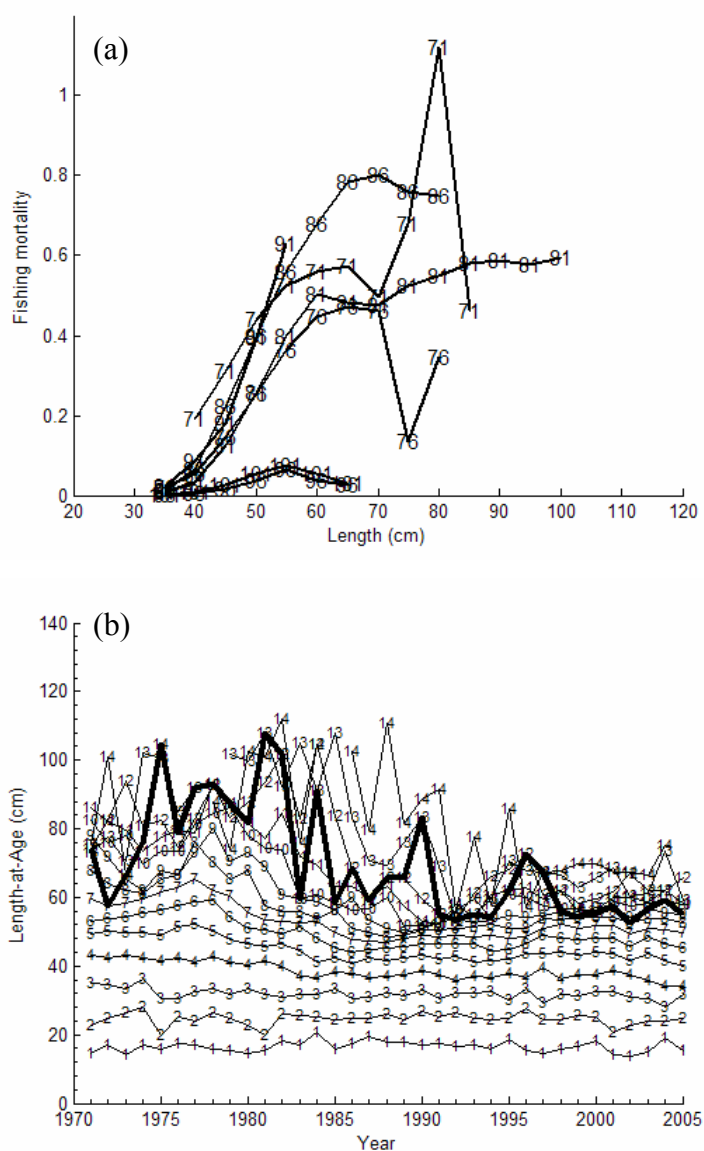
Figure 7.5: a) Variation in fishing mortality (Chouinard et al. 2006) at length (cm) grouped by 5-years: "71": 1971-1975, "76": 1976-1980, "81": 1981-1985, "86": 1986-1990, "91": 1991-1995, "96": 1995-2000, "101": 2001-2005. b) Variation in length-at-maximum-fishing-mortality (cm, thick line) and length-at-age (cm, data-labels are ages, Chouinard et al. 2006) for sGSL cod from 1970 to 2005.

7.4 Discussion

Analysis of variation in mature cod LaD with GDD demonstrated declines in both slope, cm(°C·day)$^{-1}$, and intercept, cm, with increasing year-class (**Chapter 4**). As noted in the Scotian Shelf haddock (**Chapter 3**) this pattern may indicate a decline in growth for cod in this area that is temperature-independent, causing me to reject the hypothesis that the variation in sGSL cod size-at-age is explained by variation in temperature. In this chapter I attempt to explain the remaining variation in LaD by exploring my remaining hypotheses, that variation in sGSL cod size-at-age can be explained by variation in 1) food consumption, 2) size-selective fishing or 3) a combination of the two.

