ENVIRONMENTAL QUALITY ASSESSMENT OF GEORGES BANK FOR ATLANTIC COD (*Gadus morhua*)

by

Ana M. Sellers

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Ana M. Sellers

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Approved:

Dr. Jeffrey A. Tyler

Dr. Jill Rulfs

Dr. J. Michael Jech

Abstract

The Georges Bank area in the northwest Atlantic Ocean plays an important role in New England's economy. Overfishing has led to a rapid decrease in cod population numbers, leading to a collapse in certain stocks. Currently, the rate of decrease in cod numbers has slowed; however, population numbers are still low.

In this study, I use Growth Rate Potential (GRP) to assess the current environmental quality of Georges Bank and its suitability to support a cod population. GRP is the amount of growth predicted for a fish with known prey availability and environmental conditions. With prey availability and temperature data obtained during the fall fisheries acoustics surveys in 2000, 2001 and 2002, I developed spatially explicit GRP maps, using bioenergetic and foraging models, for Atlantic cod to determine the ability of the Georges Bank environment to support a cod population. Results show that Georges Bank is able to support growth for adult Atlantic cod.

In addition to GRP analysis, I studied nucleic acid concentrations of Atlantic herring. Nucleic acids play an important role in growth and development, and have been used to assess physical condition of fish as well as and current growth rates. In this study, I determine total nucleic acid concentrations of Atlantic herring caught during three different spawning stages: pre-, post-, and non-spawning, to determine how nucleic acid concentrations and energy allocation vary seasonally. Results support the hypothesis that nucleic acid concentrations can be used as condition indicators, and are highly sensitive to the spawning stage of fish showing a significant difference between the three groups, which may affect their ability as condition indicators.

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General Introduction

The Georges Bank area of the northwest Atlantic Ocean has played an important role in New England's economy since the 1700s (Kurlansky, 1997). This area is one of the most productive marine environments and supports one of the richest fisheries, holding one of the largest Atlantic cod populations in the world (Backus, 1987). However, centuries of overfishing have led to a decline of the cod population, ending in a collapse of several stocks and closure of the Canadian and U.S. fishing grounds in 1993 (Cook, 2002). Currently, the rate of decrease in cod numbers has slowed significantly, although population numbers are still low.

In this study, I use Growth Rate Potential (GRP) to assess the environmental quality of Georges Bank and its suitability to support a cod population. GRP is the amount of growth predicted for a fish with known prey availability and environmental conditions (Brandt, 1992). Prey availability was determined by means of acoustic measurements collected during the Northeast Fisheries Science Center (NEFSC) 2000, 2001 and 2002, fall fisheries acoustic surveys, to assess Atlantic herring, cod's major food source. Temperature data were also collected during the research cruises, aboard the NOAA FR/V Delaware II. With these data, I developed spatially explicit GRP maps using bioenergetic and foraging models for Atlantic cod to determine the ability of the Georges Bank environment to support a cod population.

In addition to GRP analysis, I studied nucleic acid concentrations of Atlantic herring. Nucleic acids play an important role in growth and development, and have been used to assess physical condition of fish as well as current growth rates (Clemmesen, 1993). Since ribonucleic acid (RNA) is the organizer for protein synthesis, RNA

concentrations reflect instantaneous growth rate and nutritional status of an individual (Bulow, 1970). In this study, I determine nucleic acid concentrations of Atlantic herring caught during three different stages of their spawning season: pre-spawning, post-spawning and non-spawning, to determine how nucleic acid concentrations vary seasonally. This will reflect how growth rate is affected by seasons and how energy allocation changes due to spawning stage.

This study was originally intended to use RNA:DNA ratios using fluorescence techniques, as growth rate measurements of Atlantic herring and use them to validate the growth predictions of GRP analyses. Because of difficulties collecting tissue samples in the field, the volatility of RNA, and the obstacles encountered when attempting the fluorescence techniques, this was not possible. Also, a better correlation between this study's GRP analyses, and nucleic acid analysis, would have been to collect Atlantic cod's muscle tissue samples and compare cod's growth rate, by means of RNA:DNA ratios, to the GRP results. This was not possible because of the inability to catch Atlantic cod during the research cruises.

However, results support the hypothesis that nucleic acid concentrations can be used as condition indicators because of their ability to show recent growth of fish. Also, results show that nucleic acid concentrations are highly sensitive and change significantly depending on the spawning stage of fish. It is important to note that nucleic acid concentrations are significantly different, showing close to a 3-fold difference in concentrations between the pre-spawning and post-spawning individuals. These individuals were collected only 2 weeks apart, and show no difference in mean weights and lengths, making it impossible to observe a difference without nucleic acid analyses.

CHAPTER 1. Environmental Quality Assessment of Georges Bank using acoustic and modeling techniques

Introduction

The Georges Bank region, in the northwest Atlantic Ocean, has supported one of the most abundant Atlantic cod (*Gadus morhua*) populations, therefore playing a key role in New England history. However, centuries of overfishing the banks have lead to a decreasing trend of cod population numbers, ending in a collapse of several stocks, and a closure of the U.S. and Canadian cod fisheries in 1993 (ICES, 2003). Currently, scientific and management efforts have slowed the decline in cod abundance, although numbers continue to be low.

Efforts to understand the dynamics of cod populations in Georges Bank have focused on assessing the main forage fish populations such as Atlantic herring (*Clupea harengus*). The Northeast Fisheries Science Center (NEFSC) a branch of the National Marine Fisheries Service (NMFS) conducts annual fisheries acoustic surveys to study the state of the herring stocks. In this study, I use data collected during these surveys, as well as other data, to assess the quality of the environment on Georges Bank for the potential growth of Atlantic cod.

This research project aims to assess the quality of Georges Bank's environment as measured by Growth Rate Potential (GRP) of Atlantic cod. GRP describes the ability of an environment to support positive growth of a specific species and contributes to the understanding of the environment's condition in terms directly relevant to the fitness of the species (Brandt, 1992, Tyler 1998, Brandt & Tyler, 2001). This assessment is achieved by integrating acoustic estimates of forage fish abundance and water

temperatures collected during the NEFSC research cruises. With this analysis, I aim to investigate whether environmental factors are in fact contributing to the decrease in cod population numbers.

History of the New England fisheries

Atlantic cod fisheries were the foundation of the early New England economy, and their importance has been recorded since the beginning of the 17th century. Groundfishing, the fishing of species that live close to the bottom, was the first colonial industry in America (NMFS, 2003). Fishermen in Marblehead, Massachusetts were apparently the first residents to catch groundfish regularly, starting in the 1700s (Kurlansky, 1997). Since then, a great number of ports have landed cod, and the fisheries have been an integral part of the New England economy. Currently, many things are different: the numbers of New England ports have increased, and fishing techniques have progressed from hand fishing, to extensive use of electronic gear such as acoustic fish finders and global positioning systems. However, the importance of the fisheries to the economy has not changed since its early days.

Cod trade lifted New England from a distant colony to an international commercial power (Kurlansky, 1997). Cod composed the heart of the New England groundfishery, which had for centuries been one of the world's most productive fisheries (Dobbs, 2000). During the early 19th century, cod populations were so abundant in Georges Bank, the Canadian Ministry of Agriculture believed that the fisheries would continue to be forever fertile. So important was the cod to the economy that a wooden codfish hung from the Massachusetts House of Representatives until 1895, when the figure was ceremoniously removed from the door step, and wrapped in an American flag

(Kurlansky, 1997). Demand for cod made the colonies a self-sufficient, politically powerful, and gave them financial means to seek and win independence.

The North Atlantic fisheries, including New England and Canadian fisheries are known for their great abundance of fish species. Factors such as water currents and depth gradients make the New England and Canadian fisheries some of the most abundant fishing grounds in the world, which include Georges Banks, the Grand Banks, and many other shoals found in the area. Because of optimal combinations of physical and biological factors, large amounts of phytoplankton and zooplankton are found in the area, which enhances the prey base for supporting numerous species of fish (Backus, 1987). It is the richness and high productivity of the banks that produced cod by the millions (Kurlansky, 1997).

Early in the 20th century, cod, and other groundfish species were noted to be decreasing, leading to a surge in scientific exploration. In the 1930s scientists began to look for reasons why the cod and haddock populations were decreasing. Fisheries management was initiated, but these management strategies were not enough to deal with the rapid decrease of the populations, especially with the introduction of foreign fishermen in American and Canadian waters. Fleets from Russia, Poland, Japan, and Germany, among others, fished on Georges Bank after hearing word of the great abundance of groundfish (NMFS, 2003). Finally, with the introduction of the Magnuson Act in 1976, the Exclusive Economic Zone (EEZ) was extended to 200 nautical miles off the coast, giving jurisdiction of Georges Bank to the American and Canadian governments. Since then, scientists have been working on finding the cause of the

decline of populations and attempting different approaches to restore groundfish populations.

Current state of the Cod Fishery

Overfishing and ineffective management eventually led to a collapse of the cod populations bringing dramatic consequences on communities with economies depending on this industry. Not until the 1990s did fishermen begin to realize the decline in the groundfish. Before, they were "fishing hard and catching more, now they were fishing hard and catching less" (Dobbs, 2000). In 1996, cod was declared a "vulnerable" species by the International Union for the Conservation of Nature, as well as the Committee on the Status of Endangered Wildlife in Canada. In 2001 an assessment from the International Council for the Exploration of the Sea stated that fishing mortality had to be reduced to the lowest possible level in order to stop the decrease in population numbers (Cook, 2002). To this date, six Canadian stocks have collapsed to the point of declaring a total moratorium on fishing (Hutchings & Myers, 1994), and the populations off the eastern USA are at unprecedented low levels (Murawski, 1996).

The consequences of a collapse in the fisheries are an economic and social downfall. The decrease in fish populations not only affects the fishermen and those who are directly related to the fisheries, its repercussions affect everyone. Revenue from fishing for the New England states has decreased almost $6 million in the last 5 years (ICES, 2003). Landings have faced a 7% decrease from 1999 to 2000, leading to an increase in market price. As John Galbraith, from the National Marine Fisheries Service states: "the lack of rebound is really disturbing, cod is the most obvious, and it affects everyone who lives on the coast, not just fishermen" (Dobbs, 2000)

Since the collapse of the fisheries, Atlantic cod populations have not been able to regain their numbers, despite numerous attempts from scientists and managers. Several approaches have been taken in attempt to bring back the cod populations, and reinstate the fisheries: length regulations for commercial fishermen were appointed, catch quotas were reduced, and the fisheries were even temporarily closed in 1993 (ICES, 2002). All these efforts were in vain and cod stocks remain below the long term average of a 37 year survey time series (NEFSC, 2001). The shift in population, and the failure of the New England groundfish, especially cod, to rebound even in the protected areas of Georges Bank, had led some to wonder whether overfishing had created some fundamental change in ecosystem structure that would prevent the groundfish's return (Kurlansky, 1997).

