

2014

# Modeling Consumption Rates Of Atlantic Herring (*Clupea harengus*)

Mitchell Jones  
*University of Vermont*

Follow this and additional works at: <https://scholarworks.uvm.edu/graddis>



Part of the [Aquaculture and Fisheries Commons](#)

---

## Recommended Citation

Jones, Mitchell, "Modeling Consumption Rates Of Atlantic Herring (*Clupea harengus*)" (2014). *Graduate College Dissertations and Theses*. 302.

<https://scholarworks.uvm.edu/graddis/302>

This Thesis is brought to you for free and open access by the Dissertations and Theses at ScholarWorks @ UVM. It has been accepted for inclusion in Graduate College Dissertations and Theses by an authorized administrator of ScholarWorks @ UVM. For more information, please contact [donna.omalley@uvm.edu](mailto:donna.omalley@uvm.edu).

MODELING CONSUMPTION RATES OF  
ATLANTIC HERRING (*CLUPEA HARENGUS*)

A Thesis Presented

by

Mitchell A. Jones

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements  
for the Degree of Master of Science  
Specializing in Natural Resources

October, 2014

Accepted by the Faculty of the Graduate College, The University of Vermont, in partial fulfillment of the requirements for the degree of Master of Science specializing in Natural Resources

Thesis Examination Committee:

\_\_\_\_\_ **Advisor**  
Jason Stockwell, Ph.D.

\_\_\_\_\_  
J. Ellen Marsden, Ph.D.

\_\_\_\_\_ **Chairperson**  
Arne Bomblies, Ph.D.

\_\_\_\_\_ **Dean, Graduate College**  
Cynthia J. Forehand, Ph.D.

August 28, 2014

## ABSTRACT

Pelagic forage fishes play critical roles in productive marine food webs by providing a link between zooplankton and piscivores and transferring energy from feeding grounds to other ecosystems. The amount of energy moved to higher trophic levels or new systems is directly linked to the consumption rate of pelagic forage fishes. In the Gulf of Maine, Atlantic herring (*Clupea harengus*) is the dominant forage fish; the purpose of this study is to determine their specific consumption rate (g prey/g fish/day). Using fish collected in autumn 2012 and spring 2013, we applied a mercury mass-balance model to estimate individual and population consumption of Atlantic herring in the Gulf of Maine. Our results suggest that the specific consumption rate increases from age 1.5 until age 6 (years) and then asymptotes. These estimates were contradictory to much of what exists in the literature; for most fishes, specific consumption estimates decrease with age and overall are much lower than our estimates. We looked further into our results to explore the underlying cause of the increase in specific consumption rate. We combined the mercury mass-balance model with a Wisconsin (WI) bioenergetics model and ran several simulations adjusting the most sensitive factors in each—prey mercury in the former and activity in the latter. The results of our simulations showed that an increase in activity relative to age and mass can best explain the increase in the consumption rate of Adult herring. This suggests that an ontogenetic shift to migration in adult Atlantic herring results in increased energy demand with age, and ultimately increased consumption.

# TABLE OF CONTENTS

	Page
LIST OF TABLES.....	iii
LIST OF FIGURES.....	iv
CHAPTER 1: LITERATURE REVIEW.....	1
1.1 The Gulf of Maine.....	1
1.2 Atlantic Herring Ecology.....	2
1.3 <i>Calanus finmarchicus</i> Ecology.....	3
1.4 Wasp Waist Systems.....	5
1.5 Trophic Cascades.....	6
CHAPTER 2: AGE SPECIFIC CONSUMPTION ESTIMATES FOR ATLANTIC HERRING IN THE GULF OF MAINE.....	8
2.1 Introduction.....	8
2.2 Methods.....	10
2.3 Results.....	13
2.4 Discussion.....	15
2.5 Conclusion.....	16
CHAPTER 3: ESTIMATING AGE SPECIFIC CONSUMPTION OF ATLANTIC HERRING BY COMBINING MERCURY AND BIOENERGETICS MODELS.....	25
3.1 Introduction.....	25
3.2 Methods.....	28
3.3 Results.....	31
3.4 Discussion.....	32
CHAPTER 4: BIBLIOGRAPHY.....	42

## LIST OF TABLES

Table	Page
Table 1: Parameter descriptions for mercury mass-balance model .....	18
Table 2: Parameter descriptions for the Wisconsin bioenergetics model .....	37

LIST OF FIGURES

Figure	Page
Figure 1: Mean ( $\pm$ SD) wet mass (g) of Gulf of Maine Atlantic herring sampled in fall 2012 and spring 2013. Dotted line indicates best fit logistic growth curve used as model input ( $M_{age} = \frac{210}{(1 + 11.59 \cdot e^{0.55 \cdot age})}$ ; $R^2 = 0.945$ ). . . . .	19
Figure 2: Modeled daily specific growth rate for Gulf of Maine Atlantic herring (mg/g/day).....	20
Figure 3: Mean mercury concentration ( $\pm$ SD) in Gulf of Maine Atlantic herring sampled in autumn 2012 and spring 2013. Dotted line indicates best-fit logistic growth curve used at model input ( $Hg_{age} = \frac{Hg_{max}}{(1 + 21.78 \cdot e^{0.53 \cdot age})}$ ; $R^2 = 0.946$ ).....	21
Figure 4: Herring specific consumption rate (g/g/day) as a function of fish age based on a diet of <i>C. finmarchicus</i> . The solid line shows the consumption estimate based on mean mercury prey content; dashed lines represent $\pm 15\%$ , and dotted lines represent $\pm 30\%$ of prey mercury content.....	22
Figure 5: Correlation between total annual consumption of Atlantic herring and spawning stock biomass (top) or mean population age (bottom).....	23
Figure 6: Total annual consumption (MT) for the Atlantic herring population in the Gulf of Maine from 1999 to 2011. The black bar shows the consumption estimate based on mean mercury prey content, the dark gray bar $\pm 15\%$ of the mean mercury prey content, and the light gray bar $\pm 30\%$ .....	24
Figure 7: Flowchart showing the hybrid consumption model. Adjusted parameters in the model are shown in bold . . . . .	36
Figure 8: Measured mercury burden in Atlantic herring at age (solid line) and estimated mercury burden of Atlantic herring (dotted line) based on consumption estimates from an unaltered WI bioenergetics model input into an unaltered mercury mass-balance model. Points indicate mean measured mercury burden.....	38
Figure 9: Measured mercury burden in Atlantic herring at age (solid line), estimated mercury burden of Atlantic herring based on a WI bioenergetics model with activity (dashed line) or prey mercury (dotted line) doubled, tripled, quadrupled, or quintupled. Points indicate mean measured mercury burden.....	39

Figure 10: Measured mercury burden in Atlantic herring at age (solid line), estimated mercury burden of Atlantic herring based on a WI bioenergetics model with activity (dashed line) or prey mercury (dotted line) multiplied by current mass divided by mass at age 1. Points indicate mean measured mercury burden..... 40

Figure 11: Specific consumption of Atlantic herring at age based on original mercury mass-balance model (Chapter 2; dashed line), hybrid model with prey mercury content held constant and activity multiplied by current mass divided by mass at age 1 (solid line), and Wisconsin model with activity multiplied by current mass divided by mass at age 1 (dotted line)..... 41



## CHAPTER 1: LITERATURE REVIEW

### 1.1 The Gulf of Maine

The Gulf of Maine lies in a transition zone between the Labrador Current and the Gulf Stream, which creates a productive region of vertical mixing over Georges Bank that supports multiple fisheries (Fry 1988; Pickart *et al.* 1999; Pershing *et al.* 2001). Over the last four decades, fluctuations in the North Atlantic Oscillation (NAO) have altered the currents, affecting the Gulf of Maine's temperature, stratification, and salinity (Pershing *et al.* 2005; Green and Pershing 2007). Records show that in the late 1980s, atmospheric pressure at sea level in the central Arctic began to decline precipitously. This change in pressure increased the outflow of low saline water from the Arctic, through the Labrador Sea, resulting in a freshening of the shelf waters of the North Atlantic. The shallow outflow of relatively cold, fresh water, which had previously flown through the Fram Strait east of Greenland, resulted in colder, fresher, and more stratified North Atlantic waters in the 1990s compared to the 1980s (Green and Pershing 2007).

The largest single-year decrease in the NAO index in the 20th century occurred in 1996 (Greene and Pershing 2003). The decrease in atmospheric pressure led to a further shift in circulation on the Slope Sea on the North Atlantic continental shelf.

Consequently, by 1998 the Labrador subarctic slope water completely replaced the Atlantic temperate slope water in the deep basins of the Gulf of Maine. This scenario, known as a minimal modal state, dramatically affected the plankton communities in the Gulf of Maine, reducing the abundance of key species such as the calanoid copepod

*Calanus finmarchicus*. Within the next few years the NAO returned to positive values and by 1999 the Slope Sea had returned to its previous conditions, a maximal modal state (Green and Pershing 2003).

## **1.2 Atlantic herring ecology**

Atlantic herring, *Clupea harengus* (“herring” hereafter), is the dominant fish species in the North Atlantic. The species is pelagic, forms large schools and shoals, and feeds primarily on zooplankton (Stevenson and Scott 2005). The general range of herring extends in patches from the Straits of Gibraltar in Europe to southern New Jersey (Bigelow and Schroeder 1953). In the North Atlantic, the species ranges from Labrador to Cape Hatteras. Herring can live up to 18 years and grow in excess of 390 mm. In the western North Atlantic, however, herring rarely exceed 12 years or 350 mm. Adult herring make long migrations each year, traveling up to 1,000 km from the Gulf of Maine south, down the coast (Kanwit and Libby 2009).

Herring feed heavily on *C. finmarchicus* and northern krill, *Meganyctiphanes norvegica*, in spring and summer (Darbyson *et al.* 2005; Bailey and Pershing 2013), and spawn from August to November in shallower water depending on their location in the Gulf of Maine (Sinclair and Tremblay 1984; Kelly and Stevenson 1985). Herring larvae overwinter in the inshore areas of the Gulf of Maine, while adults migrate as far south as Chesapeake Bay (Stevenson and Scott 2005).

Herring abundance has fluctuated greatly since the 1960s, with a collapse in the

1970s caused by overfishing, followed by recovery in the late 1980s (Overholtz *et al.* 2008). The spawning stock biomass has been fairly constant since the 1990s (NFSC 2012). Fluctuations have been out of phase with groundfish populations that prey on herring, with some suggestion that the relatively high herring biomass contributes to the lack of recovery of groundfish populations (Bakun *et al.* 2009; but see Brodziak *et al.* 2004).

### **1.3 *Calanus finmarchicus* Ecology**

*Calanus finmarchicus* dominates the zooplankton community in the Gulf of Maine (Fish 1936; Runge 1988). The copepod provides a key link between planktonic microorganisms and benthic and pelagic fishes, and can be used to predict the distribution and condition of higher trophic level predators (Runge 1988; Brander *et al.* 2001; Campbell *et al.* 2001; Michaud and Taggart 2007). The range of *C. finmarchicus* extends from Cape Hatteras to the Arctic Ocean (Fleminger and Hulseman 1977), and the life cycle involves six nauplius stages (N1–6) followed by six copepodite stages (C1–6); C6 is the mature adult stage (Lebour 1916).

In the Gulf of Maine, *C. finmarchicus* take approximately one month to develop from the N1 to the C1 stage, two weeks to develop to C5, and an additional month for the final molt to the C6 stage (Fish 1936). In late winter/early spring C5 copepodites molt to the adult C6 stage before the spring phytoplankton bloom (Miller *et al.* 1991; Plourde *et al.* 2001). Males develop from the upper size range of the C5 cohort and females typically

develop from the smaller size range (Miller *et al.* 1991). In laboratory studies, food quality, food quantity, and container size all positively influenced the proportion of males in the population (Campbell *et al.* 2001). After mating, the C6 adults die, with males dying off before females (Fish 1936).