While condition estimates are often employed as a first approximation of food consumption variation, changes in condition may be an artifact of changes in a population's weight-at-length relationship rather than truly indicative of food consumption variation (**Chapter 3**). In **Chapter 6** I attempt a more direct estimate of variation in food consumption for sGSL cod by estimating DR using stomach contents samples and the Pennington method explored in **Chapter 5**. Though DR estimates (and resulting year-class specific CFC) varied in time (Fig. 7.2), variation in CFC$_E$-to-age-10 did not explain the decline in size-at-age (i.e. slope of LaD-at-GDD relation). As was demonstrated in **Chapter 6**, DR estimates for the sGSL cod are limited by sampling year and month (season) and, thus, it is possible that increased stomach sampling frequency might improve CFC estimates for this stock. In addition, the integration of DR in the CFC metric is dependent on the choice of threshold DR (DR_{Th}). DR_{Th} is the minimum food required for metabolism (i.e. no growth) and will vary with size, temperature and activity level (Hansen et al. 1993). Since metabolism is difficult to estimate and highly variable (Hansen et al. 1993) DR_{Th} was designated at 0 g·day^{-1} for this study. Improvements to the resolution of the DR time series and accuracy of the DR_{Th} parameter may allow for more accurate analysis of the effects of varying food consumption on cod LaD. Still, present DR estimates are clearly not able to explain the temperature-independent variation in LaD even at marginal levels, leading me to reject the hypothesis that variation in sGSL cod size-at-age is explained by variation in food consumption estimates integrated over the mature life of the fish. The lack of measurable effect of diet changes on sGSL cod size-at-age has been noted before and led to the hypothesis that the

influence of diet composition on sGSL cod growth may be overestimated or outweighed by other factors (Waiwood and Majkowski 1984).

Prior to the moratorium in 1993, sGSL cod were subject to extensive exploitation that was size-selective with fishing pressure concentrated on larger cod throughout the study period (Fig. 7.5ab). As detailed in **Chapter 3**, this type of size selection is typical of most fishing gear where minimum mesh size is employed to allow the smallest fish to escape (Sinclair et al. 2002). Sustained exploitation selecting for large fish predicts declines in growth (slope of the LaD-at-GDD relation) and age-at-maturity (Beacham 1987, intercept of the LaD-at-GDD relation) over time as observed for sGSL cod. Thus, I can not reject my hypothesis that variation (decline) in sGSL cod size-at-age is explained by variation in size-selective fishing.

I do not reject the possibility that variation in other factors play a role in the observed changes in size-at-age in this stock. Density-dependent effects are thought to influence growth rates of fish by predicting decreased growth at high population abundance due to competition for food, habitat, etc. Evidence for density dependent effects for sGSL cod have been suggested as cod growth rates were found to be inversely correlated with population abundance during the 1970s and 1980s (Sinclair et al. 2002). However, during the 1990s, abundance was at or near historical minima inferring lower competition and higher growth rates not found in the size-at-age series (Sinclair et al. 2002). In addition, other evidence (e.g. diet changes) beyond correlations between growth and abundance are required to conclude the influence of competition (density-dependence) on growth rate (Hanson and Chouinard 1992). As shown above, I have found no compelling evidence of a diet change in this stock sufficient to be indicative of density-dependent competition.

By examining variation in temperature and food consumption in metrics relevant to the phenotypic expression of growth physiology (length-at-age) of the fish, I have isolated a decline in cod size-at-age that is most parsimoniously explained by size-selective fishing. While environmental variables such as temperature and food consumption can alter growth rates, it seems the effects of size-selective fishing mortality act in such a way as to overwhelm effects of environmental variation experienced by this stock (Sinclair et al. 2002). Variability in size- and age-at-maturity is the link between

individual growth and the reproductive potential of a population (Beacham 1987). Thus, factors affecting size- and age-at-maturity will affect the viability and economic potential of a stock. Since the 1993 moratorium on sGSL cod fishing, size-selective fishing pressure on this stock has been low to neutral (Sinclair et al. 2002). However, Sinclair et al. (2002) found that size-selective mortality was the dominant effect even among the most recent years, suggesting size-selective fishing mortality has a strong effect on the mean population size-at-age that remains long after the fishing selection pressure is reduced.