The question as to why cod populations do not show any changes despite all the attempts to bring them back remains unanswered. Walters & Pearse (1996) conducted a study on the catchability of cod, at different population sizes, attempting to find a reason why populations are still declining after reductions in fishing power. Walters & Pearse (1996) concluded that catchability increases as population size decreases. Myers (1996) conducted a similar study, finding no evidence of higher mortality at low population levels. Another possibility for cod decline is that there is an underestimation of fishing mortality, and an overestimation of fish biomass (Steele, 1992). Dutil & Lambert (2000), argue that in Canadian waters the average size of individuals decreased dramatically because of high levels of fishing mortality in the 1970s and 1980s, resulting in lowered fecundity levels, and low population growth. Other hypotheses suggest that the decrease in population numbers is due to environmental conditions (deYoung & Rose, 1993; Lear & Parsons, 1993).

Growth Rate Potential

Growth Rate Potential (GRP) is the amount of growth predicted for a fish with known prey availability and environmental conditions (Brandt et al, 1992). GRP is computed using data on prey availability, and physical oceanographic measurements obtained in the field as parameters for bioenergetics and foraging models (Brandt, 1992; Brandt & Kirsch, 1993; Goyke & Brandt, 1993). Because fish growth responds greatest to temperature, I use temperature as the measurement of the physical environment. Because fish growth integrates both natural variability and anthropogenic causes of ecosystem change, GRP has been used as an indicator of ecosystem health (Brandt & Kirsch, 1993; Horne et al, 1996; Luecke et al, 1999).

Previous studies have analyzed potential growth for spatially homogeneous environments; however, assuming that the environment is a 'single, well-mixed' container may lead to errors in the outcomes since prey availability and temperature often have patchy behaviors (Brandt et al, 1992). Goyke & Brandt (1993) found that spatially explicit bioenergetic models are useful tools for examining environmental quality in spatially complex aquatic systems. Spatially explicit models allow us to analyze how spatial heterogeneity affects the quality of an environment (Tyler, 1998). Although GRP analyses have several limitations such as overlooking predation, competition and habitat selection, they are reliable measurement tools of relative environmental quality for fish populations (Tyler & Brandt, 2001), since the ability of a fish to achieve its maximum growth potential is a relative measure of a fish's well-being and ultimate survival.

This study analyzes Atlantic cod's environment, and its ability to support positive growth, if a population were present. These analyses were conducted using spatially

explicit GRP maps of Georges Bank. For this study, I integrated field data on prey densities and water temperatures. Prey density was measured with underwater acoustics, assuming Atlantic herring to be the major food source for Atlantic cod. Water temperature also played an important role since fish are poikilotherms, meaning that their body temperature varies with the environmental temperature, making their metabolic processes highly controlled by temperature.

Methods

Field Work

Area of Study

I measured growth rate potential for adult Atlantic cod by means of acoustic surveys conducted along Georges Bank, approximately 100 miles east of Woods Hole, Massachusetts (Fig. 1) aboard the NOAA R/V Delaware II. Georges Bank is a 150 km wide, 280 km long topographic shoal, which rises more than 100m above the Gulf of Maine (Backus, 1987) and its depths range from 366m to 27m in its shallowest points. Because of the radical changes in depth and wide ranges of temperature and light conditions, Georges Bank is home to very high abundances of phytoplankton and zooplankton. This makes it an area of high productivity, with more than 100 species of fish. It is possible that many more species actually occur on the bank since the recorded species were surveyed by means of ground fish surveys, which focused on the fisheries aspect of the bank (Backus, 1987).

Data collection for this study took place during the fall NEFSC fisheries acoustic surveys in 2000, 2001 and 2002, which take place in September and first two weeks of October. Data were collected 24 hours a day on a series of systematic parallel transects running north to south. Figures 2 to 4 show the location of the transects for the 2000, 2001 and 2002 survey cruises respectively. Survey operations included acoustic data collection with a Simrad EK500® scientific echosounder, for acoustic measures of fish density, biological data collection using a High-Speed Mid-Water trawl (HSMRT), as

well as temperature data collection using a Sea-Bird Conductivity-Temperature-Depth (CTD) probe.

Acoustic Data Collection

Acoustic data in the form of relative fish densities were measured at a rate of one "ping" every two seconds. The echo sounder emits a series of pings which scatter off objects in the water column at different intensities depending on the size of the object. The returning echoes are collected by the echo sounder and integrated over a sampling volume (volume scattering strength, Sv). Volume scattering strength is a relative measure of abundance. The EK500 pings simultaneously at frequencies of 12, 38 and 120 kHz. For this project, I used only the 38 kHz because it is the standard frequency used for acoustic estimates of Atlantic herring (J.M. Jech, personal communication, April, 2003). An Sv threshold is applied to the data to eliminate or minimize scattering by targets other than swimbladder fish. Using Echoview® software, these data were post-processed during the research cruise to identify acoustic backscatter due to Atlantic herring. The spatial distribution of herring was also measured and mapped. The data were sorted into transects and divided into cells 0.1 nautical miles (185.2 meters) long by 1 meter deep. Acoustic fish aggregations in each transect data set were designated as regions containing herring. The biomass measurements were determined to be herring using acoustic aggregation patterns observed. Resulting data were divided into two separate worksheets: a worksheet containing the data for every cell of the transect, and a worksheet containing the regions determined to be herring.

High-Speed Mid-Water Trawls (HSMRT)

To measure the species composition, and obtain biological information on the fish, High Speed Mid-Water Rope Trawls (HSMRT) were conducted along the transects. HSMRTs were also conducted to obtain mean length data for acoustic data processing, condition and spawning stage of Atlantic herring, and target and species composition.

The HSMRT is a coned-shaped commercial mid-water trawl with a mouth opening of $300m^2$ and is designed to be fished at high speeds (NEFSC, 2001). Trawls were conducted on an average of twice per day, however, trawl frequency was strongly dependant on the acoustic data, as well as weather conditions. The HSMRT was towed at approximately 4 knots, for 10 to 90 minutes, depending on the observed outcomes of the tow (i.e. tows were not standardized). At the end of the trawl, the catch were sorted and measured, and Atlantic herring was further analyzed for gender, maturity and stomach content, data not used for this study.

Temperature Data Collection

Temperature data were collected using a Seabird conductivity-temperature-depth probe (CTD). Vertical CTD casts were taken at the beginning and end of every transect, as well as before each trawl. Temperature data were also collected during each trawl using Vemco® minilog temperature and depth probes attached to the head and foot ropes of the trawl net. Temperature data are necessary to determine the location of the thermocline, since Atlantic herring tend to be found in a specific temperature range, as well as to determine GRP for the environment.

Computer Analysis

All computer analysis, with the exception of the Echoview® software, was conducted using Interactive Data Language (IDL) (Research Systems, 1996).

Acoustic Data Processing

I include here a very brief overview of the acoustic data processing and conversion from backscatter into numeric densities. For detailed descriptions and derivation of the formulas, refer to Jech & Luo (2000).

The Simrad® EK500 scientific echosounder emits a series of acoustic pings which reflect off objects in the water column and records them as acoustic backscatter. Acoustic size is the ability of a target to scatter sound back to the transducer (Jech & Luo, 2000). The SonarData Echoview® Fisheries Acoustic software was used to divide the transects into arrays of cells, 0.1 nautical miles (185.2 meters) long by 1 meter deep, and calculated a mean backscatter, $\overline{Sv}(dB)$, value to each cell. This mean backscatter for the cell includes every target encountered in the water column. Echoview allows us to identify specific areas as "regions" which are sections within the matrix of cells specified as 100% herring. We delineated each one of these regions during the research cruise depending on aggregation patterns and haul trawl data. For cells that are on the edge of the regions, and encompass only a portion of the designated herring region, Echoview calculates the proportion of the backscatter that is contributed by the region.

Sv is a relative measure of numeric density (#/m^3). In order to calculate numeric density we needed an estimate of the target strength (TS) for an individual target. Because herring aggregate in densities too high for acoustic discrimination of individual targets, we used a fish length to TS regression, derived from Foote, 1987:

$$TSherring = 20\log(\overline{L}) - 71.9dB \quad (1)$$

where L (in cm) is the mean length for Atlantic herring (L = 24.0 cm), obtained from trawl data.

For this analysis, numeric densities for only those cells designated as "herring" were calculated. All other cells have a density equal to zero. Numeric densities were calculated for each cell by means of equation 2:

$$DENSITYregion(\#/m^3) = \frac{10^{\frac{\overline{Svregion}}{10}}}{10^{\frac{\overline{TSherring}}{10}}} \quad (2)$$

The densities obtained for the cell are for everything encountered in the cell, whereas the densities obtained for the regions, are considered solely Atlantic herring.

Temperature Data Processing

Temperature values for each cell are required to calculate growth rate potential (GRP). Since temperature data were not collected continuously throughout each transect, we interpolated between CTD casts and minilog profiles. I computed linear interpolations of the temperatures, weighted by the proximity of the cell being analyzed to an existing temperature cast. From this interpolation, temperature maps were obtained for each cell of each transect.

GRP Computations

GRP is the amount of growth predicted for a fish with known prey availability and environmental conditions (Brandt et al, 1992). GRP Map Maker (Tyler, 1998) uses

both bioenergetics and foraging models to produce spatially explicit maps of GRP of a given environment. In this study, I generated GRP maps for each of the individual transects in each year. All detailed procedures and formula derivations can be found in Tyler, 1998.

BIOENERGETICS MODEL

Bioenergetics models produce fish growth estimates using a mass balance approach. Predicted growth is the energy remaining from consumption gains after all energy expenditures of metabolic costs consisting of respiration (R), specific dynamic action (movement) (S), egestion (F), and excretion (U) costs accounted for:

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

Species-specific Atlantic cod bioenergetics parameters used for this study were obtained from published data of physiological experiments (Hansson et al, 1996). Prey availability data correspond to the herring densities derived from acoustic measurements obtained in the field. These models use a length-weight regression to convert length of herring into a biomass, in order to calculate consumption. The length weight regression used is:

$$W = aL^b \tag{4}$$

where w = weight (kg), L= length (mm), a = 5.37 x 10^{-5} , and b = 2.4478 (NEFSC).

Since fish are poikilotherms, metabolic processes are strongly affected by temperature. The amount of prey items consumed, as well as the maximum consumption for an individual is strongly regulated by temperature. Also, respiration costs, along with movement costs are dependant on temperatures, making temperature measurements imperative for GRP analyses.

FORAGING MODEL

Foraging models are based on the encounter rates of the predator and the prey. In this study Atlantic cod is considered the forager with Atlantic herring as its prey. These models are computed by assuming the fish searches for food in a cylindrical volume of water, and it encounters all prey items in that volume. This volume takes into account the reactive distance (RD) of the fish, assumed to be equal to the predator length, as well as the distance swum during foraging. Distance swum (DS) is determined by the swim speed of the fish, the foraging time, as well as the average body length. Volume searched multiplied by prey biomass density and by foraging efficiency results in prey consumed, which is the fraction of prey that the fish will capture from this volume. In this study, I assume the predator forages for 12 hours, and the volume searched is based on average cod size of 130 cm, obtained from bottom trawl survey data. The swim speed assigned was 0.2 body lengths per second, since cod's foraging behavior is opportunistic (Love, 2003), in other words, an individual will wait and consume prey items encountered during this period. A foraging efficiency factor is incorporated into the model to account for the fact that not everything a fish encounters is consumed; In this case, I used a foraging efficiency of 0.001.