Distinct cohorts of *C. finmarchicus* have been observed in some areas. For example, in the western Gulf of Maine there are two distinct spawning periods: the first in late March/early April and the second in late June/early July. A third, less distinct spawning event, occurs in September. In the eastern side of the Gulf of Maine, however, two less-defined spawning events take place, lagging behind the western spawning by about a month (Fish 1936). The duration of the spawning season and the timing of emergence from the winter diapause determine the number of cohorts per year. The rate of development of *C. finmarchicus* varies throughout their range with changing temperature and food availability (Fish 1936; Campbell *et al.* 2001). Size and mass are inversely related to temperature and positively correlated with food availability (Campbell *et al.* 2001).

If the final spawning event for *C. finmarchicus* is too late in the fall, that cohort will not be able to reach the C5 stage to overwinter and will fail. Up to 95% of *C. finmarchicus* overwinter as C5 individuals (Bamstedt and Tande 1988). During this time, C5s have lipid sacs filled with wax esters (Miller *et al.* 1998; Evanson *et al.* 2000). During diapause, C5s settle in the water column to a depth of approximately 500 m (Miller *et al.* 1991). The copepod does not feed during the winter and consequently loses mass as it metabolizes lipid stores (Fiksen and Carlotti 1998). Although their

metabolisms slow significantly, C5s are not completely immobile and will still exhibit avoidance behavior when molested (Bamstedt and Tande 1988; Miller *et al.* 1991).

Several hypotheses exist about what causes the arousal of individuals from diapause. The first is that an increasing photoperiod rouses *C. finmarchicus*. This hypothesis was tested on *C. helgolandicus* with success (Grigg and Bardwell 1982). Other factors, however, may also be at play. For instance, another hypothesis is that an endogenous, long-range timer triggers arousal (Miller *et al.* 1991). A final hypothesis is that there is no mechanism to the arousal—there is simply an end to the diapause-maintaining factors that keep individuals in their resting phase (Miller *et al.* 1991).

#### **1.4 Wasp-Waist Systems**

Wasp-waist ecosystems are characterized by intermediate trophic levels with low species richness and high relative abundance, which create a vector for energy transfer from lower to higher trophic levels (Rice 1995; Bakun 1996; Jordan *et al.* 2005). In highly productive marine ecosystems the link is made by small pelagic forage fish between plankton and piscivores (Cury *et al.* 2000; Chase 2002; Hunt and McKinnell 2006). In addition to moving energy up the food web, migrating forage fish (e.g., alewife *Alosa pseudoharengus*, herring) move energy from feeding grounds to less productive marine and aquatic systems (Durbin *et al.* 1979; Polis *et al.* 1997; Varpe *et al.* 2005). Energy subsidies to terrestrial systems by forage fishes include predation by seabirds, fishing, and use as fertilizer or animal feed (Holt 1996; Wanless *et al.* 2005). Forage

fishes are affected by overfishing, climate change, and flux in plankton community, and fluctuations in their abundance can have a significant impact on the entire ecosystem (Cyterski *et al.* 2002; Frank *et al.* 2005; Albert and Taconand 2009; Bakun *et al.* 2009).

### **1.5 Trophic Cascades**

Reduction of top predators can lead to trophic cascades where small pelagic fishes increase, large zooplankton decrease, and phytoplankton increase (Reid *et al.* 1999; Frank *et al.* 2005; Casini *et al.* 2008; Varpe and Fiksen 2010). A dramatic shift with increases of small pelagic fishes, such as clupeids, can restructure the zooplankton community and negatively affect the larvae of top predators through predation and competition, reducing their recruitment (Casini *et al.* 2009; Österblom *et al.* 2007). Shifts in the stable state are driven first by a reduction in upper trophic level predators and then maintained by density-dependent consumption by small pelagic fish (Casini *et al.* 2009; Österblom *et al.* 2007). Bottom-up control on higher trophic levels by increased abundances of small pelagic fish can “trap” their predators at low abundances by preying on or out-competing early life stages of their predators (Cury *et al.* 2000; Bakun 2006; Fauchald *et al.* 2011).

Overfishing can result in a disruption of top-down controls exhibited by apex predators, while climate change influences plankton biomass and bottom up forcing in marine ecosystems (Casini *et al.* 2008; Bailey and Pershing 2013). Numerous studies have examined top-down (Reid *et al.* 2004; Frank *et al.* 2005; Casini *et al.* 2009; Varpe and Fiksen 2010) or bottom-up (Ricchardson and Schoeman 2004; Pershing *et al.* 2005;

Buren *et al.* 2014) dynamics, and there is a divide in the literature about which is the driving force of change. If the process is bottom-up and prey is limiting, we would expect the consumption demand by herring populations to be correlated to the available zooplankton biomass.

## CHAPTER 2: AGE SPECIFIC CONSUMPTION ESTIMATES FOR ATLANTIC HERRING IN THE GULF OF MAINE

### 2.1. Introduction

Herring occupy a key intermediate trophic level in many productive marine food webs and serve as a vector of energy transfer from plankton to piscivores (Cury *et al.* 2000; Chase 2002; Hunt and McKinnell 2006). Atlantic herring (*Clupea harengus*) is the dominant pelagic forage fish in the North Atlantic (Bakun *et al.* 2009). Over the last several decades, significant fluxes in Atlantic herring biomass throughout the North Atlantic have been correlated with shifts in the plankton community structure and groundfish stocks (Overholtz 2002; Frank *et al.* 2005; Greene and Pershing 2007; Casini *et al.* 2009; Bailey and Pershing 2013). In the Gulf of Maine, herring spawning stock biomass has fluctuated by more than an order of magnitude since 1965 when assessments began. The stock declined precipitously in the 1970s (to 53,000 MT from a high of 700,000 MT in the 1960s), recovered through the 1980s and 1990s (to a new high of 840,000 MT), declined again until 2010 (to 300,000 MT), and most recently has increased (518,000 MT) (Northeast Fisheries Science Center 2012). In addition to changing biomass, herring age structure has also varied over the last decade, most recently declining from 4.5 years in 1999 to just over 3 years old in 2011 (Northeast Fisheries Science Center 2012).

Mounting evidence suggests that the structure of the Gulf of Maine food web is controlled by bottom-up forces including sea-surface temperature and plankton densities (Greene and Pershing 2007; Greene 2013). The energy-dense copepod, *Calanus*



*finmarchicus*, is the primary prey of herring in the North Atlantic (Darbyson *et al.* 2003; Varpe *et al.* 2005). The abundance of this copepod is difficult to assess and can fluctuate by orders of magnitude over several years (Bailey and Pershing 2013). Estimates of how much *C. finmarchicus* is consumed by Atlantic herring populations will help to better forecast how flux in *C. finmarchicus* abundance will translate through the system.

Adult herring on both sides of the North Atlantic make extensive annual migrations between feeding, spawning, and over-wintering grounds (Stevenson and Scott 2005; Varpe *et al.* 2005). Tagged herring released in the Gulf of Maine and southern New England have been recovered up to 1000 km away (Kanwit and Libby 2009). Age-based estimates for specific consumption rates have been calculated for herring in the Baltic Sea (Rudstam 1988). However, the bioenergetics model used to make those estimates (Kitchell *et al.* 1977) has been criticized for its sensitivity to, and underestimation of, fish activity and subsequent consumption estimates (Rowan and Rasmussen 1996).

Contaminant mass-balance models have been used to estimate consumption independently of fish activity (Rowan and Rasmussen 1996; Trudel *et al.* 2000; Trudel and Rasmussen 2001). The highly migratory nature of herring makes contaminant mass-balance a plausible approach to modeling consumption because it eliminates the need to estimate the energetic cost of their migrations.

The purpose of this study was to provide an estimate of specific consumption rates at age for Gulf of Maine Atlantic herring using a mercury-mass-balance model (Trudel *et al.* 2000; Trudel and Rasmussen 2001). We used contemporary estimates of mercury loads in herring and their primary prey *C. finmarchicus*, with historic population structure

estimates of herring, to estimate specific and total annual consumption rates from 1999 to 2011.

## 2.2 Methods

### *Sample collection*

Herring were collected in the Gulf of Maine (Jeffreys Ledge and Jordan Basin) and on Georges Bank by National Marine Fisheries Service bottom trawl surveys during fall 2012 and spring 2013. Fish were frozen immediately and processed in the laboratory within three months of capture. Total length (mm), wet mass (g), and sex were recorded for each fish and otoliths were extracted for age estimation.

Fish collected in the spring were given integer ages (1, 2, 3...) in years. For fish captured in the fall, interim months were accounted for by adding six months, resulting in ages 1.5, 2.5, 3.5... years. Growth (g/g/day) was estimated based on the difference in mean mass between cohorts.

*Calanus finmarchicus* were collected in the Gulf of Maine from Wilkinson Basin (250 m depth) and Jeffreys Ledge (50 m depth) using two dual-ring net plankton tows in autumn/winter 2012 and frozen at -80°C until mercury analysis.

### *Total mercury analysis*

Whole fish were homogenized individually and a subsample of approximately 15 g of homogenate per fish was refrozen until the mercury analysis. Fish from both sampled areas in the Gulf of Maine were selected for analysis to cover the observed range of sizes. Total mercury was measured in accordance with U.S. EPA Method 7473 using a

Milestone DMA-80 Direct Mercury Analyzer (Milestone Srl, Bergamo, Italy) at Clarkson University (Potsdam, NY). Detailed methods are described in Zananski *et al.* (2011). The total mercury content of *C. finmarchicus* was measured using the same method.

Individuals were pooled, however, to obtain enough biomass to reach the 0.1 g minimum for analysis.

#### *Mercury mass-balance model*

Individual herring consumption rate ( $I$ ; g/g/day) was modeled for each age class using the mercury mass-balance equation developed by Trudel *et al.* (2000) and Trudel and Rasmussen (2001):

$$I = \frac{C_{t+\Delta t} - C_t \cdot e^{-(E+G)\Delta t}}{\alpha \cdot C_d [1 - e^{-(E+G)\Delta t}]} (E + G)$$

where  $C_t$  is mercury concentration of herring ( $\mu\text{g/g}$ ),  $t$  is time (days),  $E$  is elimination rate ( $\mu\text{g/g/day}$ ),  $G$  is specific growth rate (g/g/day),  $\alpha$  is assimilation rate of mercury (0.80; Trudel and Rasmussen 2001), and  $C_d$  is mercury concentration of prey ( $\mu\text{g/g}$ ; described in text in ng/g). In fish, mercury associates with proteins and not lipids. Therefore, in our model we did not include  $K$ , daily loss of mercury due to spawning, because we assumed losses would be negligible in lipid-rich eggs (Harris *et al.* 2003; Trudel and Rasmussen 2006).

The specific growth rate for each age was estimated as follows:

$$G = \frac{1}{\Delta t} \cdot \ln\left(\frac{M_{t+\Delta t}}{M_t}\right)$$

where  $M$  is fish wet mass (g). We made the assumption that the difference between mean wet mass in consecutive cohorts (e.g., age 1 and 2) was equal to the annual growth of the younger cohort.

The elimination rate was estimated as follows:

$$E = \varphi \cdot M^{\beta} \cdot e^{\gamma \cdot T}$$

where  $\varphi$  (0.0029),  $\beta$  (-0.2), and  $\gamma$  (0.066) are empirically derived constants (Trudel and Rasmussen 1997; Trudel and Rasmussen 2001).  $T$  is average annual temperature in the Gulf of Maine on Georges Bank and the western Gulf of Maine where the fish were collected (7.02 °C). Data were obtained from the Bedford Institute of Oceanography hydrographic database (<http://www.bio.gc.ca/science/data-donnees/base/climat-climat-eng.php>).