Chapter 8

Conclusion

Accurate estimation of growth in fishes is necessary for many studies of fish physiology (e.g. bioenergetics) and ecology (e.g. population and ecosystem modelling) as well as for the estimation of the effects of fishing. Environmental variables such as temperature and prey field as well as internal (e.g. genetic make-up) and external (e.g. size-selective fishing) forces influence fish growth and resulting observed size-at-age. These influencing factors may vary in time (e.g. among years) and space (e.g. latitude) producing observed size-at-age variation among years, year-classes, populations and stocks, etc. The quantitative analysis of variation in fish size-at-age requires an accurate estimation of this temporal and spatial variation among the factors affecting fish growth. Moreover, this factor variation must be estimated in a manner relevant to the physiology of the fish and must be comparable to the integrated growth measure that is size-at-age. My research explores the relevant estimation of factors thought to influence fish growth thereby allowing the quantitative explanation of fish size-at-age variation.

The physiological processes that determine growth are directly influenced by temperature (Atkinson 1994; van der Have and de Jong 1996). Time-dependent variations in temperature are reflected in time-dependent variations in development and in size-at-age. While physiological rates for endotherms (including humans) are generally independent of environmental temperature (homeothermy), the rates for fish (and other ectotherms) are a function of the thermal environment. Therefore the impact of temperature on size-at-age variation must be examined foremost (Brander 1995) and in a manner that is physiologically-meaningful for the fish. For up to 270 years in some areas of ectotherm research (e.g. agriculture and entomology, Seamster 1950; Atkinson 1994; Bonhomme 2000) and recently in fish research (**Chapter 2** and Neuheimer and Taggart 2007), the approximation of the thermal integral employed to describe size-at-age is the growing degree-day (GDD, ºC day), the time integral of the daily temperature measured above a given temperature threshold. In **Chapter 2** I demonstrate that the GDD metric is

able to explain between 92 and 99% of variation in fish size-at-age over a range of species among environments, temperature regimes, and laboratory and field studies. The GDD metric is able to explain that fraction of size-at-age variation that is the result of variation in temperature, whether that fraction represents the majority (e.g. among herring datasets, **Chapter 2**) or only a small amount (e.g. among haddock year-classes, **Chapter 3**) of the total variation in size-at-age. It appears that the GDD has similar utility in explaining variation in life history development and stage transitions (e.g. thermal constant) as well as simplifying many physiological rates (e.g. gastric evacuation and mortality rates, **Chapter 2**). Thus, the GDD appears as an essential metric that can explain a large amount of variation that is observed in fish growth and development. Such physiological scaling via GDD could be incorporated into all aspects of studies on fish physiology and ecology including fish simulation models (e.g. Neill et al. 2004) and the quantification of the influence of climate change on fish size-at-age (**Chapter 2**).

The GDD metric offers a mechanism for extricating the temperature-dependent variation in size-at-age from that due to other factors (e.g. **Chapters 2, 3** and **4**). In **Chapter 3**, I demonstrate this with Scotian Shelf haddock (*Melanogrammus aeglefinus*). Here differences in thermal histories (i.e. GDD) among year-classes are unable to explain the major trends in haddock size-at-age. Instead prolonged size-selective fishing mortality offers a parsimonious explanation for the declining size-at-age (as well as the change in condition) observed in this exploited stock. Thus, the GDD metric allowed me to isolate the temperature-independent variation in size-at-age among haddock year-classes that is most parsimoniously attributed to sustained size-selective exploitation.

I employ a similar yet more detailed methodology to disentangle the variation in size-at-age of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence (sGSL, **Chapters 4** through **7**). An examination of sGSL cod size-at-age demonstrated a decline in size-at-age among year-classes that is not explained by thermal history variation (GDD time-series) among year-classes. In **Chapters 5**, **6** and **7** I examined this temperature-independent trend in cod size-at-age with variation in food consumption as fish size-at-age is directly affected by the amount and type of food consumed by the fish (Waiwood and Majkowski 1984). Food consumption often varies in time (intra- and inter-annually) and location such that estimates of food consumption including variation in food type