Studies have been conducted to assess the effects of foraging efficiencies on GRP measurements (Mason & Brandt, 1996; Bartell et al, 1986). Mason & Brandt (1996) concluded that changing the foraging efficiency produces a change in GRP results, depending on the spatial resolution of the environment. To assess this possible problem I tested different foraging efficiencies, as well as foraging times, and studied their effect on

GRP results. From this analysis, I concluded that foraging efficiencies larger than $1e^{-5}$, and foraging times greater than 4 hours, did not show any effect on GRP results (Fig. 5).

GRP reaches a maximum value when consumption by an individual is equal to the maximum consumption possible for this particular individual. This is achieved when there is a perfect combination of optimal prey biomass and temperature values for the bioenergetics of Atlantic cod. Figure 6 shows the GRP values for a 30 kg cod in areas with a range of prey biomass and water temperature conditions. This figure was constructed using species specific bioenergetic and physiological parameters obtained from laboratory experiments (Hansson et al, 1996). The optimal values for cod growth are prey biomass higher than $1e^{-3}$ $g^{\bullet}m^{-3}$ and temperatures ranging between $12^{o}C$ and $15^{o}C$. GRP values decline as temperature decreases from $12^{o}C$ or increases from $15^{o}C$, or if prey biomass decreases below $1e^{-3}$ $g^{\bullet}m^{-3}$.

Results

The fall NEFSC research and survey cruises of the FR/V Delaware II produced a total of 55 acoustic transects in the years 2000 (13 transects), 2001 (24 transects) and 2002 (18 transects). I mapped results for each transect, as well as divided the study area for each year into regions corresponding to west of Georges Bank, central region of Georges Bank and east of Georges Bank (Northeast Peak). I further divided each transect into strata based on water depth with 50 meter increments beginning at the bottom. For each transect, I summarized bottom depth, mean temperatures, mean prey biomass, as well as depth stratification and fraction of the biomass corresponding to each strata for 2000, 2001 and 2002. I also include the fraction of the transect with positive Growth Rate Potential (GRP), mean GRP for the entire transect as well as mean GRP for only cells with positive in the transect to assess the overall quality of the environment in the transect.

Temperature maps

The temperature for all transects ranged between 19^{o}C and 4.9^{o}C, with variations depending on depth and length of the transect. Mean temperatures for all three years were consistently cooler west of Georges Bank, followed by temperatures on Georges Bank and finally the warmest temperatures were found east of Georges Bank (Fig. 7). Examining the thermoclines, with help of the temperature casts obtained in the field, shows how its depth varies throughout the study area. The depth of the top of the thermoclines varies little within each year with the mean depth of the top of the thermocline about 20m in 2000 (Fig. 8), 12 m in 2001 (Fig. 9), and 10 m in 2002 (Fig.

10). The bottom of the thermoclines showed a notable trend. In 2000 and 2002 the bottom of the thermocline was notably deeper in casts located to the east of Georges Bank than in the center and west (Fig. 8; Fig. 10). The temperature data from 2001 also show a geographical trend in the depth of the bottom of the transect, but opposite of that observed in the other years (Fig. 9). Temperatures below the thermocline showed a slight increasing trend toward the bottom, at an average of 2^{o}C, in the deeper transects (Fig. 11).

Interpolated temperature fields for each transect show fine-scale geographical variation in water temperature within the transects. Example temperature fields show a classic pattern of water temperatures with strong thermoclines in deeper waters and nearly uniform temperature profiles in shallow waters (Fig. 12). This pattern of water temperatures appeared in all years and most transects that included both shallow and deep areas.

Prey biomass

Herring were present in all transects, with the exception of transects 95, 109 and 113 of 2001, and transects 105, 107, 115, 117 and 119 of 2002. Acoustics show herring consistently residing toward the bottom of the water column, in very tight aggregations in all sample years, 2000 (Fig. 13), 2001 (Fig. 14) and 2002 (Fig. 15). These aggregations appeared between the 300m and 150m depth strata in each year, 2000 (Table 1), 2001 Table 2) and 2002 (Table 3). Herring also appeared throughout the northern edge of Georges Bank, along the slope of the bank; however, they failed to aggregate toward the shallower areas of Georges Bank. Biomass values were very consistent throughout most transects, showing a uniform distribution of herring throughout the schools.

Geographical trends in herring biomass density show no strong trend in 2000 (Fig. 16), but a slight trend of greater biomass density in areas east of Georges Bank in 2001 (Fig. 17), and 2002 (Fig.18), although none of the biomass trends are significant.

Growth Rate Potential (GRP)

High GRP values for all transects are very localized, making the mean GRP for the entire transect, which take into account all cells, very low in the data for 2000 (Table 4), 2001 (Table 5) and 2002 (Table 6). These tables also include the fraction of the environment with positive GRP, and the mean GRP for only those cells containing positive GRP values. For all three years, the mean positive GRP values are relatively close to the theoretical maximum GRP for Atlantic cod, supporting the fact that the environment is well suited for growth. Mean positive GRP shows little variance throughout each transect, given the uniformity of prey biomass, and temperature distribution where herring aggregate. Higher GRP values occur in the central, and east regions of Georges Bank, while GRP values for the west region of Georges Bank are slightly lower for 2000 (Fig. 19), 2001 (Fig. 20), and 2002 (Fig. 21).

The spatial distributions of Atlantic cod GRP values across the transects closely match those of the Atlantic herring distributions. Transects have high GRP values in areas close to the bottom of the water column in 2000 (Fig. 22), 2001 (Fig. 23) and 2002 (Fig.24) where one also finds Atlantic herring. In most cells that contain herring, GRP values are constrained by cod maximum consumption. Cumulative distribution functions (CDFs) of the GRP values for each region of Georges Bank show the distribution of the GRP values for each transect for 2000 (Fig. 25), 2001 (Fig. 26) and 2002 (Fig. 27). The

CDFs show that greater than 80% of the transect have negative GRP. Areas with negative GRP contain no Atlantic herring and any variation in GRP values results strictly from the effect of temperature on respiration. Some transects show more positive values than others, such as transect 120, of 2000 (Fig. 25), transects 85, 87 and 135 of 2001 (Fig. 26), and transect 103 in 2002 (Fig. 27).

Discussion

The spatial distribution of Growth Rate Potential (GRP) values closely matches the spatial distribution of prey biomass in the water column. While temperature does affect GRP values in these data, the large majority of herring resided in deep water that was overall uniformly cold ($6^{o}C$ - $8^{o}C$) resulting in little effect of temperature on cod GRP. Large herring aggregations appeared in the lower region of the water column which could occur for at least two reasons. First, the NEFSC conducts the acoustic surveys during the herring spawning season and herring spawn demersal eggs. In addition the herring reside near the bottom because of the lower temperatures found in this area and herring are a cold water fish. Aggregations were also found along the northern edge of the bank, where depth gradients occur. These are areas of high productivity resulting from high nutrient and sunlight availability, and a wide range of temperatures, leading to high numbers of phytoplankton and zooplankton, thus increased fish activity after spawning, when herring resume feeding. Atlantic herring appeared in most of the studied transects, although a number of transects in 2001 and 2002 did not contain any fish aggregations. 2002 had a particularly large number of empty transects, compared to 2000 and 2001. NEFSC scientists believe that spawning season occurred earlier that year, and the herring aggregations had moved off Georges Bank (J.M. Jech, personal communication, March 2003).

GRP is strongly affected by the combination of temperature and prey biomass values. Figure 6 illustrates this by showing the optimal values of prey biomass and temperature, and how they appear together might affect GRP. This can also be observed in the results by comparing transects 126 and 128 of 2000. In these transects, the prey

biomass density is approximately similar, however the temperature varies from 10.5^{o}C in transect 126 to 11.1^{o}C in transect 128. This increase in temperature changes the fraction of the environment with positive GRP from 6.89 to 10.66. This shows the importance of temperature in cod bioenergetics. There is also a slight difference between mean positive GRP values west, central and east regions of Georges Bank. GRP values where somewhat higher on the eastern edge of Georges Bank. This slight increase in GRP might be due to the higher temperatures found east of Georges Bank, compared to the western regions. The reason why maximum GRP values do not occur, even though the large prey biomass aggregations and optimal temperature ranges were found, is that optimal values did not occur simultaneously. In spite of this, mean positive GRP values for the temperature where herring resided were close to maximum in all transects, supporting the hypothesis that Georges Bank is a thriving environment, able to support positive growth for adult Atlantic cod. In fact, the herring biomass in locations where they did reside exceeded that needed to meet the energetic requirements for cod maintenance many times, further suggesting that the Georges Bank environment holds sufficient resources to support adult Atlantic cod.

Atlantic cod populations have notably declined, and specifically, Georges Bank cod populations have been at record low levels for more than 30 years (Myers, 1996), leading to a collapse in several stocks and closure of the fishery in 1993 (2003 ICES report). On the other hand, Atlantic herring populations in Georges Bank and its surrounding regions have reached historic high numbers (2003 NEFSC report). It is yet to be explained why Atlantic cod populations are on a decreasing trend in a time with such abundant prey.

Multiple studies have assessed the discrepancy of the species population numbers, and the reasons for the unprecedented low numbers of cod (deYoung & Rose, 1993; Lear & Parsons, 1993; Lambert & Dutil, 1997b; Steele, 1992; Jakobsen, 1994). There is constant monitoring of the populations by the Northeast Fisheries Science Center (NEFSC) by means of the yearly groundfish survey, the longest running scientific survey in the country and commercial fishing regulations are constantly revised using the findings of these surveys. Fishing quotas have slowed the decrease in cod populations, however, numbers remain very low. It is important to note that based on prior research, NEFSC conducts the herring fisheries acoustic surveys recognizing that herring are evenly distributed along Georges Bank. This study shows that there are only very slight geographical differences in herring aggregations, temperature or GRP values in Georges Bank, supporting the NEFSC assessment methods.

Several other studies have assessed different causes of this problem stating that the reason why stocks failed to recover after the closure of the fisheries in 1993, is because of environmental changes (deYoung & Rose, 1993; Lear & Parsons, 1993; Lambert & Dutil, 1997b). This study assesses the environmental conditions for Georges Bank, and its ability to support growth for Atlantic cod if a population were present. The data support a conclusion that in its current state the Georges Bank environment is in fact able to support positive growth. Temperature values, even though are not in the optimal growth, 12^{o}C-15^{o}C range, are close to optimal, still supporting positive growth for Atlantic cod, and the abundance in prey biomass further enhancing growth for adult cod in the Georges Bank.

After determining the suitability of Georges Bank to support growth, the question of why Atlantic cod are in such low levels still remains. Fishing mortality might play a strong role in the low population numbers. Even though strong fishing quotas have been instated and are enforced, restricting sea-hours for commercial fishing boats, setting length minimums for caught fish, and setting weight limits on the catches, the effort might still be too weak. According to Steele (1992), there is an underestimation of fishing mortality, while there is an overestimation of prey fish biomass by regulating agents. Jakobsen (1994) observed a substantial increase in populations when fishing was radically reduced, so the fact that cod populations have not increased in spite of the quotas might result from an underestimation of fishing mortality. A possible problem may arise from increased juvenile mortality by bottom trawlers.