To simplify our modeling and allow us to interpolate from age 1 to 9, we smoothed the observed data. First, herring mass and mercury burden were input to the mercury-mass balance model as best-fit functions of age to reduce noise in the results. To estimate growth we calculated the difference between mass of cohorts on the best-fit line. We also initially assumed herring consumed 100% *C. finmarchicus*, their dominant prey in the North Atlantic (Darbyson *et al.* 2003; Varpe *et al.* 2005). Determining the mercury content of *C. finmarchicus* proved difficult due to the small number of samples (n=4) and sea water contamination in one sample, which likely diluted mercury concentrations. Because prey mercury content is one of the most sensitive parameters in the mercury mass-balance model (Trudel *et al.* 2000), we varied the mercury concentration of prey in the model by  $\pm 15\%$  and  $30\%$  from the mean *C. finmarchicus* to encompass a range of

possible mercury values, as well as a varied diet.

Using our modeled specific consumption rates for each age class and the stock structure and biomass estimates available from 1999 to 2011 (Northeast Fisheries Science Center 2012), we estimated the total annual consumption for the Gulf of Maine herring population for the years 1999 to 2011. Age structure was reported as percent of total biomass for each age class from 1 to 9 years. We multiplied those proportions by total fish biomass estimates to determine the biomass of each cohort. We then extrapolated our consumption estimates ranging from 1.5 and 8.5 years to encompass the 1- to 9-year-old fish. We estimated annual consumption for each cohort by multiplying our specific consumption estimates by the biomass of each cohort. Summing the consumption for all cohorts gave total annual consumption.

## 2.3 Results

### *Age and growth*

We collected a total of 168 Gulf of Maine Atlantic herring for mass, age, and growth estimates. Age estimates ranged from 1.5 to 8.5 years. Mass increase followed a logistic growth curve ( $M_{age} = \frac{210}{(1 + 11.59 \cdot e^{0.55 \cdot \text{age}})}$ ;  $R^2=0.945$ ; Figure 1). Growth rate declined with age from 0.0013 g/g/day at age 1.5 years to 0.0001 g/g/day at age 8.5 years (Figure 2).

### *Mercury content of Atlantic herring and *C. finmarchicus**

Of the 168 total herring collected, a subset of 68 herring was sampled for total

mercury content. Whole-body mercury levels in herring increased and became more variable with age (Figure 3). Mercury concentration was lowest (14.49 ng/g) at age 1.5 years and highest (77.9 ng/g) at age 7.5 years, and our best fit rose logistically ( $Hg_{age} = \frac{0.10}{(1 + 21.78 \cdot e^{0.53 \cdot age})}$ ;  $R^2=0.946$ ). The mean mercury content ( $\pm$  SD) of *C. finmarchicus* was  $1.844 \pm 0.634$  ng/g; therefore we used a range of prey mercury inputs ( $\pm 15\%$  and  $30\%$  of the mean) in our model.

### *Consumption estimates*

Estimated specific consumption rate for herring based on the mean prey mercury content (1.844 ng/g) increased from 0.0434 g/g/day at age 1.5 years to between 0.1156 and 0.1230 g/g/day at age 6 when it neared its asymptote (Figure 4). Decreasing prey mercury content in the model by 15% and 30% resulted in a 17.6% and 42.8% increase in specific consumption rate estimates for all ages, respectively. Similarly, increasing prey mercury by 15% and 30% decreased consumption estimates by 13.0% and 23.1%, respectively (Figure 4).

Individual specific consumption rate estimates were extrapolated to the estimated Gulf of Maine herring population for the years 1999 to 2011. During this period, the mean estimated herring age dropped from 4.4 to 3.0 years (Northeast Fisheries Science Center 2012). A comparison of total consumption with average stock age and spawning stock biomass suggests consumption is more tightly correlated to age ( $R^2 = 0.699$ ) than spawning stock biomass ( $R^2 = 0.488$ ; Figure 5). The estimated specific annual

consumption of the population dropped by ~30% from 35.5 to 25.7 g/g/year over this period. Total annual consumption for the Gulf of Maine population ranged from a high of 51,408,900 MT in 2001 to 7,064,800 MT in 2010 (Figure 6).

## 2.4 Discussion

Our results show a three-fold increase in the specific consumption rate of herring in the Gulf of Maine from 0.0434 g/g/day at age 1.5 years to 0.131 at age 8.5 years. The increase with age is opposite to trends found in Baltic herring, where estimates suggest a decrease in the specific consumption rate from 0.047 g/g/day at age 1 to 0.027 g/g/day at age 8 (Rudstam 1988). While juvenile consumption rates are similar between the two studies, our estimates suggest that adult herring in this study consume approximately five times more prey biomass than Baltic herring.

This discrepancy likely has less to do with herring consumption than the methods used to derive the estimates. The bioenergetics model used by Rudstam (1988), which was based on Kitchell *et al.* (1977), underestimates consumption when compared to mercury-mass-balance models (Rowan and Rasmussen 1996). The source of the discrepancy, according to Rowan and Rasmussen (1996), is an underestimation of activity.

We suggest that seasonal migrations of adult herring greatly increase energy demand and are the driving force behind the increased consumption. Each spring and fall, adult herring migrate as far as 1000 km from the Gulf of Maine to overwintering areas in the Mid-Atlantic and southern New England region, with larger herring traveling farther

(Hildebrand 1963; Stevenson and Scott 2005; Kanwit and Libby 2009). Juveniles do not embark on these long winter migrations, but remain in deep basins in the Gulf of Maine in the winter (Boyar 1968; Stevenson and Scott 2005). Furthermore, adults migrate south to warmer waters and juveniles overwinter in colder waters of the Gulf of Maine. This means adults have higher metabolic rates than if they stayed in the colder water of the Gulf of Maine, and higher metabolic rates require increased consumption. Based on our result, the magnitude of energy expenditure or differences in winter metabolic rate may not be captured in the respiration parameters of Rudstam (1988).

Total annual consumption by Atlantic herring was tightly coupled to stock biomass. However, total consumption is more highly correlated with the population's age structure. We found that a drop in the average age in the population from about 4.5 to 3.0 years old from 1999 to 2011 resulted in a 30% reduction of consumption-to-biomass ratio due to the lower specific consumption rates of younger fish. Therefore, herring population age structure is pivotally important when estimating total consumption. Varpe *et al.* (2005) suggested a consumption-to-biomass ratio of 5.2 for herring in the Baltic Sea using consumption estimates based on Kitchell *et al.* (1977). Our estimates for consumption-to-biomass ratio were between 9.6 and 15.6, approximately two to three times that of Varpe *et al.* (2005).

## **2.5 Conclusion**

We used a mercury mass-balance model based on Trudel *et al.* (2000) to estimate age-based specific consumption rates for individual herring and the total annual



consumption of the Gulf of Maine herring population. Our estimates were two to four times higher for adult herring than published values, suggesting that the energetic demand of herring is much higher than previously reported. The higher consumption values of adults may be due to an increased energetic demand associated with seasonal migrations. Our model may be improved by including juveniles younger than age 1.5 and by obtaining more precise data on prey and prey mercury content.

Table 1: Parameter descriptions for mercury-mass-balance model

Symbol	Parameter Description	Value
$I$	Consumption rate	g/g/day
$C_t$	Mercury concentration of herring	$\mu\text{g/g}$
$t$	Time	days
$E$	Elimination rate	g/g/day
$G$	Growth rate	g/g/day
$\alpha$	Assimilation rate	0.80
$C_d$	Mercury concentration of prey	ng/g
$W_t$	Fish mass	g
$\varphi$	Coefficient of mercury elimination	0.0029
$\beta$	Allometric exponent of mercury elimination	-0.2
$\gamma$	Temperature coefficient of mercury elimination	0.066
$T$	Temperature	7.02 °C

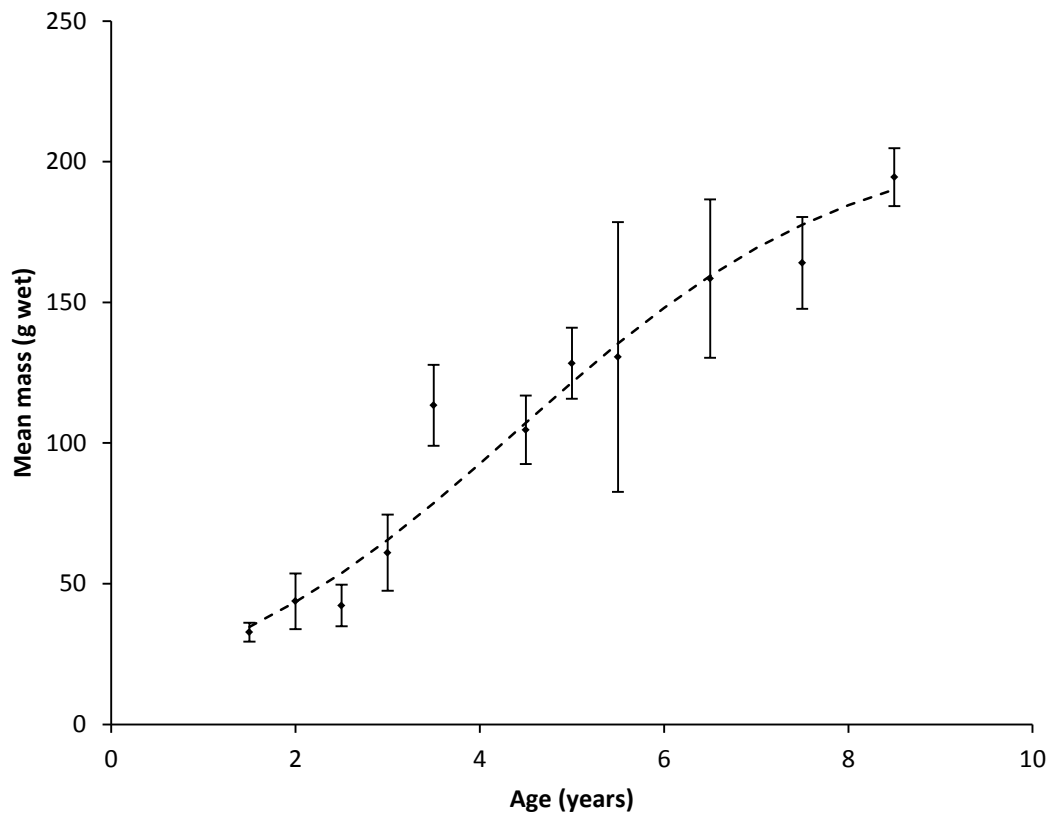


Figure 1: Mean ( $\pm$  SD) wet mass (g) of Gulf of Maine Atlantic herring sampled in fall 2012 and spring 2013. Dotted line indicates best fit logistic growth curve used as model input ( $M_{age} = \frac{210}{(1 + 11.59 \cdot e^{0.55 \cdot \text{age}})}$ ;  $R^2 = 0.945$ ).