consumed must be made sufficiently frequently and specific to the stock in question (Hanson and Chouinard 2002). While condition estimates are often employed as a first approximation of food consumption variation, changes in condition may be an artifact of changes in the weight-at-length relationship for a population rather than an indication of actual changes in food consumption (**Chapter 3**). An alternative to inferring variation in food consumption from condition estimates is the estimation of actual food consumed by the fish from stomach contents data through an evacuation model. Based on the probable factors describing variation in daily stomach content weight, I employed a simple model to determine sensitivity of the diel change in stomach content weight to factors thought to influence consumption and the accuracy of the Pennington evacuation model in estimating food consumption from stomach content weight estimates (**Chapter 5**). The Pennington method (with shaping parameter, $a = 0.5$) is shown to be a suitable method of estimating daily ration when parameterized with predator size, temperature and food energy-density. The Pennington method was employed, along with sGSL cod stomach contents data from 1987 to 2004, to estimate temporal variation in food consumption (daily ration, DR, g·day^{-1}) for this stock (**Chapter 6**).

Quantitative analysis of sGSL cod stomach contents demonstrated significant variations in diet and DR with cod size and at a number of temporal scales (year, month, hour, **Chapter 6**). As it is the integrated food consumption that results in the phenotypically expressed size-at-age of the fish, DR estimates were integrated as cumulative food consumption (CFC, g) estimates (**Chapter 7**). Use of CFC metrics appears to be limited in the published literature (e.g. Buckel et al. 1995) and is restricted to the quantification of fish food consumption over short time scales (months). Here I examine CFC variation over longer time scales (years) allowing me to explore food-dependent size-at-age variation among year-classes. CFC time-series varied among year-classes but were unable to explain the temperature-independent decline in year-class size-at-age extricated in **Chapter 4**. The lack of a measurable effect of diet changes on sGSL cod size-at-age has been noted before leading to the hypothesis that the influence of diet composition on sGSL cod growth may be overestimated or outweighed by other factors (Waiwood and Majkowski 1984).

I extricated declines in cod size-at-age independent of variation in temperature (as with the haddock in **Chapter 3**) and food consumption. Finally I examined the role that sustained fishing pressure may play in influencing this size-at-age pattern. Fishing exploitation innately acts as a selective influence on an ecosystem. Species-selective mortality can change the community structure and nutrient cycling while size-selective mortality can alter population growth rates and production (Bax 1998). If a portion of the phenotypic variation in size-at-age is rooted in genetic variation, it is possible that size-selective fishing mortality may represent a strong force of selection on a population (Engelhard and Heino 2004; Hutchings 2005) resulting in evolutionary changes in growth and maturation (Law 2000; Stokes and Law 2000). Both Scotian Shelf haddock and sGSL cod stocks experienced periods of fishing selecting for the largest fish in the population (**Chapters 3** and **7**). The proposed effects of this sustained size-selection (**Chapter 3**) are consistent with the declines in size-at-age among year-classes that are found in these exploited stocks. While environmental variables such as temperature and food consumption can alter growth rates, it appears that the effects of size-selective fishing mortality overwhelm the effect of environmental factors in Scotian shelf haddock and sGSL cod (e.g. Sinclair et al. 2002).

Variability in size- and age-at-maturity is the link between individual growth and the reproductive potential of a population (Beacham 1987). Thus, factors affecting size- and age-at-maturity will affect the viability and economic potential of a stock. While fishing pressure on sGSL cod has been low since the 1993 moratorium, size-selective mortality appears as the dominant effect on cod growth even in most recent years, suggesting that the strong effects of size-selective fishing (i.e. fishing mortality often exceeds natural mortality by a factor of 2 or 3; Engelhard and Heino 2004; Hutchings 2005) remain long after the fishing selection pressure is reduced (Sinclair et al. 2002).

In conclusion, the complex interactions of the many factors affecting fish growth must be disentangled before size-at-age variation can be explained and/or predicted. A number of possible combinations of internal and external factors may act to produce the observed temporal variations in size-at-age. I argue that explanatory or predictive models of size-at-age variation can only be made by pursuing the most parsimonious explanations. Such explanations can only be resolved through the extrication of the

influence of these factors – and only by using metrics that accommodate and reflect the physiological time-scales relevant to the fish.

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