Juvenile cod are approximately the same size of adult Atlantic herring, which have been found in bottom trawl nets. It is possible that juvenile cod are being caught by bottom trawlers, and they are discarded because they do not meet marketable sizes. However, fish caught in nets are in a weakened state, if not already dead, so discarding juvenile cod caught in a bottom trawl can greatly increase the cod mortality from fishing without appearing as a part of the reported fishing mortality rate. High mortality of juvenile cod caught as bycatch can greatly affect recruitment into the adult population.

The fact that commercial catches of cod have increased during the same period that scientific estimates of cod population sizes have decreased does not support a claim that commercial catches more accurately reflect the actual trends in cod populations. Walters & Pearse (1996) found that fish catchability increases as population numbers decrease. In addition, landings remain the same as population decreases (Myers, 1996).

If landings remain the same as population decreases, cod numbers are being increasingly depleted, as measured by percent of the population. All these factors may be affecting cod populations, impeding the increase in numbers. As stated in Rose & deYoung (2000), the dramatic decline in cod populations would not have occurred without the fisheries, and fishing mortality can increase rapidly in cod, so managers have to be immensely cautious when setting quotas (Myers, 1996). Regardless of all efforts, cod populations remain in a historic low, without any signs of improvement, even though the environment is thriving.

CHAPTER 2. Nucleic acid concentration analysis of non-, pre-, and post-spawning Atlantic herring.

Introduction

Atlantic cod (*Gadus morhua*) has been documented as one of the most cherished species for the Northwest Atlantic fisheries since the early 1700s (Kurlansky, 1997), and Atlantic herring (*Clupea harengus*) is one of the major food sources for cod (Love, 2003). Cod stocks have experienced a dramatic decline in population numbers leading to social and economic downfalls in the New England fishing communities, as well as the maritime provinces of Canada and even European countries (Dobbs, 2000). At the same time, herring populations are documented to be at historic highs (NEFSC, 2001). This discrepancy has lead to some questions as to whether herring might be experiencing low per capita food availability as a result of their high density resulting in reduced growth. In this study, I attempt to bring light to this discrepancy by determining the ability of nucleic acid concentration analysis to assess the condition of Atlantic herring in Georges Bank and the Gulf of Maine.

Nucleic acids play a major role in growth and development of organisms (Clemmesen, 1993) and are used to assess the condition of fish. Ribonucleic acid (RNA) concentrations have been used as indicators of instantaneous growth, and health condition in fishes since Sutcliffe showed its accuracy in 1970 (Bergeron, 1997). RNA concentration is a sensitive parameter to determine the growth rate of an organism because it is the organizer of protein synthesis (Bulow, 1970). In a large number of fish species, nucleic acid concentrations have been found to correlate with growth rate and nutritional status (Jobling, 1988; Mathers et al, 1992). Other approaches have been added

to nucleic acid quantifications to have a better understanding of the physiological condition of fishes, such as enzyme analyses (Mathers et al, 1992), temperature manipulations (Ferguson & Danzmann, 1989), and food ration changes (Arndt et al, 1996), among others. However, it is agreed upon that protein synthesis of white muscle tissue expressed as RNA concentrations may be used as a reliable estimate of instantaneous growth rate.

There are many advantages in using nucleic acid concentration techniques as indicators of growth and condition of fishes. It is often difficult to measure growth on marine fishes because of the inability to successfully mark and track schooling fishes. RNA concentration techniques as indicators of growth are advantageous because of the ability to detect changes over a shorter time span than direct measures of the change in size over time (Arndt, 1996). Because of the increased sensitivity to indicate somatic changes, and the short time span necessary for RNA concentrations to vary, they have been used as indicators of seasonal growth characteristics within fish populations as well (Westerman & Holt, 1988; Kuropat, 2002).

Atlantic herring have a seasonal life cycle, which strongly affects their behavior. Adult herring migrate to open water to spawn (Stratoudakis et al, 1998) and their spawning season in the Gulf of Maine and Georges Bank is from late September to the end of October (Gulf of Maine Aquarium, 2003). Theoretically, spawning fishes devote all their energy to gonadal development (Ledeiros & Himmelman, 2000; Hansen, 2001), and in Atlantic herring's case, to migration costs (Gulf of Maine Aquarium, 2003), during the pre-spawning season, and I will assess this in my study.

I hypothesize that the seasonality in herring lifecycles and their changes in behavior, affect their growth and overall condition. In this study, I estimated the concentration of RNA in herring white muscle tissue by means of spectrophotometric readings at a wavelength of 260 nm. Since concentration of cellular DNA is insensitive to changes in environmental conditions (Dortch, 1983) and it is practically constant in somatic tissues (Clemmesen, 1993), when constant tissue sample sizes are used, the variation in spectrophotometric readings are the effect of variations in RNA concentrations, where higher amounts of RNA are due to increased growth and better condition of the individuals.

Methods

I collected Atlantic herring white muscle tissue samples on 3 separate occasions throughout the year 2002: summer samples in June, 2002, by means of a commercial purse seiner in the Gulf of Maine and fall pre-spawn and post-spawn samples using a high speed mid-water rope trawl (HSMRT) during the NEFSC fisheries acoustic fall survey aboard NOAA FR/V Delaware II, in September and October of 2002 respectively. Using a sterile 5 mm biopsy punch, I collected all samples from dorsal area white muscle tissue, and stored them in liquid nitrogen. I then transferred and stored the samples at -80^{o}C until nucleic acid analysis. In addition to the tissue samples, I collected fork-length (in millimeters) and weight (in grams) data on each individual. Because of excess vibration on the deck of the purse seiner, I failed to collect reliable weight data as a result of malfunctioning of the scale; however, fork-length data was still recorded. Length and weight data can be found in Appendix A.

I extracted nucleic acids from white muscle tissue samples of non-spawning, pre-spawning and post-spawning groups (n = 22,19,18 respectively) following a modification of the Perchuk (2000) protocol. I autoclaved and cleaned all the surfaces and instruments with diethyl pyrocarbonate (DEPC) treated water (0.1%) prior to the extractions. I homogenized 0.15 g ($\pm$ 0.01 g) of muscle tissue in 2mL of warm extraction buffer (50 mM Tris, pH 8, 0.1 M NaCl, 0.1M EDTA, 0.5% SDS containing Proteinase-K to 50 μg/ml) for approximately 20 seconds or until tissue was completely dissolved, using a Beckman POLYTRON Tissue homogenizer. Incubation in a 55^{o}C water bath followed, for a minimum of 3 hours in order for the Proteinase-K to complete digesting all proteins. Samples were treated with one volume of equilibrated phenol, rocked for 30 minutes and

centrifuged for phase separation. I transferred the aqueous phase into a clean tube, added half of a volume of equilibrated phenol, and half of a volume of chloroform, and rocked for 30 minutes. Phases were separated by centrifugation and aqueous phase was again transferred into a clean tube. I added two volumes of ice cold 100% ethanol and stored the samples overnight at -20^{o}C.

After the samples were centrifuged in a Beckman high speed centrifuge at 10,000 g, and the ethanol removed, I allowed the pellets to dry completely. I resuspended the pellets in TE (10 mM Tris-Cl, pH 8, 1 mM EDTA) and to the solution, added NaCl to 0.7 M, Tris pH 8 to 0.1 M, and 1/9 volume of 10% C-TAB and 0.7 M NaCl. To this, I added one volume of chloroform, and rocked for 10 minutes. Phases were again separated through centrifugation, added two volumes of 100% ethanol to the aqueous phase and left overnight at -20^{o}C. Samples were centrifuged at 10,000 g, ethanol was removed and the pellet was allowed to dry completely. Finally, I resuspended the pellets in 100 μL of TE, and stored at -80^{o}C until spectrophotometric readings were conducted.

The samples were brought up to a final volume of 1 mL, using TE buffer, for spectrophotometric reading. After blanking the spectrophotometer with TE buffer, I calculated RNA concentrations from the absorbance readings at a wavelength of 260 nm using a Cecil, CE2020 Spectrophotometer.

I used analyses of variance (ANOVA) to test the difference in nucleic acid concentrations among the groups to assess the effect of the season on the growth of each of the individuals of the groups. First, all three groups were compared to each other to assess the overall variance in nucleic acid concentrations due to seasonality. Next, the non-spawning group was compared to the combined pre- and post- spawning groups to

determine the significance of the difference between non-spawning versus spawning individuals. Finally, a comparison was made between the pre-spawning and post-spawning groups to determine the variance in energy expenditure between these individuals.

Results

I analyzed three separate groups: non-spawning, pre-spawning and post-spawning Atlantic herring (n = 22, 19, and 18 respectively) for nucleic acid concentrations in white muscle tissue samples to determine the condition of the individuals (Figure 1.). Since cellular DNA is constant within a species, changes in absorbance readings reflect changes in RNA concentrations, thus showing changes in recent growth. Results show the variability in energy expenditure of Atlantic herring is highly seasonal. During the non-spawning season, corresponding to June of 2002, spectrophotometric absorbencies at a wavelength of 260 nm, which correspond to total nucleic acids, are the highest (mean = 1.438 OD units, variance = 0.065). During the pre-spawning season, corresponding to September of 2002, absorbance values fall dramatically (mean = 0.2497 OD units, variance = 0.028). Finally, during the post-spawning season, corresponding to October of 2002, absorbance values show an upward trend (mean = 0.6009 OD units, variance = 0.016).

An analysis of variance test (ANOVA) shows a significant difference between non-spawning, pre-spawning and post-spawning groups. First, I tested for overall differences in the three groups. I concluded that all three group are significantly different ($F=203.024$, $p<0.0001$). I tested for differences between non-spawning and spawning seasons (June 2002, and combined September and October 2002) with orthogonal contrasts to observe the seasonality of growth condition. There was a significant difference between these groups ($df = 29.436,33.297$; $t = 17.055,7.261$; $p < 0.0001$). I also tested for differences between pre-spawning and post-spawning groups (September and October, respectively), to observe the difference between individuals experiencing

gonadal growth versus somatic growth after spawning. There was a significant difference between the pre-spawning and post-spawning groups ($df = 56$; $t = 19.299,5.475$; $p < 0.0001$) showing a shift in energy expenditure from immediately before spawning, to shortly after spawning.

Discussion

In this study I determined the recent growth and condition of Atlantic herring during three different time points of their reproductive cycle: pre-spawning (September), post-spawning (October) and non-spawning (June) using nucleic acid concentrations. I concluded that there is significant seasonal variation in concentrations of nucleic acids between each of the groups (Fig. 28). Feeding behavior and energy allocation are possible causes for the seasonal variability of nucleic acid concentrations. During spawning season, all net energy gain is redirected to gonadal growth. This is observed in the dramatic decrease in nucleic acid concentrations in white muscle tissue, which correlates to a decrease in somatic growth. Shortly after spawning, the individuals begin reallocating their energy gain toward muscle growth, culminating in a full reallocation of energy expenditure during the non-spawning season, where all energy gains are directed toward muscle growth. An analysis of variance (ANOVA) test was conducted to determine the correlation between non-, pre- and post-spawning groups. Results from this test further support our conclusions, where all three group's nucleic acid concentrations were significantly different from each other.