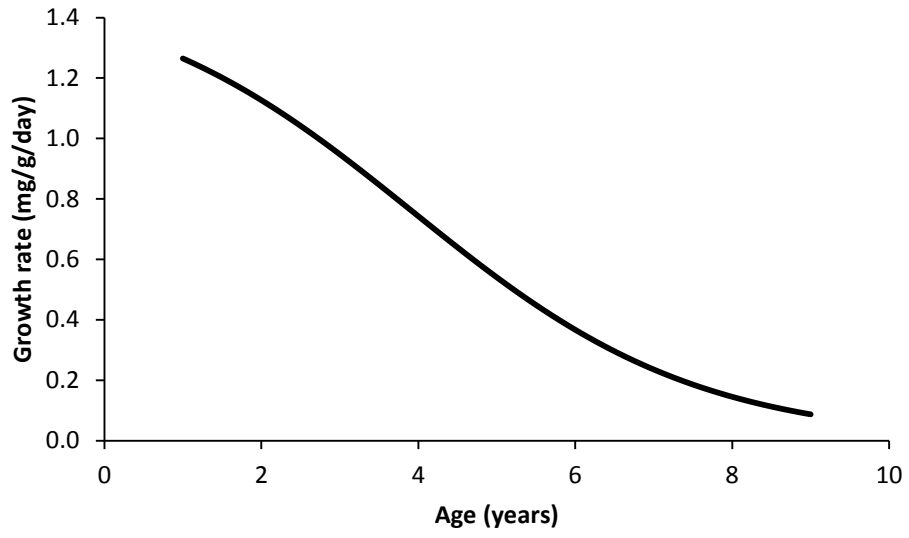


Figure 2: Modeled daily specific growth rate for Gulf of Maine Atlantic herring (mg/g/day).

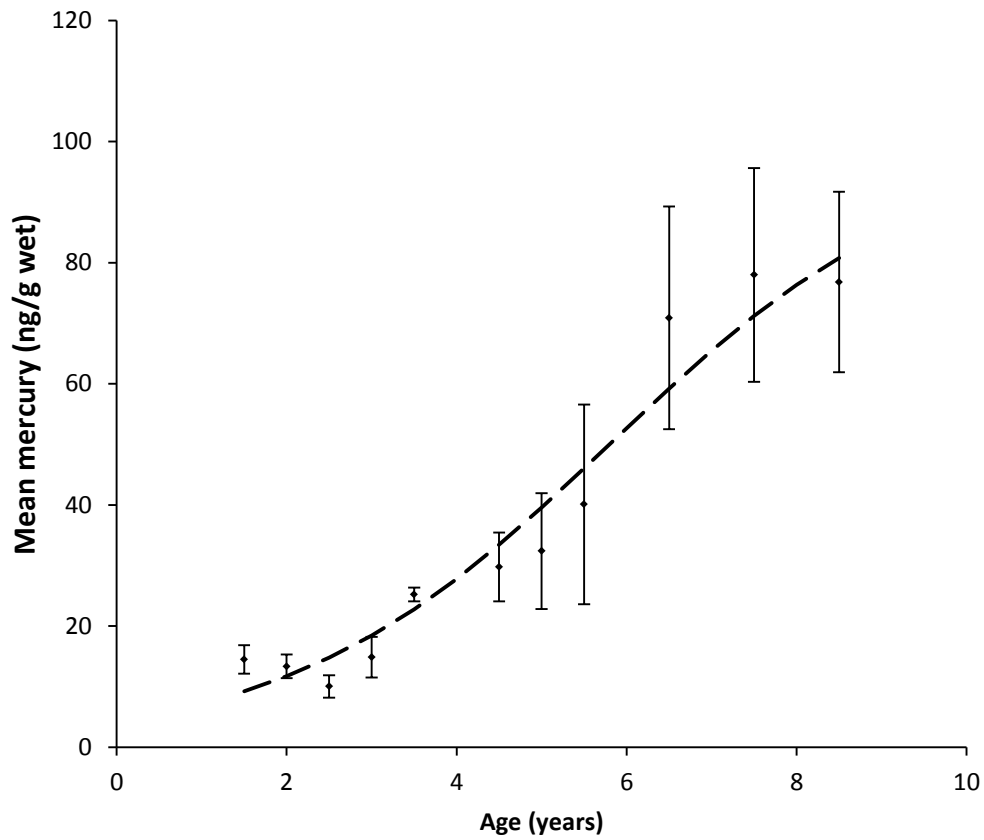


Figure 3: Mean mercury concentration ( $\pm$  SD) in Gulf of Maine Atlantic herring sampled in autumn 2012 and spring 2013. Dotted line indicates best-fit logistic growth curve used at model input ( $Hg_{age} = \frac{Hg_{max}}{(1 + 21.78 \cdot e^{0.53 \cdot age})}$ ;  $R^2 = 0.946$ ).

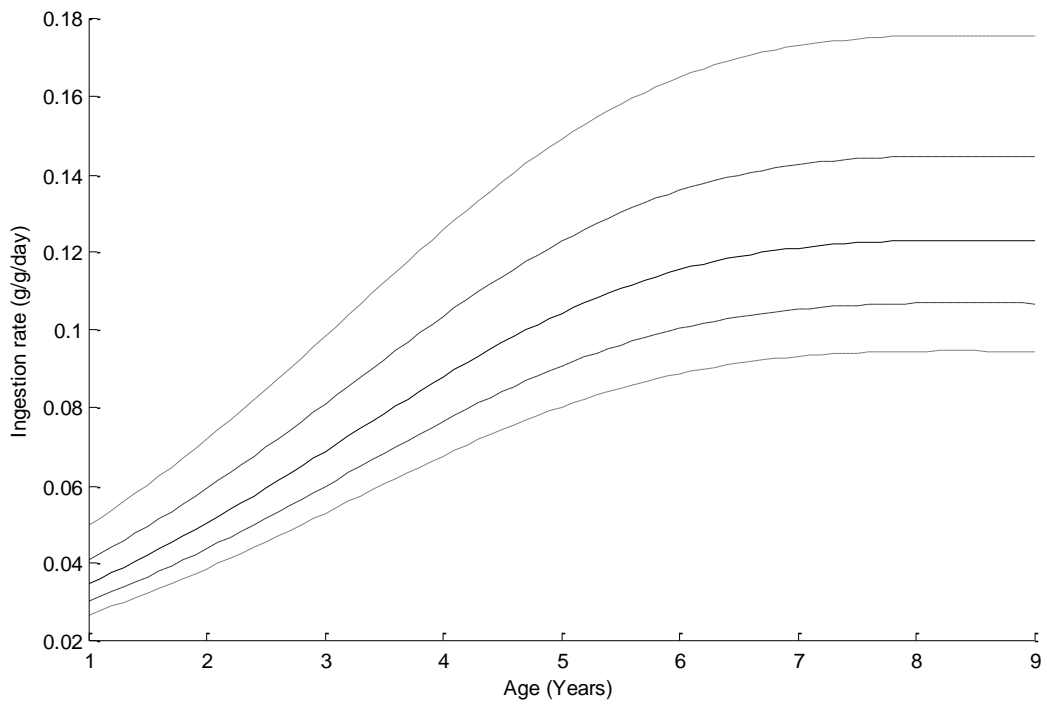


Figure 4: Herring specific consumption rate (g/g/day) as a function of fish age based on a diet of *C. finmarchicus*. The solid line shows the consumption estimate based on mean mercury prey content; dashed lines represent  $\pm 15\%$ , and dotted lines represent  $\pm 30\%$  of prey mercury content.

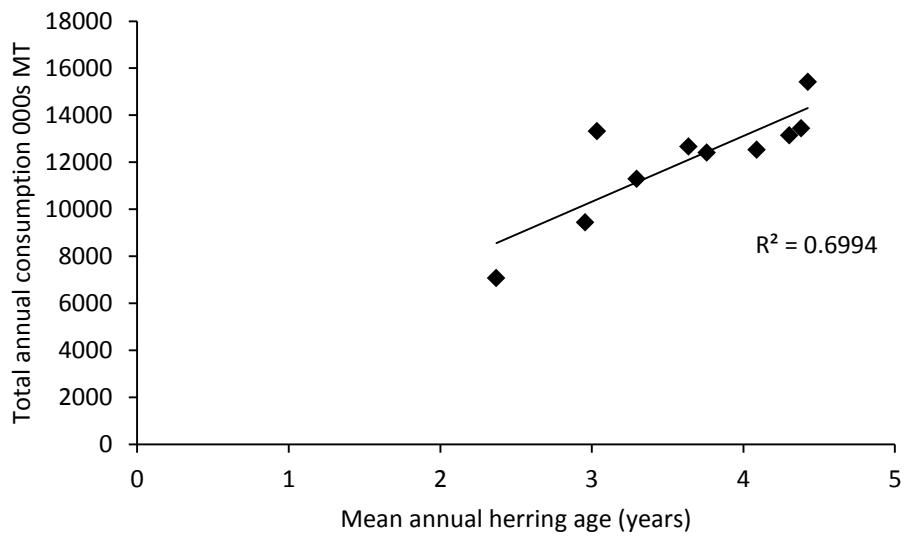
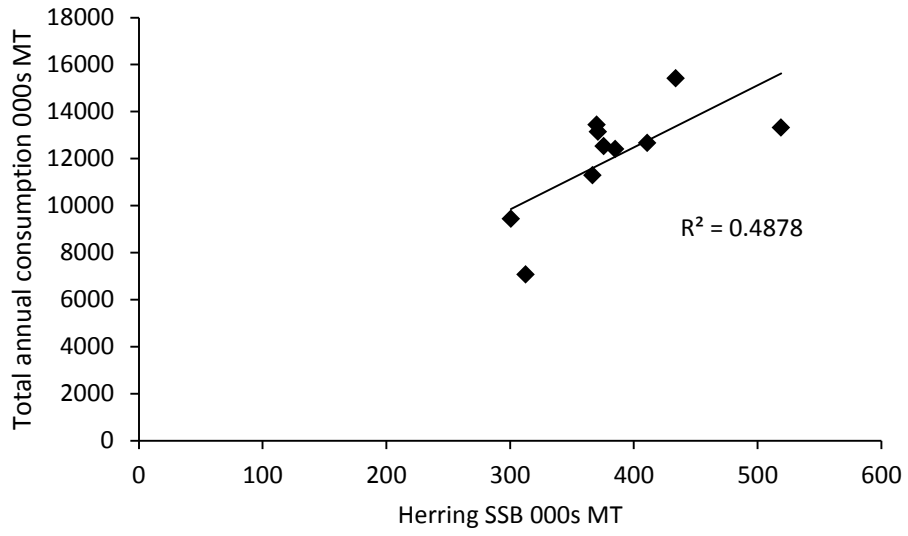


Figure 5: Correlation between total annual consumption of Atlantic herring and spawning stock biomass (top) or mean population age (bottom).

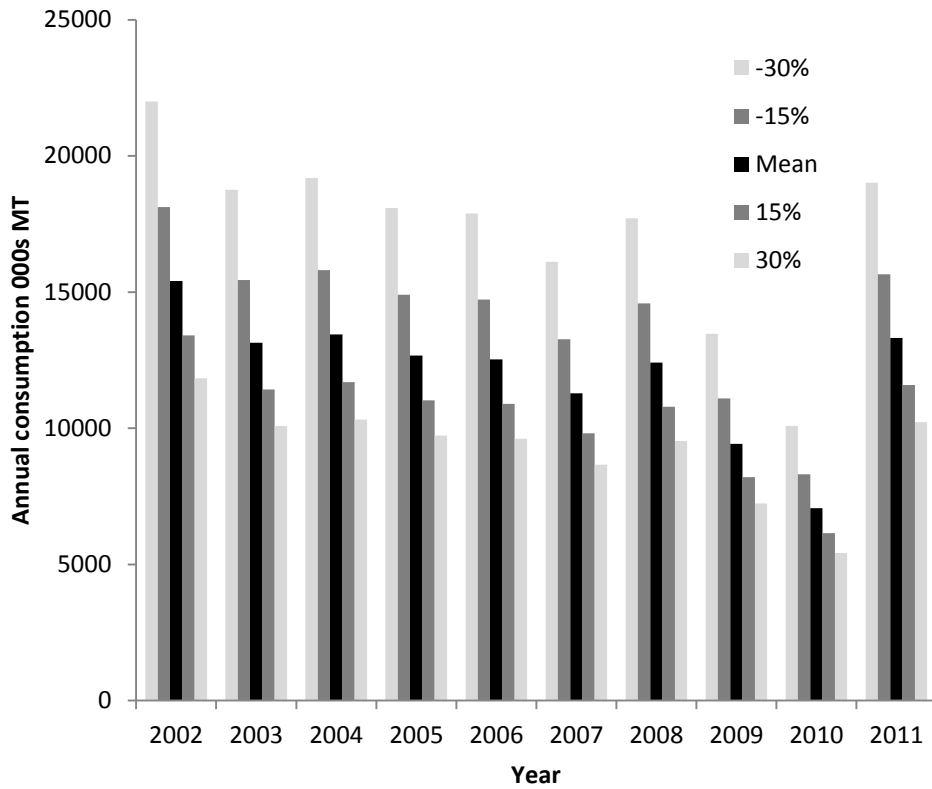


Figure 6: Total annual consumption (MT) for the Atlantic herring population in the Gulf of Maine from 1999 to 2011. The black bar shows the consumption estimate based on mean mercury prey content, the dark gray bar  $\pm 15\%$  of the mean mercury prey content, and the light gray bar  $\pm 30\%$ .



## **CHAPTER 3: ESTIMATING AGE-SPECIFIC CONSUMPTION OF ATLANTIC HERRING BY COMBINING MERCURY MASS-BALANCE AND BIOENERGETICS MODELS**

### **3.1 Introduction**

Predation and consumption are fundamental principles of ecology (Connell 1961; Paine 1966). Knowing how much an organism eats helps us understand the affects of predation on prey abundances (Hansen *et al.* 1993; Overholtz and Link 2007), how energy moves through and between systems (Polis *et al.* 1997; Varpe and Fiksen 2005), ontogenetic shifts in a species (Werner and Hall 1988), and growth in different environmental conditions (Kerr 2011). While quantifying consumption in any species generally requires complex models, fish consumption provides additional challenges, including the difficulty of direct observation, laboratory replication, and the ability to endure long periods without eating (Hallfredsson *et al.* 2007; Ferriss and Essington 2014).

Fish consumption has been quantified using several methods, including direct observation, gut content analysis, and various models (Eggers 1977; Kitchell *et al.* 1977; Elliot and Persson 1978; Trudel *et al.* 2000). Each approach has strengths and weaknesses. Direct observation can provide valuable information on the predation process, but is difficult in situ and time consuming in the laboratory. Additionally, when prey is small, assumptions must be made about the success of each predation attempt (Gibson and Ezzi 1992). Gut content analysis provides definitive information about what prey are consumed, but only provides a snapshot. Repetitive sampling over time can resolve this issue, but is time and labor intensive in the field and laboratory.

Modeling can be an effective approach to examine longer-term (greater than the season sampled) fish consumption. Consumption models are generally mass-balance models that estimate consumption by balancing energy inputs and outputs, which may vary throughout the year or the life of a fish. Once a good baseline estimate is attained, inputs can be adjusted to make predictions about consumption under different conditions. Bioenergetics and contaminant mass-balance models are both commonly used for this purpose. The WI bioenergetics model (Kitchell *et al.* 1977) has been used extensively in freshwater and marine environments for estimating fish consumption (Diana 1983; Boggs and Kitchell 1991; Wahl and Stein 1991; Stockwell and Johnson 1997) and uses energy densities of fish and their prey to derive a consumption estimate by summing the costs of metabolism, growth, and waste (Kitchell *et al.* 1977; Stewart *et al.* 1981). Bioenergetics models, however, have been criticized for their sensitivity to, and under estimation and fixed value of, fish activity (Hansen *et al.* 1993; Rowan and Rassmussen 1996). Contaminant mass-balance models have been used to estimate consumption independently of fish activity (Rowan and Rassmussen 1996; Trudel *et al.* 2000; Trudel and Rassmussen 2001). These models measure heavy metals that bioaccumulate in fish and their prey. Using excretion and assimilation rates, contaminant mass-balance models directly estimate a specific consumption rates for fish (Trudel *et al.* 2000). Several species of lake fish have been estimated to have activity levels up to four times greater using the contaminant mass-balance model compared to the bioenergetics model (Rowan and Rassmussen 1996). However, the contaminant model has been criticized for over-estimating consumption and underestimating contaminant levels in prey (He and Stewart

1997; Ferris and Essington 2014). Each of these models has pros and cons, and a single modeling approach that can make estimates for all species of fish is difficult due to the diversity of life histories. The best approach may be to examine the life history of a species and choose a model that matches strengths and minimizes weaknesses of the model based on the fish's ecology.

Adult Atlantic herring on both sides of the North Atlantic make extensive annual migrations between feeding, spawning, and overwintering grounds, whereas juveniles move relatively little (Stevenson and Scott 2005; Varpe *et al.* 2005). Tagged herring released in the Gulf of Maine and southern New England have been recovered over 1,000 km away (Kanwit and Libby 2009). Fish with highly migratory behavior have high energy costs (Dewar and Graham 1994; Nottestad *et al.* 1999), which may exacerbate any underestimation of activity in bioenergetics models, leading to a further underestimation of consumption. The ontogenetic shift to migration in herring provides an interesting opportunity to compare how consumption estimates from different models may change with increased activity.

A recent model combines the contaminant and bioenergetics models to balance the strengths and weaknesses of each (Ferris and Essington 2014). The “hybrid” model uses the consumption estimate from a bioenergetics model to back-calculate contaminant levels (e.g., mercury) using a mercury mass-balance model. The calculated mercury levels are then iteratively compared to measured mercury levels. Prey mercury burden and fish activity, the most sensitive parameters in each model, can be manipulated to improve the fit of the estimates to the measured values. Consumption can then be

calculated using the adjusted values.

In a previous study (see Chapter 2), herring consumption estimates using a mercury mass-balance model were much higher than those from the WI bioenergetics models. The specific consumption estimates were higher and showed an increase with age, compared to a decrease in specific consumption with age for Baltic herring (Rudstam 1988). We used the general framework from Ferris and Essington (2014), combining the mercury mass-balance model with a WI bioenergetics model and adjusting parameters within each, to mirror the observed increase in whole body mercury load with age in Atlantic herring taken from the Gulf of Maine in 2012 and 2013 (Chapter 2). We used this model to test the following four hypotheses to account for the differences in consumption estimates between mercury mass-balance and WI bioenergetics models:

**H1:** Consumption is overestimated by the mercury model because prey mercury content is underestimated.

**H2:** Consumption is underestimated by the WI model because fish activity is underestimated.

**H3:** Consumption is underestimated by the WI model because fish activity increases with age.

**H4:** Consumption is overestimated by the mercury model because older herring consume prey with high prey mercury content.

### 3.2 Methods

Collection, processing, and mercury analysis of herring were described in Chapter 2. Briefly, herring were collected from the Gulf of Maine in autumn 2012 and spring and

autumn 2013. Fish were frozen and later processed in the lab for total length (mm), wet mass (g), sex, age (years), and maturity. Age and mass were used to calculate growth using change in mass between cohorts. Total mercury was measured in accordance with U.S. EPA Method 7473 using a Milestone DMA-80 Direct Mercury Analyzer (Milestone Srl, Bergamo, Italy) for herring and *Calanus finmarchicus* at Clarkson University, Potsdam, New York.

The individual herring consumption rate was modeled for each age class using the WI bioenergetics model (Table 2; Kitchell *et al.* 1977; Rudstam 1988; Hansen *et al.* 1997; Rose *et al.* 2008) and mercury mass-balance model (Trudel *et al.* 2001).

To test our hypotheses we used a hybrid model (Figure 7; Ferris and Essington 2014). First, specific consumption rates from the WI bioenergetics model were calculated for each age class. The consumption equation from the mercury mass-balance model was then rearranged so that consumption was an input to estimate mercury burden. We next compared the estimated mercury burden from the hybrid model to observed mercury levels in herring. We were then able to manipulate prey mercury and activity to get a better fit between the estimated and observed herring mercury burden. We used this model framework (Figure 7) to test each of our hypotheses by manipulating prey mercury or fish activity.

Underestimation of the prey mercury burden is a chief criticism of contaminant models (Ferris and Essington 2014). Planktonic prey can be particularly difficult to measure due to their small size, relative to the sample size needed for mercury estimation (Braune 1987). We tested hypothesis H1, that underestimating prey mercury content can

account for the differences between mercury and bioenergetics model specific consumption estimates, by increasing the measured prey mercury burden in the mercury model by factors of 2, 3, and 4.

Previous studies using contaminant models have estimated that fish activity in lakes can consistently be 2 to 4 times higher than estimates from WI bioenergetics models (Rowan and Rassmussen 1996). We tested our second hypothesis H2, that underestimating the activity level can account for the differences between mercury and bioenergetics model specific consumption estimates, by increasing the activity multiplier in the WI model by factors of 2, 3, and 4.

Because neither of the previous two simulations satisfactorily explained the discrepancy in mercury burden, we tested two additional hypotheses. Hypothesis H3 addressed the increase in migration distance with age in herring (Nottestad *et al.* 1999; Stevenson and Scott 2005). We hypothesized that increasing activity as a fish ages could account for the differences between mercury and bioenergetics models. H3 was tested by multiplying activity by the proportional growth (mass) standardized to mass at age 1. We tested hypothesis H4, that an increase in prey mercury burden with age could explain the discrepancies in consumption estimates between mercury and bioenergetics models, in a similar manner. In the mercury model, we multiplied prey mercury content by the mass of the fish divided by the mass of the fish at age 1. We evaluated our hypotheses by comparing the goodness of fit between the observed and predicted mercury content of herring using  $R^2$  from linear regressions.

Once we achieved a good fit between the estimated and measured herring

mercury burden, we used the adjusted parameters in the Wisconsin bioenergetics model and mercury mass-balance model to estimate consumption.

### 3.3 Results

The herring mercury burden estimated in the initial hybrid model was relatively constant across age compared to the measured values (Figure 8). While mercury burden at age 1 was similar between modeled estimates and measured values, by age 9 measured values were ~9 times greater than estimated values.

Adjusting prey mercury concentration to double, triple, quadruple, or quintuple measured levels (H1) simply increased the estimated mercury burden in herring over all age classes, and did not change rate of accumulation with age (Figure 9). Making the same adjustments to the activity multiplier (H2) yielded similar results, with an overall increase in mercury burden and little change in slope. The  $R^2$  values for these simulations ranged from -0.81 to 0.422.

When prey mercury was held constant and the activity multiplier was multiplied by mass at age divided by mass at age 1 (H3), the estimated mercury burden improved the agreement between measured mercury burdens in herring to  $R^2 = 0.96$  (Figure 10). When the same adjustment was made to prey mercury burden and activity was left alone (H4), a similar fit was achieved ( $R^2 = 0.97$ ).

The specific consumption rate estimated using the hybrid model (H3 or H4 simulations) fell lower than the specific consumption estimates of the original mercury mass-balance model, and higher than the estimates of the bioenergetics model with an

adjusted activity multiplier (Figure 11).

### 3.4 Discussion

Our hybrid model results provide several scenarios that could explain the increase in the specific consumption rate of herring with age as estimated by the mercury mass-balance model. Proportional increases in activity and prey mercury content with fish age explained the increased specific consumption with age. The increase in activity as fish get older, however, makes better ecological sense. The ontogenetic shift from overwintering in the Gulf of Maine as juveniles to migrating as far as 1000 km as adults suggests that adults would have greater energetic costs (Nottestad *et al.* 1999; Stevenson and Scott 2005; Kanwit and Libby 2009). Because of this ontogenetic shift, we did not anticipate that a simple fixed increase in herring activity across all ages would adequately explain the increase in mercury burden. Results from our model simulation supported this prediction.