Similar results have been found in other marine species: many fishes (Blom at al, 1997; Arndt et al, 1996; Hansen, 2001), bivalves (Ledeiros & Himmelman, 2000), cephalopods (Cortez, 1995) and crustaceans (Moss, 1994), corroborating our findings. In cod, feeding markedly decreased during spawning season, increasing gonad weight, and decreasing muscle reserves (Hansen, 2001). This is followed by an increase in feeding activity during post-spawning season. A different approach was taken using sea scallops where difference in growth rates was strongly affected by delays in sexual maturation.

The differences in growth were explained by differences in timing of the spawning season and the gonadal weight investment of energy (Ledeiros & Himmelman, 2000).

Although results were as expected, there were several limitations during the course of this study which can be improved for further explorations. Even though spectrophotometric techniques have been used successfully in the past (Kuropat et al, 2002), other studies suggest that fluorometric techniques are more sensitive when it comes to detecting nucleic acid concentrations (Grant, 1996; Clemmesen, 1993; Steinhart & Eckmann, 1992). Performing RNA and DNA specific extractions and quantifications with the help of fluorometric techniques would rule out the uncertainty of our assumption of constant cellular DNA concentrations. It is imperative to be aware that samples and staining techniques for fluorometric readings are very volatile, and all the necessary precautions need to be taken since nucleic acids tend to be highly sensitive and easily degradable (Ferguson & Drahushchak, 1989)

Many other approaches can be taken, using this study as a foundation, such as collecting valid lengths and weights for every group, as well as collecting gonad weights. This would allow a comparison between the classic condition measurement of length-weight regressions, as well as comparing nucleic acid concentrations to changes in gonad weight. Making this a long term study would also be valuable to observe trends throughout a series of years, and find a correlation between nucleic acid concentrations and more global factors. The study of these global factors, such as yearly temperature changes (Foster et al, 1993), fishing mortality and migration patterns may give a better understanding of what influences nucleic acid concentrations and spawning behavior.

Although the methods in this study had certain limitations, the magnitude of the variation of nucleic acid concentrations suggests a very strong dependence between spawning season and allocation of energy gains. Researchers in the past have studied the change in nucleic acid concentrations as a result of starvation (Steinhart & Eckmann, 1992; Arndt et al, 1996) and temperature changes (Ferguson & Danzmann, 1990), showing only 4-5 fold differences in RNA and DNA concentrations. However, results indicate that spawning season has a more dramatic effect on nucleic acid concentrations showing a close to 7-fold difference between spawning and non-spawning individuals.

This study also suggests that the commonly used length-weight regressions, as measurements of growth condition of fish might lead to inaccurate conclusions, especially when sampling over a short period of time. This is observed in the pre- and post-spawning groups, sampled only two weeks apart, where the mean lengths and weights (Appendix A) show no obvious difference (mean weights = 159g; 157g, mean lengths = 252mm; 251mm, for pre-spawning and post-spawning respectively), while nucleic acid analyses show a significant difference between these groups (Fig. 28).

Results suggest that a very important factor for planning further nucleic acid concentration studies, is the variation of nucleic acid concentrations during short periods of time, such as from late September to early October. Sampling times need to be closely monitored, and spawning seasons considered at all times, as nucleic acid concentrations have been found to change significantly depending on the timing of the spawning season. This is also a consideration to take into account when attempting to validate GRP with nucleic acid analyses. If sampling times are not closely monitored and standardized, nucleic acid analyses would be faulty measurements for validation of GRP analyses.

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Table 1. Year 2000 Biomass values and fraction of biomass in each depth strata

Transect	Max.Depth (m)	BIODENS ($g.m^{-3}$)	Mean Temp. (C)	300m	250m	200m	150m	100m
106	130	0.4289	8.7	0	0	0	0.53502	0.46498
108	220	0.2178	9.1	0	0	0.54894	0.26161	0.18945
110	220	0.5935	9.7	0	0.39425	0.58993	0.01479	0.00104
112	180	1.126	9.9	0	0	0.96478	0.03522	0
114	187	12.54	7.1	0	0	0.37263	0.62719	0
116	216	2.088	7.6	0	0.00004	0.9317	0.06826	0
118	239	0.5313	9.4	0	0.96904	0.03096	0	0
120	249	0.8184	9.2	0	0.67585	0.32198	0.00217	0
122	249	0.9683	9.4	0	0.91206	0.06111	0	0.02683
124	329	7.715	9.4	0.13801	0.66226	0.19973	0	0
126	291	0.5722	10.5	0	0.21899	0.22918	0.52804	0.02379
128	303	0.6036	11.1	0.1035	0.22519	0.39526	0.27605	0
130	265	0.7728	10.1	0	0.71944	0.25918	0.02138	0

Table 2. Year 2001 Biomass values and fraction of biomass in each depth strata

Transect	Max.Depth (m)	BIODENS ($g.m^{-3}$)	Mean Temp. (C)	350m	300m	250m	200m	150m	100m
81	189	0.3622	6.9	0	0	0	0	0.31094	0.68906
83	237	0.2001	6.1	0	0	0.65753	0.34247	0	0
85	243	0.6048	6.4	0	0	0.21288	0.71057	0.06934	0
87	231	0.5896	9.6	0	0	0.38216	0.22095	0.19599	0.2009
89	186	1.918	8.6	0	0	0	0.205	0.7897	0.0053
91	185	5.896	13.5	0	0	0	0.73005	0.26993	0.00002
93	221	2.63	8.5	0	0	0.03715	0.90617	0.05668	0
97	238	0.6208	8.6	0	0	0.22954	0.71536	0.05376	0.00134
99	253	5.54	8.7	0	0	0.16236	0.08793	0.41809	0.31649
101	276	12.77	11.5	0	0.01461	0.04472	0.93656	0.00411	0
103	341	5.177	8.8	0	0.05716	0.12395	0.77867	0.00019	0.04003
105	377	1.654	11.3	0.01553	0.07409	0.02017	0.60309	0.28621	0.0009
107	304	7.877	11	0	0.01815	0.32004	0.66084	0	0
111	281	1.419	9.9	0	0.10877	0.84066	0.05057	0	0
123	292	3.02	9.6	0	0	0.10247	0.89753	0	0
125	302	1.202	9.9	0	0.00365	0.99635	0	0	0
127	306	4.2	8.8	0	0.00287	0.28714	0.70999	0	0
129	339	47.98	8.4	0.72953	0.19672	0.0059	0.04886	0.01896	0.0002
131	303	1.507	7.7	0	0.45181	0.21618	0.20021	0.00502	0
133	510	5.961	6.5	0	0.00386	0.43694	0.55866	0	0
135	251	0.3178	9.3	0	0	0.50343	0.45071	0.0418	0.00005

Table 3. Year 2002 Biomass values and fraction of biomass in each depth strata

Transect	Max.Depth (m)	BIODENS ($g.m^{-3}$)	Mean Temp. (C)	300m	250m	200m	150m	100m
81	246	1.49	9.5	0	0.38641	0.61359	0	0
83	277	0.8589	10.4	0	0.97051	0.02949	0	0
87	303	5.076	10.9	0.00461	0.81456	0.18083	0	0
89	303	5.27	10.3	0	0.03936	0.96064	0	0
91	510	7.712	11.11	0	0.00426	0.99574	0	0
93	345	1.51	7.7	0.01586	0.94855	0.03559	0	0
97	247	3.99	9.1	0	0.67279	0.30322	0.02386	0.00013
99	251	3.08	11.9	0	0.80983	0.18643	0	0
101	235	2.627	9.9	0	0.88467	0.11533	0	0
103	234	1.29	8.7	0	0.97998	0.02002	0	0
109	181	3.67	10.65	0	0	0.9699	0.0301	0
111	195	1.487	8.5	0	0	0.99699	0.00301	0
113	227	1.038	8.7	0	0.20395	0.79605	0	0

Table 4.Year 2000 GRP values

Transect	%GRP>0	mean GRP ($g.g^{-1}.d^{-1}$)	mean positive GRP ($g.g^{-1}.d^{-1}$)
106	5.18	-0.0006227	0.003092
108	4.27	-0.0006386	0.003958
110	11.1	-0.0003771	0.003842
112	5.95	-0.0006214	0.003484
114	7.66	-0.0004938	0.002995
116	6.88	-0.000512	0.003079
118	10.65	-0.0003778	0.003639
120	16.75	-0.0001092	0.003557
122	7.58	-0.0005024	0.003752
124	3.73	-0.0006685	0.004032
126	6.89	-0.0005601	0.004064
128	10.66	-0.0004381	0.003756
130	5.35	-0.0006538	0.003448

Table 5. Year 2001 GRP values

Transect	%GRP>0	mean GRP ($g.g^{-1}.d^{-1}$)	Mean positive GRP ($g.g^{-1}.d^{-1}$)
81	3.81	-0.0006132	0.00283
83	6.24	-0.0004816	0.002909
85	12.84	-0.0002434	0.003009
87	17.22	-0.000068	0.003744
89	11.2	-0.0003714	0.003469
91	7.22	-0.0006684	0.004185
93	8.88	-0.0004829	0.003022
97	8.86	-0.0004635	0.003261
99	11.55	-0.0003535	0.003275
101	6.7	-0.0006069	0.0041
103	2.38	-0.0007162	0.003636
105	3.23	-0.0007783	0.003923
107	5.7	-0.0006433	0.003962
111	2.97	-0.000727	0.003933
123	0.52	-0.0008341	0.003952
125	1.69	-0.0007911	0.003891
127	4.14	-0.0006563	0.003391
129	10.28	-0.0003988	0.003229
131	13.58	-0.000212	0.00337
133	11.61	-0.0002899	0.003101
135	21.78	-0.000039	0.003183

Table 6. Year 2002 GRP values with depth stratification

Transect	%GRP>0	mean GRP ($g.g^{-1}.d^{-1}$)	mean positive GRP ($g.g^{-1}.d^{-1}$)
81	0.52	-0.0008324	0.003408
83	1.87	-0.0008067	0.003827
87	1.82	-0.0008399	0.003585
89	0.33	-0.0008766	0.004111
91	0.96	-0.0008806	0.00407
93	1.2	-0.0007428	0.002832
97	1.61	-0.0007693	0.003509
99	3.01	-0.0008048	0.004316
101	7.27	-0.0005501	0.003632
103	9.6	-0.0004331	0.003289
109	7.92	-0.0005985	0.004316
111	5.08	-0.0006719	0.003116
113	3.49	-0.0006813	0.003243