We also addressed a major concern with the mercury mass-balance model and prey mercury content—that high consumption estimates from mercury models are a result of simply underestimating prey mercury. Herring maintain simple diets dominated by a few species of similar trophic levels throughout most of their lives (Darbyson *et al.* 2003; Varpe *et al.* 2005). Therefore, the assumption of a steady prey mercury burden throughout the life of Atlantic herring seems reasonable. Allowing for both error in measuring the mercury burden in *Calanus* and a diet that likely contains other zooplankton, adjusting the average prey mercury burden appeared reasonable. However,



a fixed prey mercury burden cannot explain the discrepancy in consumption values between the bioenergetics models and mercury models, and therefore a simple underestimation of mercury in prey is not a plausible answer to our question. We also looked at what would be mathematically necessary for prey mercury burden to explain the increased mercury burden in herring with age. We found that increasing prey mercury content proportionally with age would explain the difference. However, an increase in the mercury content of prey would suggest that either herring were constantly switching prey types and moving up the food chain or that adult herring were finding the same prey with consistently higher mercury levels as they aged. Because herring maintain a fairly constant diet and utilize the same feeding grounds throughout their life, we find it less ecologically plausible that increasing prey mercury is the cause of the increase in specific consumption estimates.

In addition to the magnitude of the migration in younger versus older herring, various aspects of the migration may also implicate an increased energetic demand. Herring filter feed in high prey densities (Gibson and Ezzi 1990), such as those found during spring and summer blooms in the Gulf of Maine (Townsend and Spinrad 1986; Thomas *et al.* 2003). However, herring switch feeding modality to particulate feeding at lower prey densities (Gibson and Ezzi 1990). In adult herring overwintering grounds along the mid-Atlantic coast of the United States, prey densities are likely lower than those found in spring blooms in the Gulf of Maine. Lower prey densities suggest herring would particulate feed. Although particulate feeding is less energetically costly than filter feeding, it is also less profitable (James and Probyn 1989; Gibson and Ezzi 1992). This suggests that in

order to maintain a daily ration by particulate feeding, more time would need to be spent foraging.

We are not the first investigators to suggest that activity can vary with body mass. In walleye (*Sander vitreus*), juvenile activity was found to correlate to body mass, predation, and food density (Madon and Culver 1993). Walleye, northern pike (*Esox niger*), and lake whitefish (*Coregonus clupeaformis*) consumption rates have also been estimated to increase with body mass using mercury mass-balance models; however, these increases were at most a doubling in specific consumption rate and varied among lakes (Trudel *et al.* 2000). Our consumption rate estimates are 1.7–7.5 times higher, suggesting that highly migratory species may have a much larger energy requirement and impact on lower trophic levels than previously thought.

The implication of our model simulations is that, depending on life history, respiration, metabolic, and consumption rates may not decrease with body size. Fishes whose activity as adults far exceeds activity as juveniles cannot be assumed to have fixed activity rates. We suggest that this may be especially true of highly migratory pelagic marine fishes. These results are contrary to what we previously believed about the feeding habits of herring, and leave the door open for future studies on winter foraging and migration costs of herring on the mid-Atlantic coast of the United States.

Our methods worked off ideas put forward by Ferris and Essington (2014) using a hybrid of two models that seem to be at odds in the literature (Rowan and Rasmussen 1997; Stewart and He 1997; Trudel and Rasmussen 2006). We found that combining approaches provided a more in depth insight to fish consumption and allowed us to see

how weaknesses in each model can work in tandem. While the method requires more input (mercury burdens and energy densities) and greater parameterization, we believe it allowed for greater control to make adjustments that aligned with the fish's life history.

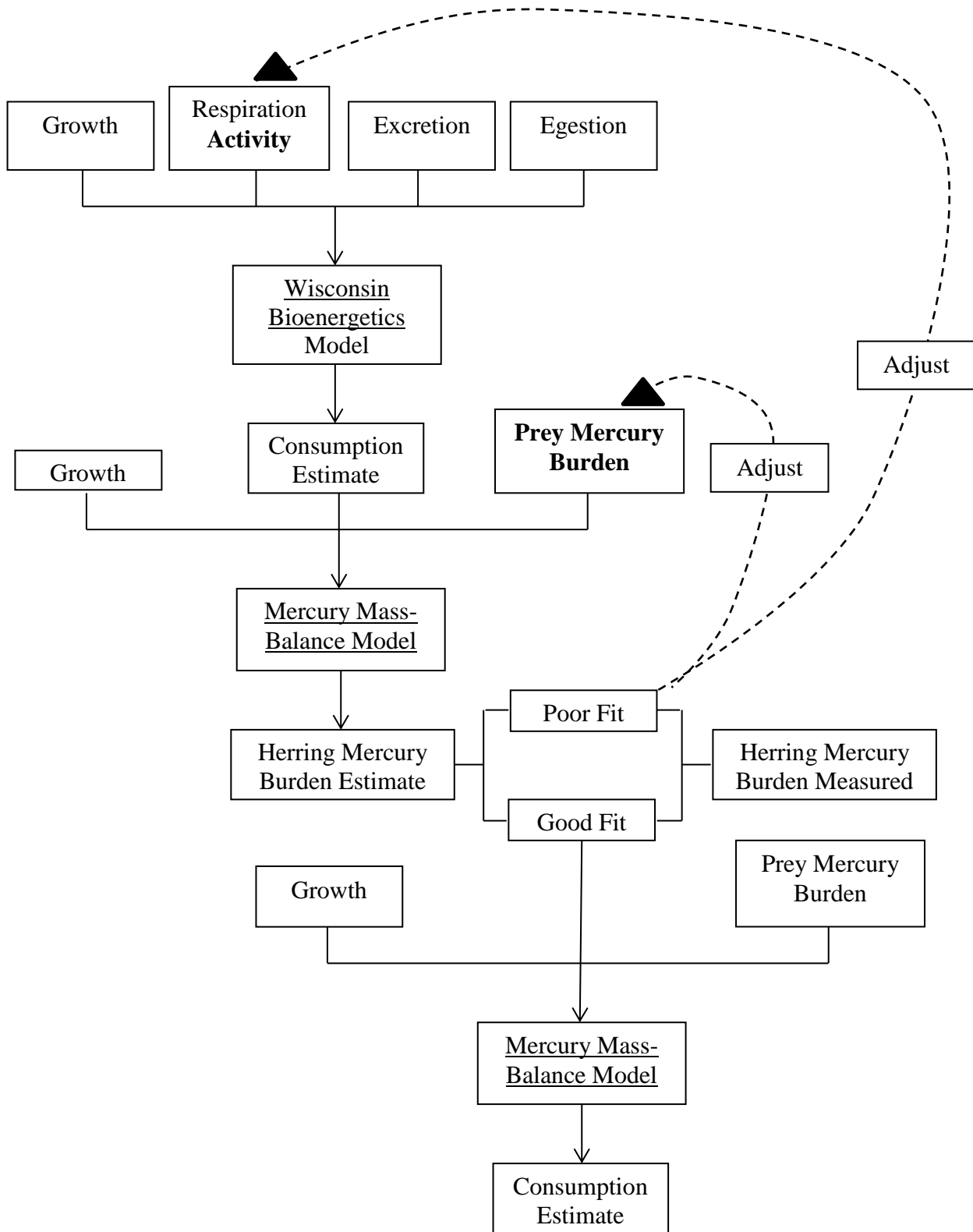


Figure 7: Flowchart showing the hybrid consumption model. Adjusted parameters in the model are shown in bold.

Table 2. Parameter descriptions for the Wisconsin bioenergetics model.

Symbol	Parameter description	Value
C <sub>A</sub>	Intercept of the allometric mass function	0.642
C <sub>B</sub>	Slope of the allometric mass function	-0.256
C <sub>Q</sub>	Lower water temperature (°C) at which temperature dependence is CK1 of maximum rate	13
CTM	Water temperature (°C) at which dependence is 0.98 of the maximum	15
CTL	Temperature (°C) at which dependence is a reduced CK4 of the maximum rate	23
CK1	Small fraction of maximum rate	0.1
CK4	Reduced fraction of the maximum rate	0.01
R <sub>A</sub>	Specific weight of oxygen	0.0033
R <sub>B</sub>	Slope of the allometric mass function	-0.227
R <sub>Q</sub>	Rate at which respiration increases over relatively low temperatures	0.0548
RTO	Desired velocity (cm/s)	0.03
RTL	Cut-off temperature	9
RK1	Intercept for swimming speed above cut-off temperature	15
RK4	Mass dependence coefficient for swimming speed at all water temperatures	0.13
ACT	Intercept of the relationship of swimming speed at water temperatures below RTL	3.9
BACT	Water temperature dependence coefficient of swimming speed at water temperatures below RTL	0.149
SDA	Specific dynamic action coefficient	0.175
F <sub>A</sub>	Constant proportion of consumption	0.16
U <sub>A</sub>	Constant proportion of assimilated energy	0.1

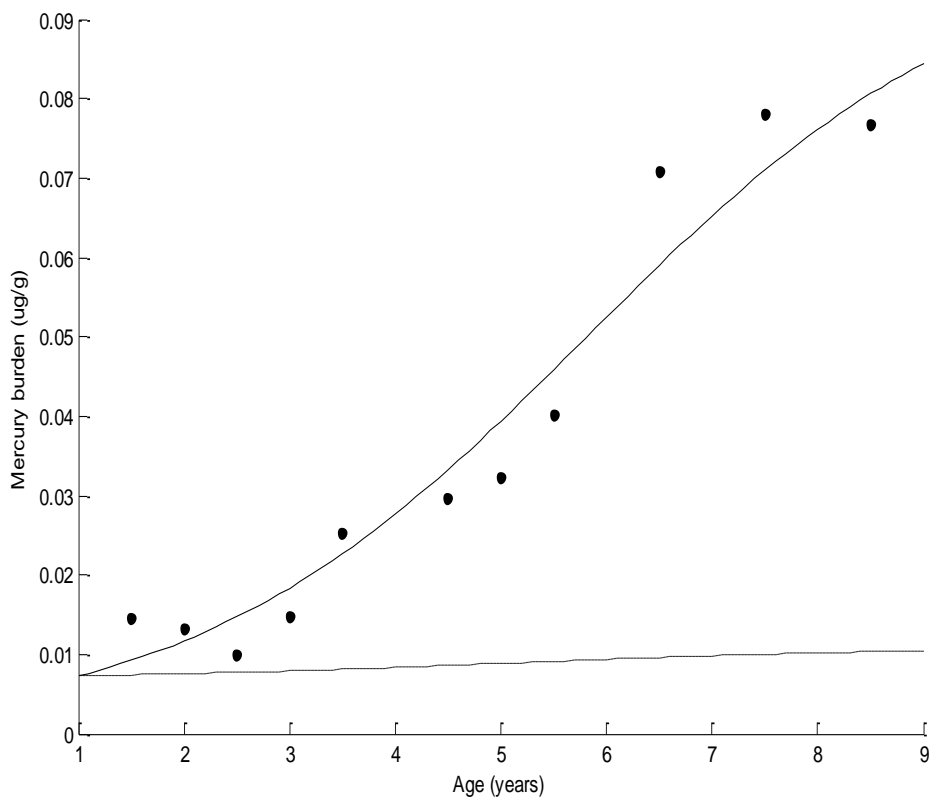


Figure 8: Measured mercury burden in Atlantic herring at age (solid line) and estimated mercury burden of Atlantic herring (dotted line) based on consumption estimates from an unaltered WI bioenergetics model input into an unaltered mercury mass-balance model. Points indicate mean measured mercury burden.

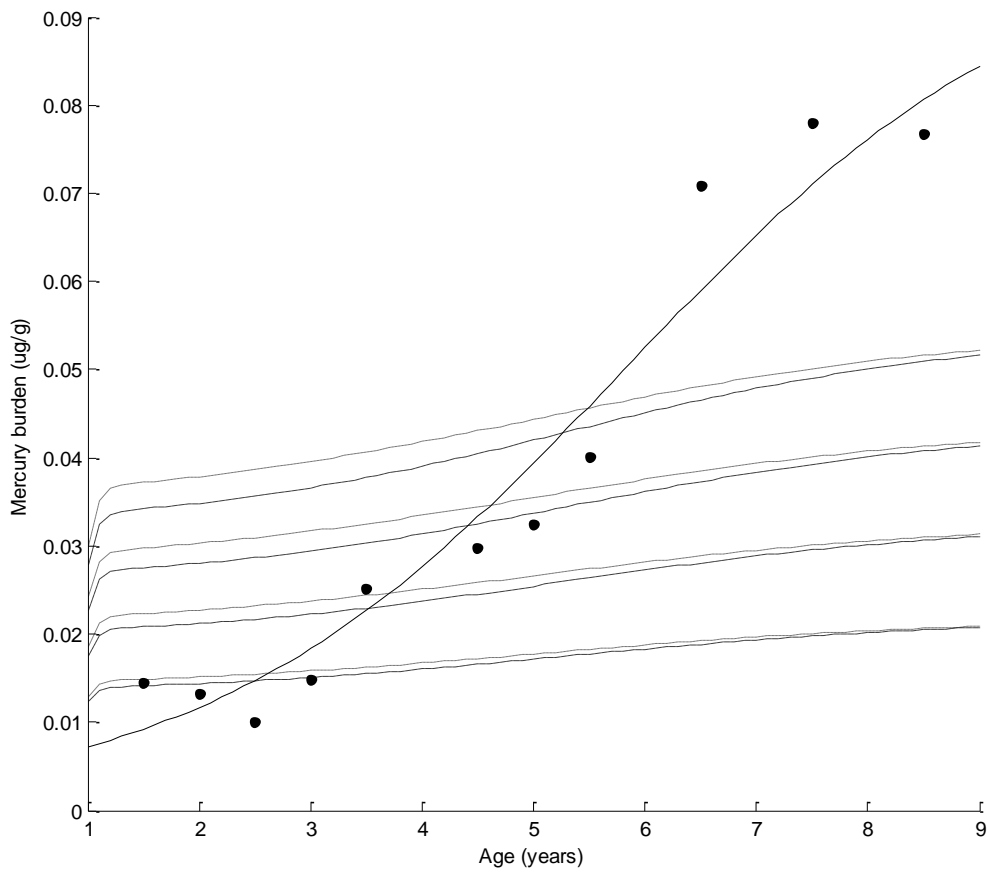


Figure 9: Measured mercury burden in Atlantic herring at age (solid line), estimated mercury burden of Atlantic herring based on a WI bioenergetics model with activity (dashed line) or prey mercury (dotted line) doubled, tripled, quadrupled, or quintupled. Points indicate mean measured mercury burden.

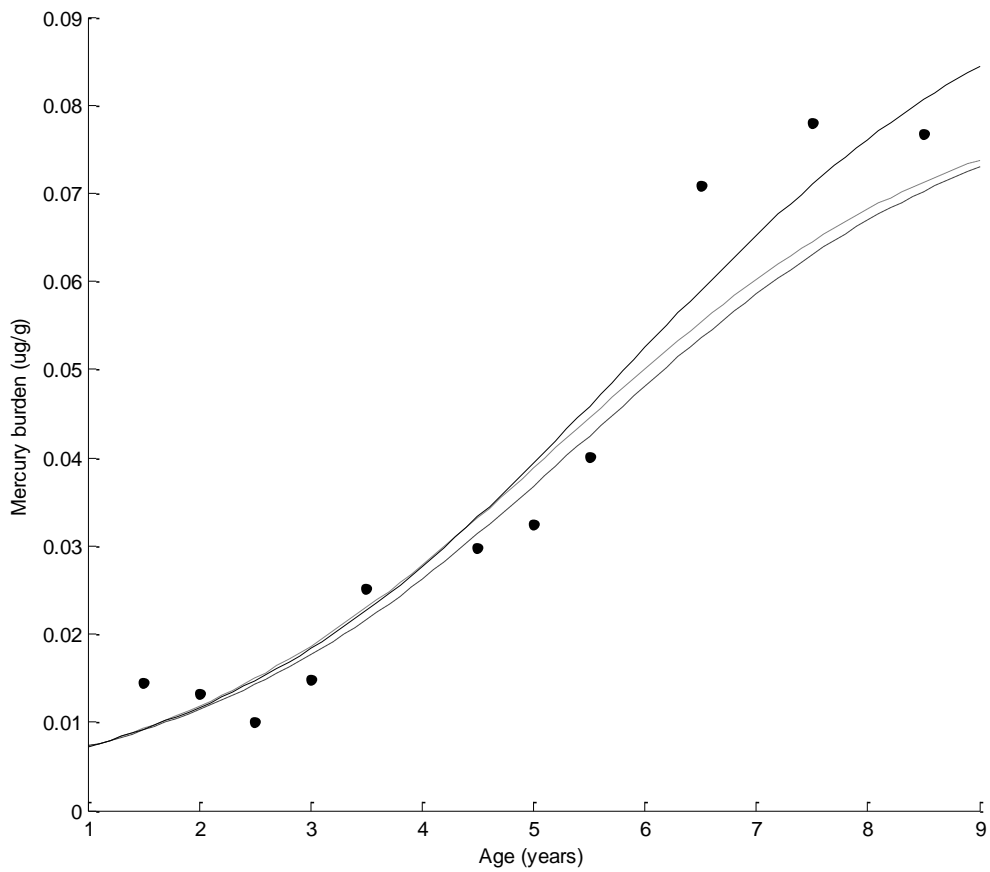


Figure 10: Measured mercury burden in Atlantic herring at age (solid line), estimated mercury burden of Atlantic herring based on a WI bioenergetics model with activity (dashed line) or prey mercury (dotted line) multiplied by current mass divided by mass at age 1. Points indicate mean measured mercury burden.



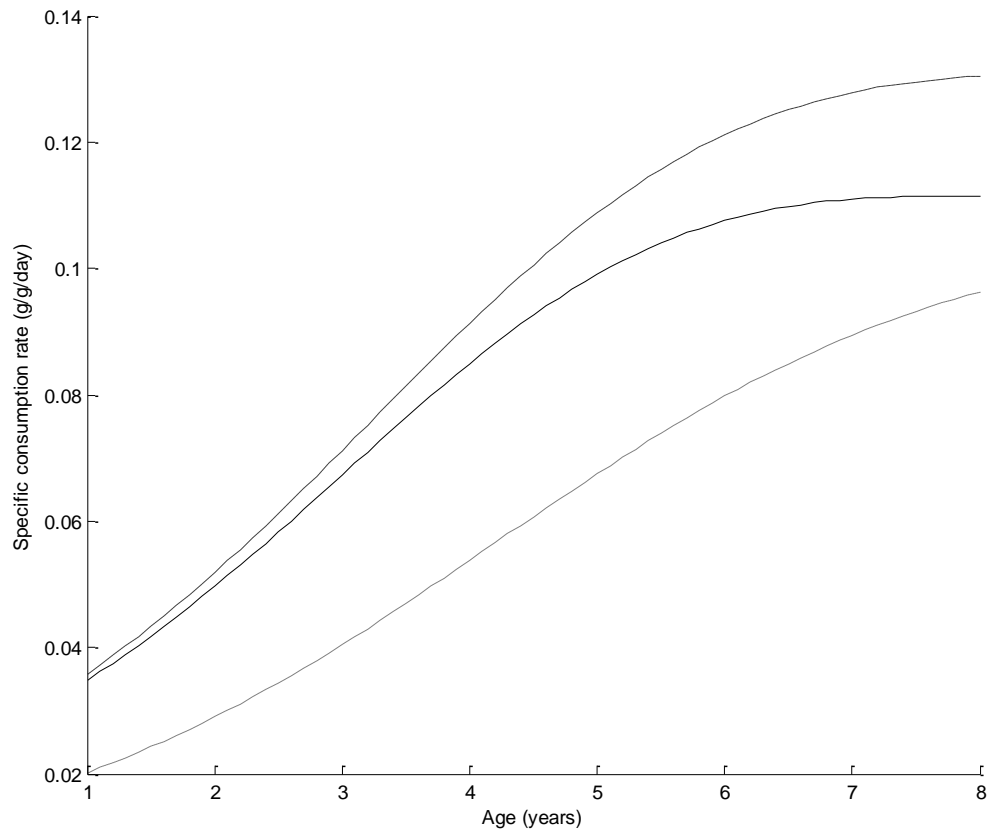


Figure 11: Specific consumption of Atlantic herring at age based on original mercury mass-balance model (Chapter 2; dashed line), hybrid model (with prey mercury content held constant and activity multiplied by current mass divided by mass at age 1 (solid line), and Wisconsin model with activity multiplied by current mass divided by mass at age 1 (dotted line).

## CHAPTER 4: BIBLIOGRAPHY

- Albert, G.J., & Taconand, M.M. (2009). Fishing for feed of fishing for food: Increasing global competition for small pelagic forage fish. *AMBIO* 38(6), 294-302.
- Bailey, B.A., & Pershing, A.J. (2013). A nonlinear model for predicting interannual changes in *Calanus finmarchicus* abundance in the Gulf of Maine. *Journal of Agricultural, Biological, and Environmental Statistics* 18(2), 234-249.
- Bakun, A. (1996). Patterns in the Ocean: Ocean processes and marine population dynamics. *Reviews in Fish Biology and Fisheries* 7(3), 382-384.
- Bakun, A., Babcock, E.A., & Santora, C. (2009). Regulating a complex adaptive system via its wasp-waist: Grappling with ecosystem-based management of the New England herring fishery. *ICES Journal of Marine Science* 66, 1768–1775
- Båmstedt, U., & Tande, K. (1988). Physiological responses of *Calanus finmarchicus* and *Metridia longa* (Copepoda: Calanoida) during the winter-spring transition. *Marine Biology* 99(1), 31-38.
- Bigelow, H.B., Bradbury, M.G., Dymond, J.R., Greeley, J.R., Hildebrand, S.F., Mead, G.W., Miller, R.R., Suttkus, L.R., & Vladykov, V.D. (1948). *Fishes of the western North Atlantic*. New Haven, CT: Sears Foundation for Marine Research, Yale University.
- Bigelow, H.B., Schroeder, W., & Hole, W. (1953). *Fishes of the Gulf of Maine*. Washington, DC: U.S. Government Printing Office, 80-100.
- Boggs, C.H., & Kitchell, J.F. (1991). Tuna metabolic rates estimated from energy losses during starvation. *Physiological Zoology* 64(2), 502-524.
- Boyar, H.C., Marak, R.R., Perkins, F.E., & Clifford, R.A. (1973). Seasonal distribution and growth of larval herring (*Clupea harengus* L.) in the Georges Bank-Gulf of Maine area from 1962 to 1970. *Journal du Conseil* 35(1), 36-51.
- Brander, K.M., Dickson, R.R., & Shepherd, J.G. (2001). Modelling the timing of plankton production and its effect on recruitment of cod (*Gadus morhua*). *ICES Journal of Marine Science: Journal du Conseil* 58(5), 962-966.
- Braune, B.M., & Gaskin, D.E. (1987). Mercury levels in Bonaparte's gulls (*Larus philadelphia*) during autumn molt in the Quoddy region, New Brunswick, Canada. *Archives of Environmental Contamination and Toxicology* 16(5), 539-549.