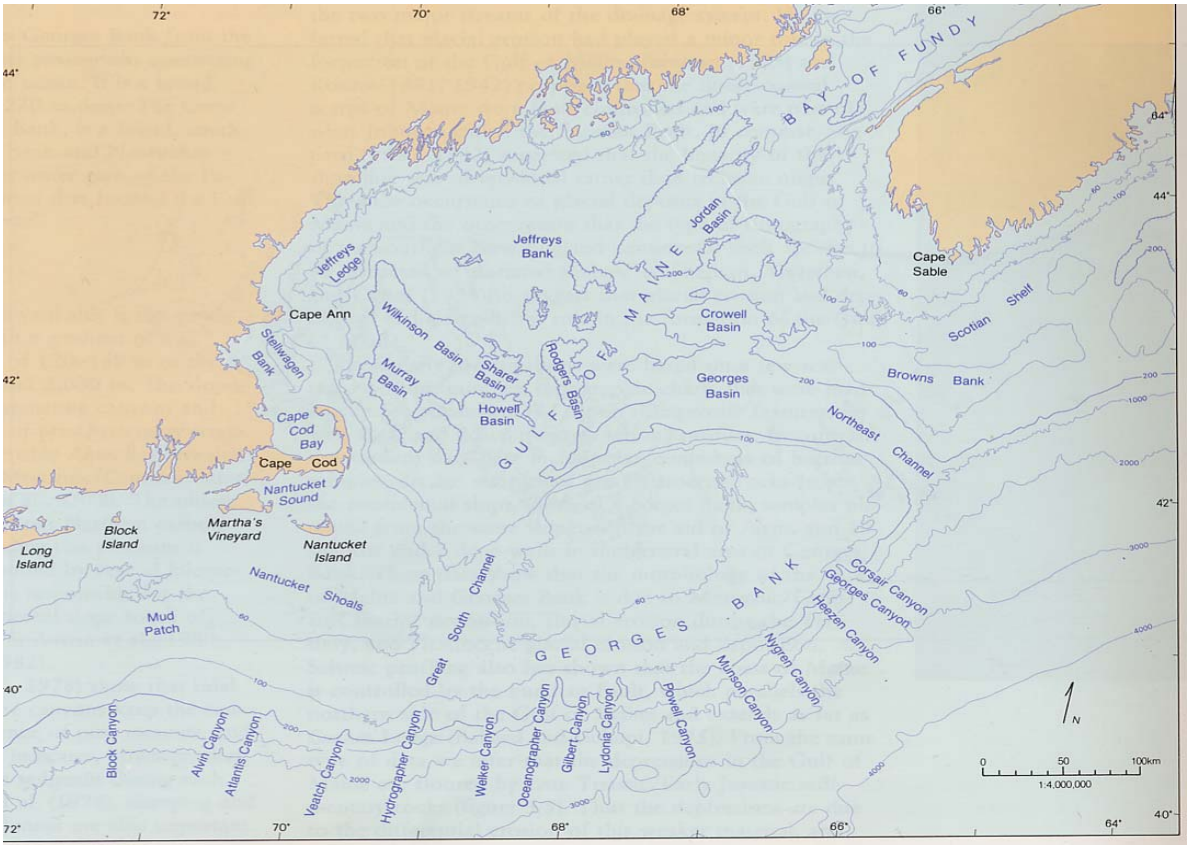


Figure 1. Topographic map of northwest Atlantic Ocean and Georges Bank

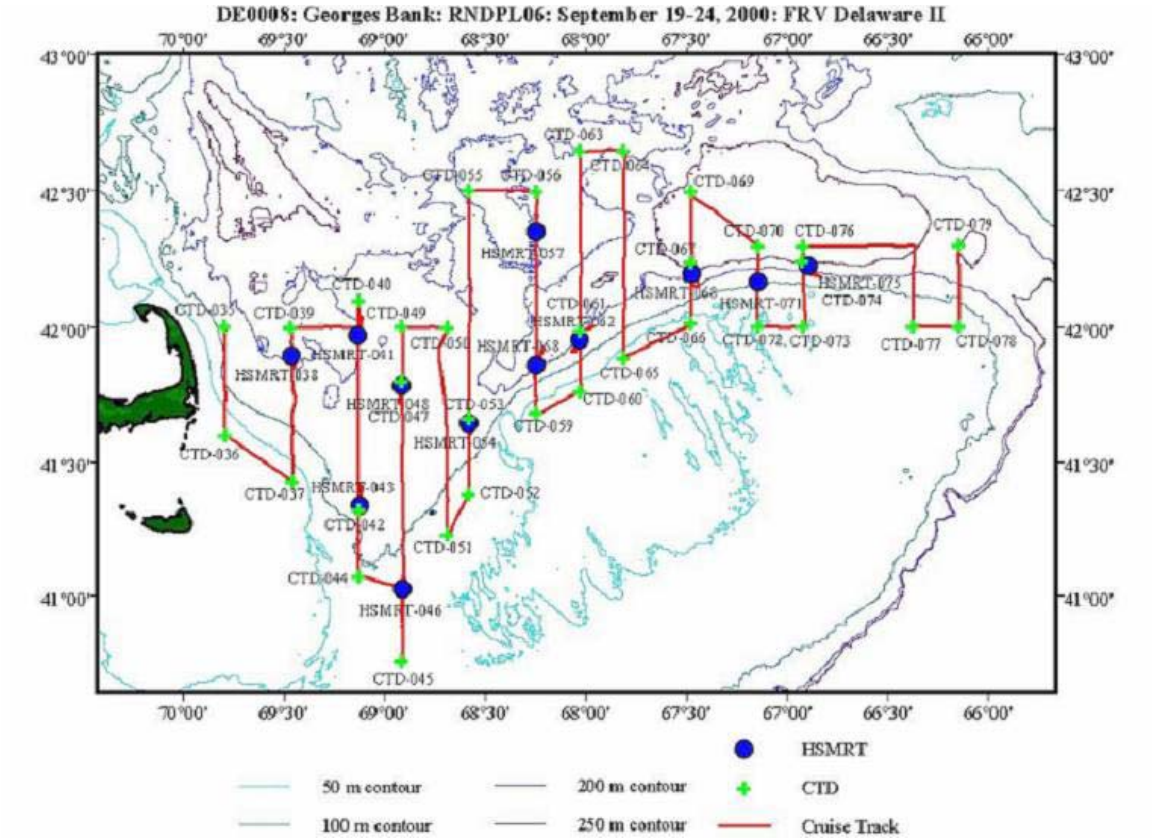
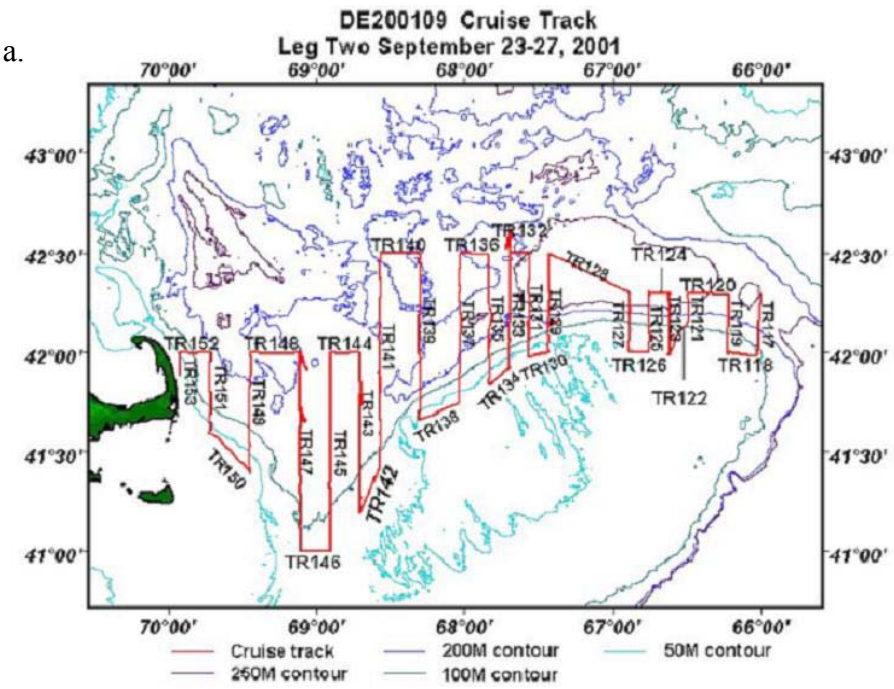


Figure 2. 2000 cruise and deployment track. Blue circles show HSMRT while green circles show CTD deployments.

a.



b.

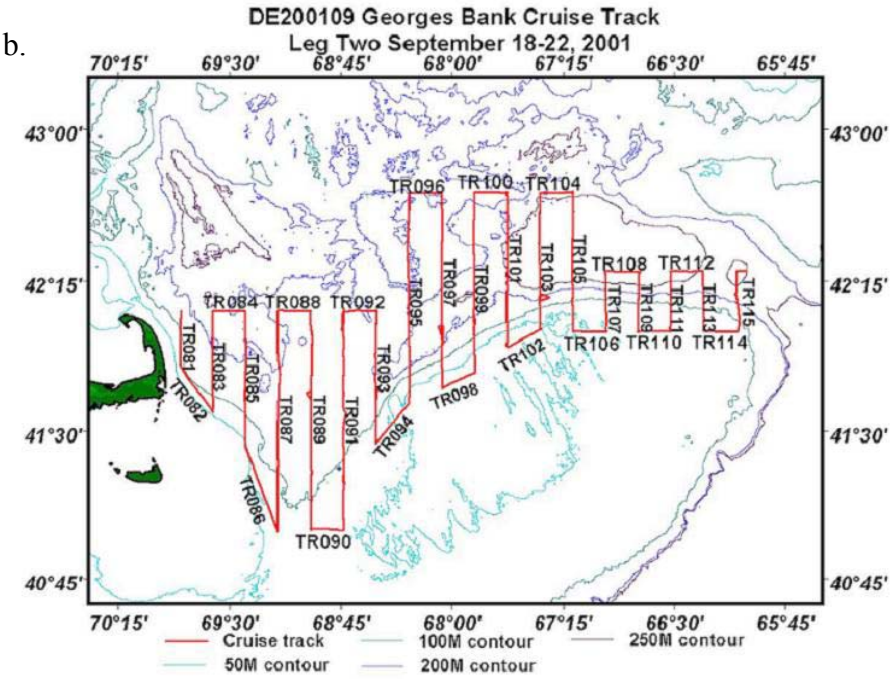


Figure 3. 2001 cruise track. a.) Transects 081 to 115
b.) Transects117 to 153.

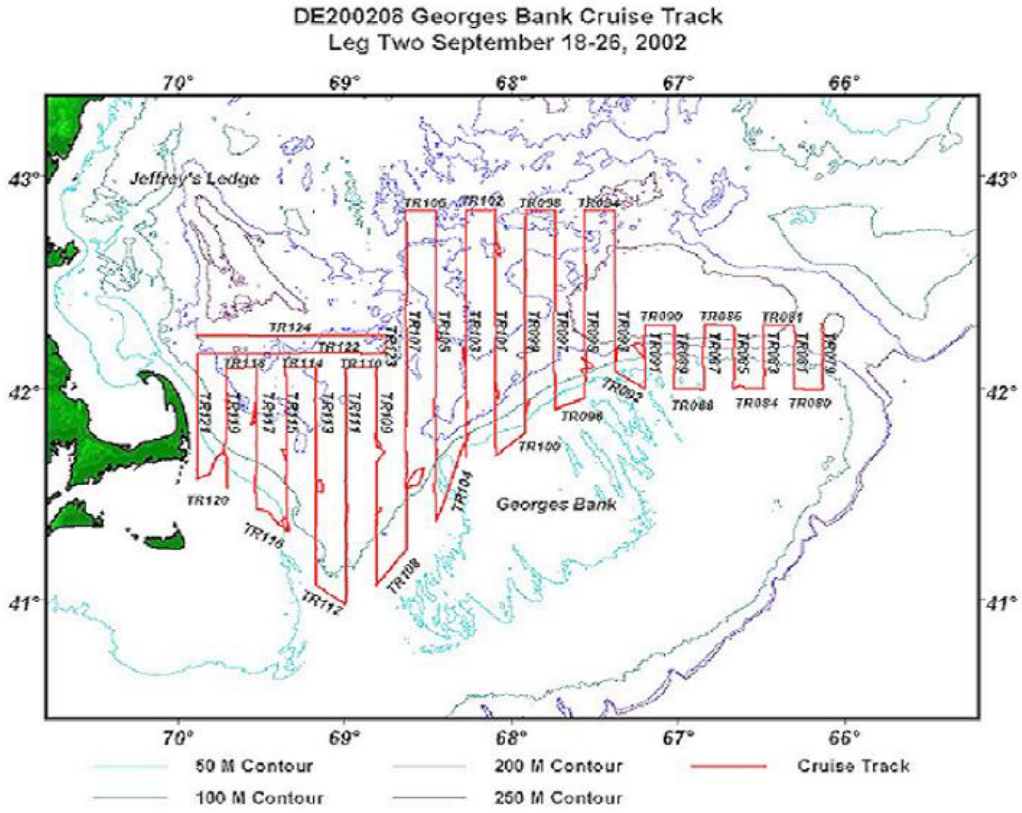


Figure 4. 2002 cruise track.