- Campbell, R., Wagner, M., Teegarden, G., Boudreau, C., & Durbin, E.G. (2001). Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series* 221, 161–183.
- Casini, M., Hjelm, J., Molinero, J.C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., & Kornilovs, G. (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences* 106(1), 197-202.
- Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.C., & Kornilovs, G. (2008). Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences* 275(1644), 1793-1801.
- Chase, B.C. (2002). Differences in diet of Atlantic bluefin tuna at five seasonal feeding grounds on the New England continental shelf. *Fish Bull* 100, 168-180.
- Connell, J.H. (1961). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31(1), 61-104.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., & Verheye, H.M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science* 57(3), 603–618.
- Cyterski, M., Ney, J., & Duval, M. (2002). Predator demand for clupeid prey in Smith Mountain Lake, Virginia. *Fisheries Research* 59(1), 1-16.
- Darbyson, E., Swain, D.P., Chabot, D., & Castonguay, M. (2003). Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. *Journal of Fish Biology* 63(5), 1235-1257.
- Dewar, H., & Graham, J. (1994). Studies of tropical tuna swimming performance in a large water tunnel-energetics. *Journal of Experimental Biology* 192(1), 13-31.
- Diana, J.S. (1983). Oxygen consumption by largemouth bass under constant and fluctuating thermal regimes. *Can. J. Zool.* 61, 1892-1895.
- Durbin, A.G., Nixon, S.W., & Oviatt, C.A. (1979). Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. *Ecology* 60(1), 8-17.
- Eggers, D. M. (1977). The nature of prey selection by planktivorous fish. *Ecology* 58(1), 46-59.

- Elliott, J.M., & Persson, L. (1978). The estimation of daily rates of food consumption for fish. *The Journal of Animal Ecology* 47(3), 977-991.
- Evanson, M., Bornhold, E.A., Goldblatt, R.H., Harrison, P.J., & Lewis, A.G. (2000). Temporal variation in body composition and lipid storage of the overwintering, subarctic copepod *Neocalanus plumchrus* in the Strait of Georgia, British Columbia (Canada). *Marine Ecology Progress Series* 192, 239–247.
- Ferris, B.E., & Essington, T.E., (2014). Can fish consumption rate be improved by linking bioenergetics and mercury mass balance models? Application to tunas. *Ecological modelling* 272, 232-241.
- Fiksen, O., & Carlotti, F. (1998). A model of optimal life history and diel vertical migration in *Calanus Finmarchicus*. *Sarsia* 83, 129–147.
- Fish, C.J. (1936). The Biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull. Mar. Biol. Lab.* 70, 118-141.
- Fleminger, A., & Hulsemann, K. (1977). Geographical range and taxonomic divergence in North Atlantic calanus (*C. helgoandicus*, *C. finmarchicus* and *C. glacialis*). *Marine Biology* 40, 233-248.
- Frank, K.T., Petrie, B., Choi, J.S., & Leggett, W.C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308(5728), 1621-1623.
- Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* 33(5), 1182-1190.
- Gibson, R.N., & Ezzi, I.A. (1992). The relative profitability of particulate feeding and filter feeding in the herring *Clupea harengus*. *Journal of Fish Biology* 40, 577-590.
- Greene, C.H. (2013). Towards a more balanced view of marine ecosystems. *Fisheries Oceanography* 22(2), 140-142.
- Greene, C.H., & Pershing, A.J. (2003). The flip-side of the North Atlantic Oscillation and modal shifts in slope-water circulation patterns. *Limnology and Oceanography* 48(1), 319-322.
- Greene, C.H., & Pershing, A.J. (2007). Oceans. Climate drives sea change. *Science* 315(5815), 1084-1085.
- Grigg, H., & Bardwell, S.J. (1982). Seasonal observations on moulting and maturation in stage V copepodites of *Calanus finmarchicus* from the Firth of Clyde. *Journal of the*

- Marine Biological Association of the United Kingdom* 62(2), 315-327.
- Hallfredsson, E.H., Pedersen, T., & Præbel, K. (2007). Estimation of digestion rates for herring *Clupea harengus* L. feeding on fish larvae. *Journal of Fish Biology* 70(2), 638-643.
- Hansen, M., Boisclair, D., Brandt, S.B., Hewett, S.W., Kitchell, J.F., Lucas, M.C., & Ney, J.J. (1993). Applications of bioenergetics models to fish ecology and management: Where do we go from here? *Transactions of the American Fisheries Society* 122, 1019-1030.
- Hanson, P.C., Johnson, T.B., Schindler, D.E., & Kitchell, J.F. (1997). Fish bioenergetics 3.0 for Windows. University of WI-Madison Sea Grant Institute, Madison.
- He, J., & Stewart, D.J. (1997). Comment—Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (<sup>137</sup>Cs). *Canadian Journal Fisheries and Aquatic Sciences* 54, 1953-1954.
- Holt, R.D. (1996). Food webs in space: An island biogeographic perspective. *Food Webs*. 313-323.
- Hunt Jr., G.L., & McKinnell, S. (2006). Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress in Oceanography* 68(2), 115-124.
- Jordán, F., Liu, W.C., & Wyatt, T. (2005). Topological constraints on the dynamics of wasp-waist ecosystems. *Journal of Marine Systems* 57(3), 250-263.
- Kanwit, J.K., & Libby, D.A. (2009). Seasonal movements of Atlantic herring (*Clupea harengus*): Results from a four year tagging study conducted in the Gulf of Maine and Southern New England. *J. Northw. Atl. Fish. Sci.* 40, 29-39.
- Kelly, K.H., & Stevenson, D.K. (1985). Fecundity of Atlantic herring (*Clupea harengus*) from three spawning areas in the western Gulf of Maine, 1969 and 1982. *J. Northw. Atl. Fish. Sci.* 6, 149-155.
- Kitchell, J.F. (1977). Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Board of Canada* 34, 1922-1935.
- Madon, S.P., & Culver, D.A. (1993). Bioenergetics model for larval and juvenile Walleyes: An in situ approach with experimental ponds. *Transactions of the American Fisheries Society* 122, 797-813.

- Michaud, J., & Taggart, C. (2007). Lipid and gross energy content of North Atlantic right whale food, *Calanus finmarchicus*, in the Bay of Fundy. *Endangered Species Research* 3, 77-94.
- Miller, C.B., Cowles, T., Wiebe, P., Copley, N., & Grigg, H. (1991). Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. *Mar. Ecol. Prog. Ser.* 72, 79-91.
- Miller, C., Morgan, C., Prahl, F., & Sparrow, M. (1998). Storage lipids of the copepod *Calanus finmarchicus* from Georges Bank and the Gulf of Maine. *Limnology and Oceanography* 43(3), 488-497.
- Northeast Fisheries Science Center. (2012). 54th Northeast Regional Stock Assessment Workshop (54th SAW) Assessment Report. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 12-18; 600 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026
- Nøttestad, L., Giske, J., Holst, J.C., & Huse, G. (1999). A length-based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* 56(S1), 26-34.
- Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., & Folke, C. (2007). Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10, 877-889.
- Overholtz, W.J. (2002). The Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*): Spatial pattern analysis of the collapse and recovery of a large marine fish complex. *Fisheries Research* 57, 237-254.
- Overholtz, W.J., Jacobson, L.D., & Link, J.S. (2008). An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine-Georges Bank Atlantic herring complex. *North American Journal of Fisheries Management* 28(1), 247-257.
- Overholtz, W.J., & Link, J.S. (2007). Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. *ICES Journal of Marine Science: Journal du Conseil* 64(1), 83-96.
- Paine, R.T. (1969). A note on trophic complexity and community stability. *American Naturalist* 103(929), 91-93.
- Pershing, A.J., Greene, C.H., & Hannah, C. (2001). Oceanographic responses to climate

in the Northwest Atlantic. *Oceanography* 14(3), 76-82.

- Pershing, A.J., Greene, C.H., Jossi, J., Obrien, L., Brodziak, J., & Bailey, B. (2005). Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. *ICES Journal of Marine Science* 62(7), 1511-1523.
- Pickart, R.S., McKee, T.K., & Harrington, S. (1999). Mean Structure and Interannual Variability of the Slopewater System South of Newfoundland\*. *Journal of Physical Oceanography* 29(10), 2541-2558.
- Plourde, S., Joly, P., Runge, J. a, Zakardjian, B., & Dodson, J.J. (2001). Life cycle of *Calanus finmarchicus* in the lower St. Lawrence Estuary: The imprint of circulation and late timing of the spring phytoplankton bloom. *Canadian Journal of Fisheries and Aquatic Sciences* 58(4), 647-658.
- Polis, G.A., Anderson, W.B., & Holt, R.D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28, 289-316.
- Reid, R., & Cargnelli, L. (1999). Essential fish habitat source document: Atlantic herring, *Clupea harengus*, life history and habitat characteristics. *NOAA Technical* (July), 1-84.
- Rose, K.A., Megrey B.A., Hay D., Werner F., & Schweigert J. (2008). Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. *Transactions of the American Fisheries Society* 137, 278-297.
- Rowan, D.J., & Rasmussen, J.B. (1996). Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (<sup>137</sup>Cs). *Canadian Journal of Fisheries and Aquatic Sciences* 53(4), 734-745.
- Rudstam, L.G. (1988). Exploring the dynamics of herring consumption in the Baltic: applications of an energetic model of fish growth. *Kieler Meeresforschungen Sonderheft* 6, 312-322.
- Runge, J.A. (1988). Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. *Hydrobiologia* 167/168, 61-71.
- Sinclair, M., & Tremblay, M. (1984). Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. *Canadian Journal of Fisheries and Aquatic Sciences* 41(7), 1055-1065.

- Stevenson, D.K., Scott, M.L. (2005). *Essential fish habitat source document: Atlantic herring, Clupea harengus, life history and habitat characteristics*, 2nd edition. NOAA Tech Memo NMFS NE 192; 84 p.
- Stewart, D.J., Kitchell, J.F., & Crowder, L.B. (1981). Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110(6), 751-763.
- Stockwell, J.D., & Johnson, B.M. (1997). Refinement and calibration of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 54(11), 2659-2676.
- Thomas, A.C., Townsend, D.W., & Weatherbee, R. (2003). Satellite-measured phytoplankton variability in the Gulf of Maine. *Continental Shelf Research* 23(10), 971-989.
- Townsend, D.W., & Spinrad, R.W. (1986). Early spring phytoplankton blooms in the Gulf of Maine. *Continental Shelf Research* 6(4), 515-529.
- Trudel, M., Tremblay, A., Schetagne, R., & Rasmussen, J.B. (2000). Estimating food consumption rates of fish using a mercury mass balance model. *Canadian Journal of Fisheries and Aquatic Sciences* 57(2), 414-428.
- Trudel, M., Tremblay, A., Schetagne, R., & Rasmussen, J.B. (2001). Why are dwarf fish so small? An energetic analysis of polymorphism in lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences* 58(2), 394-405.
- Wahl, D.H., & Stein, R.A. (1991). Food consumption and growth of three esocids: Field tests of a bioenergetic model. *Transactions of the American Fisheries Society* 120(2), 230-246.
- Wanless, S., Harris, M.P., Redman, P., & Speakman, J.R. (2005). Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294(1), 8.
- Werner, E.E., & Hall, D.J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology* 69(5), 1352-1366.
- Varpe, Ø., & Fiksen, O. (2010). Seasonal plankton–fish interactions: Light regime, prey phenology, and herring foraging. *Ecology* 91(2), 311-318.
- Varpe, Ø., Fiksen, Ø., & Slotte, A. (2005). Meta-ecosystems and biological energy transport from ocean to coast: The ecological importance of herring migration.



*Oecologia* 146(3), 443-451.

Zananski, T.J., Holsen, T.M., Hopke, P.K., & Crimmins, B.S. (2011). Mercury temporal trends in top predator fish of the Laurentian Great Lakes. *Ecotoxicology* 20(7), 1568-1576.