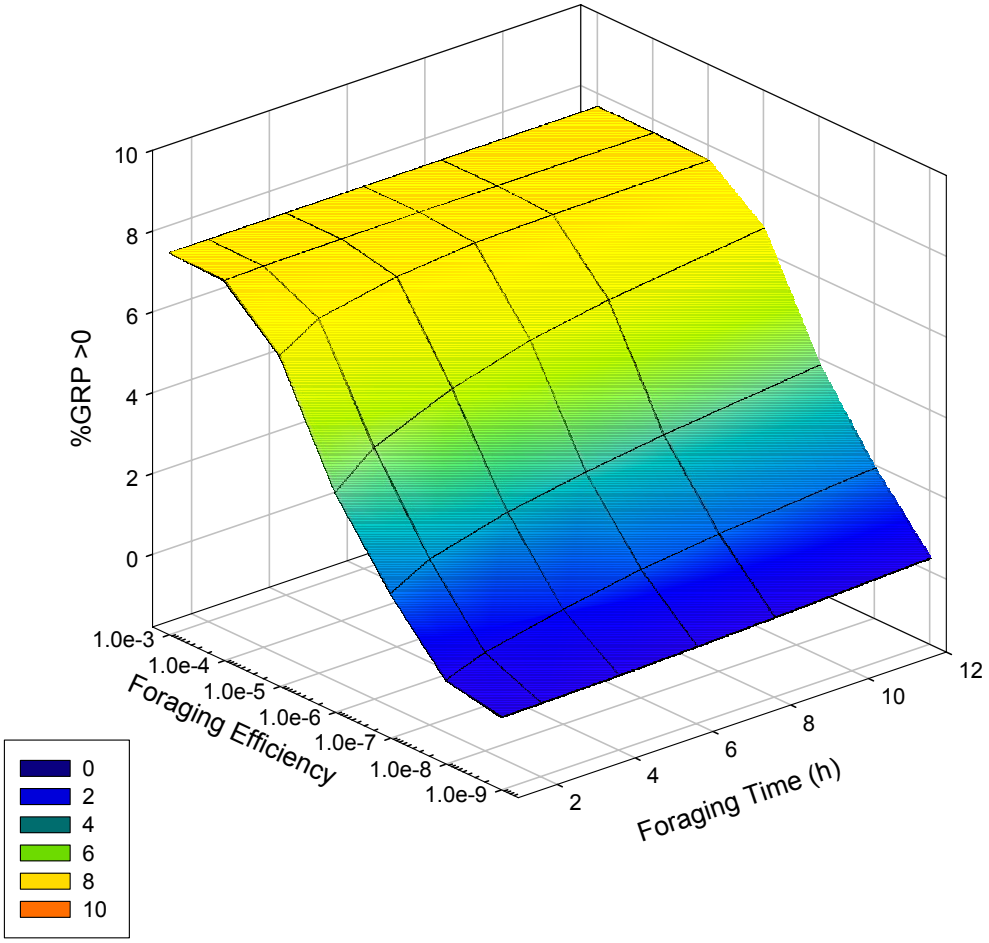


Figure 5. GRP values at different foraging times (h) and foraging efficiencies. With any foraging efficiency greater than $1e^{-5}$ and foraging time greater than 4 hours, GRP values remain unchanged.

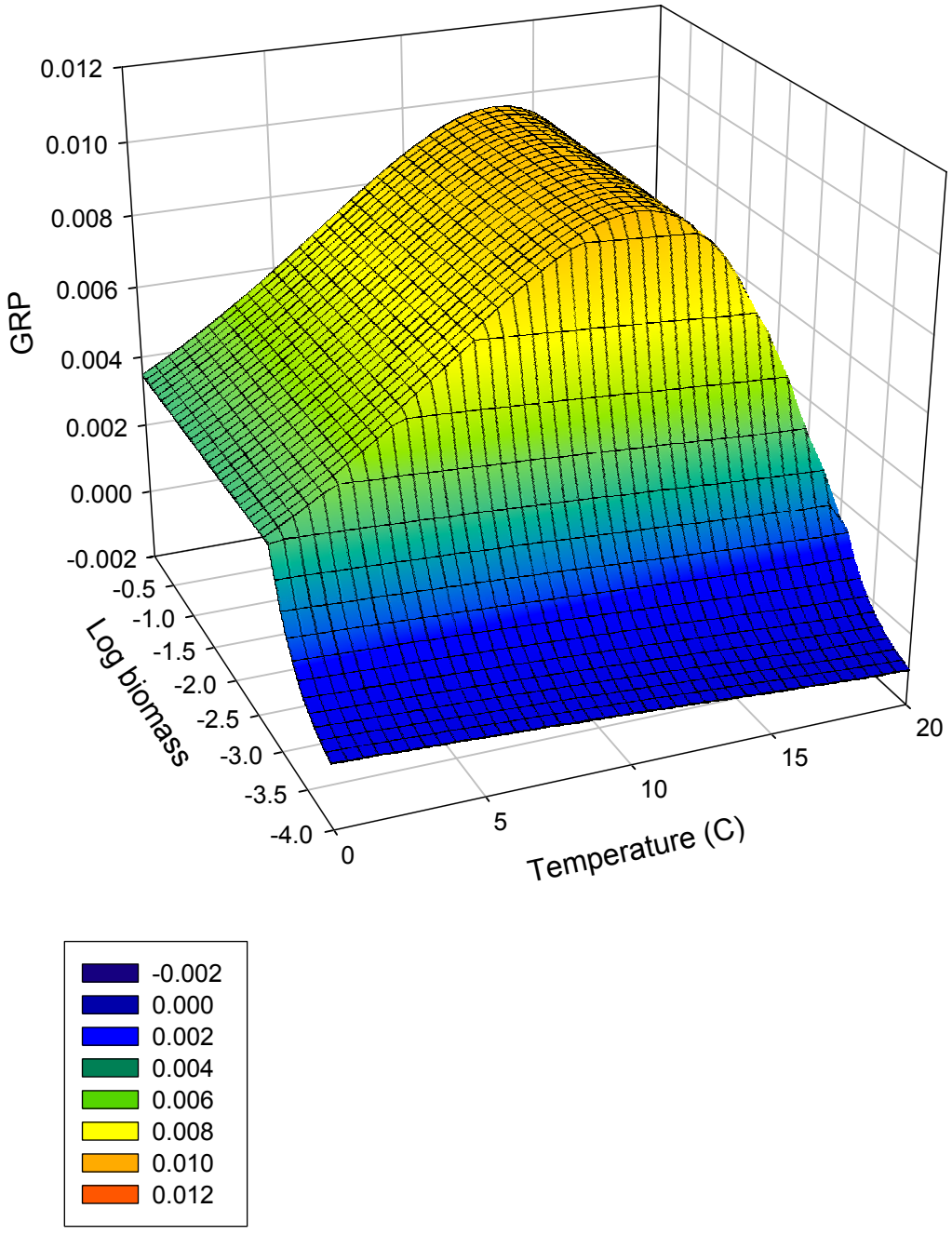


Figure 6. Optimal temperature and prey biomass values for theoretical maximum GRP.

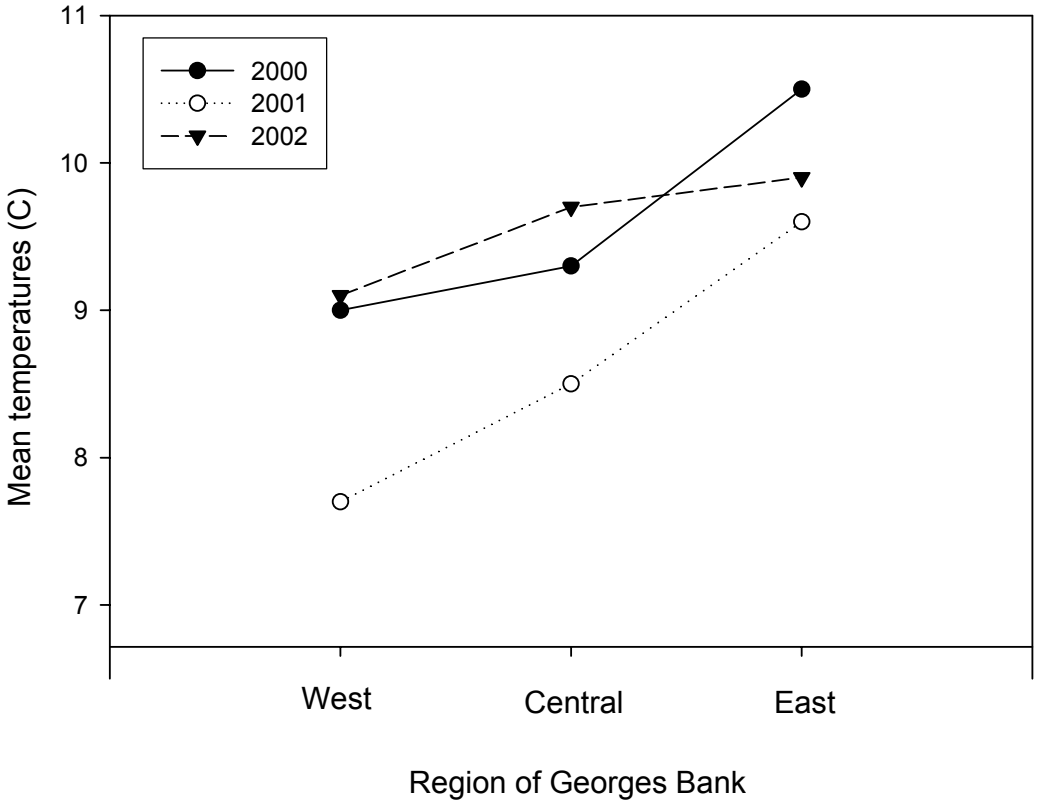


Figure 7. Mean temperatures for west, central and east regions of Georges Bank for 2000, 2001 and 2002 showing an increasing trend from west to east in all years.

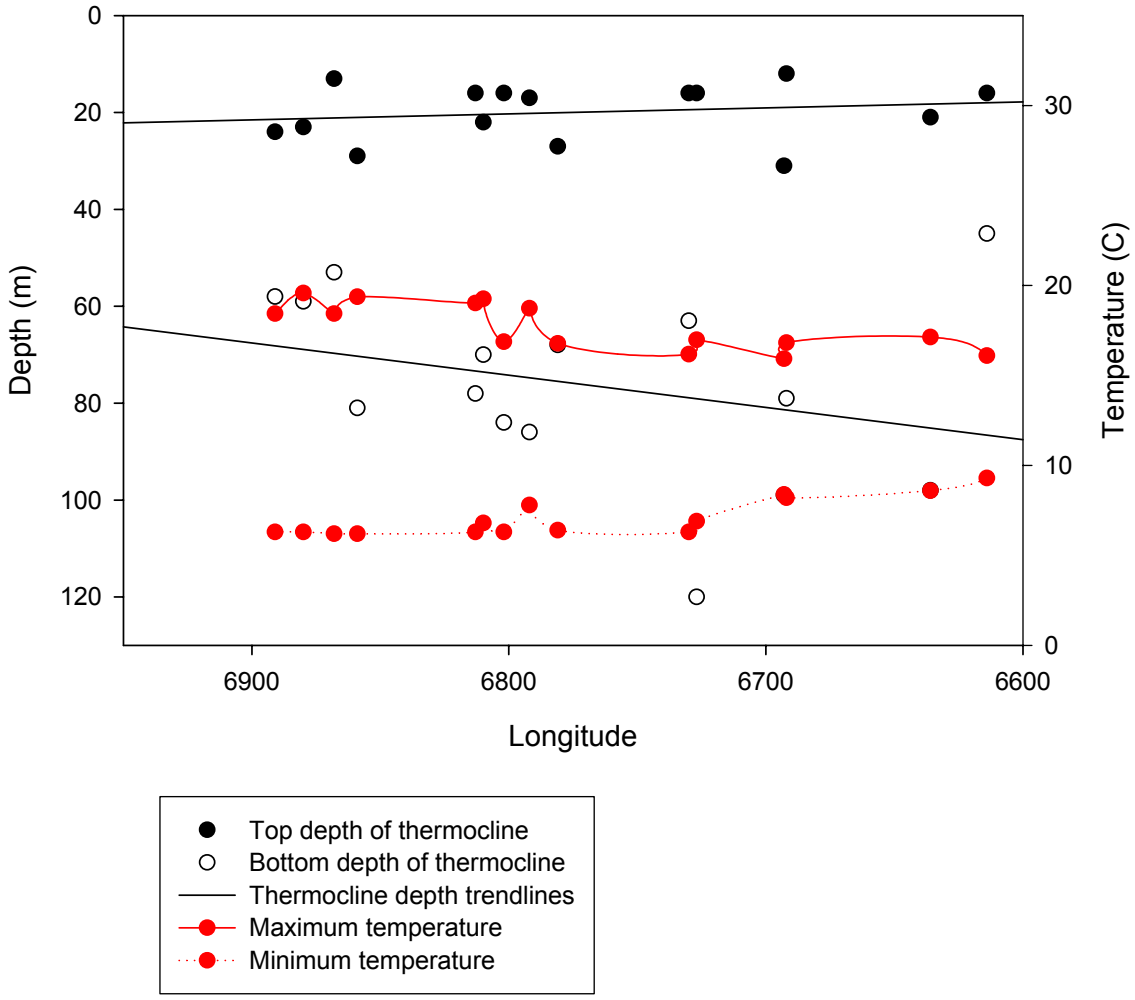


Figure 8. Temperature range and thermocline dynamics of 2000 from west to east of Georges Bank. Trendlines for the top depth of the thermocline has R^2=0.09, and bottom depth R^2=0.03

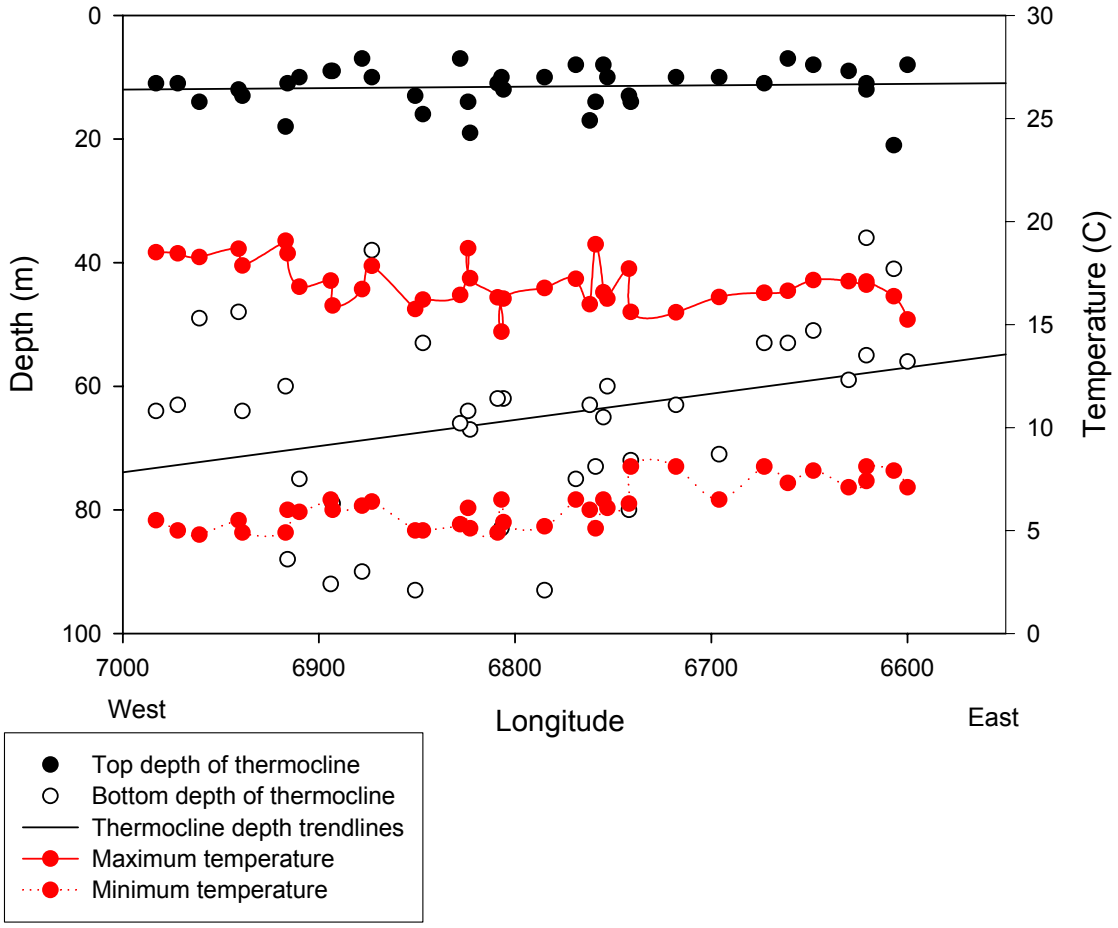


Figure 9. Temperature range and thermocline dynamics of 2001 from west to east of Georges Bank. Trendline for top depth of the thermocline has a R^2=0.006 and for bottom depth of the termocline, R^2=0.102

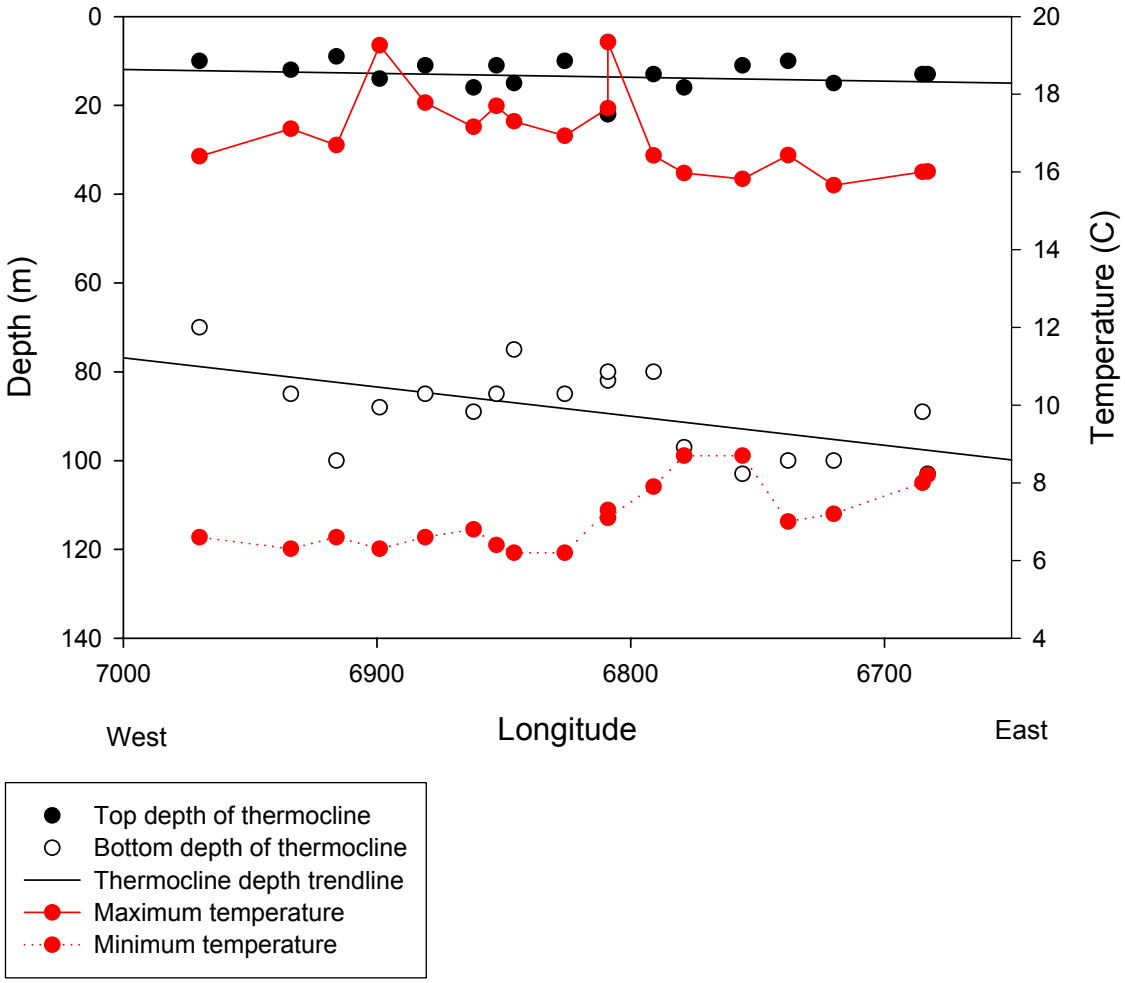


Figure 10. Temperature range and thermocline dynamics of 2002 from west to east of Georges Bank. Trendline for the top depth of the thermocline has R^2=0.04 and for bottom depth of the thermocline R^2=0.32

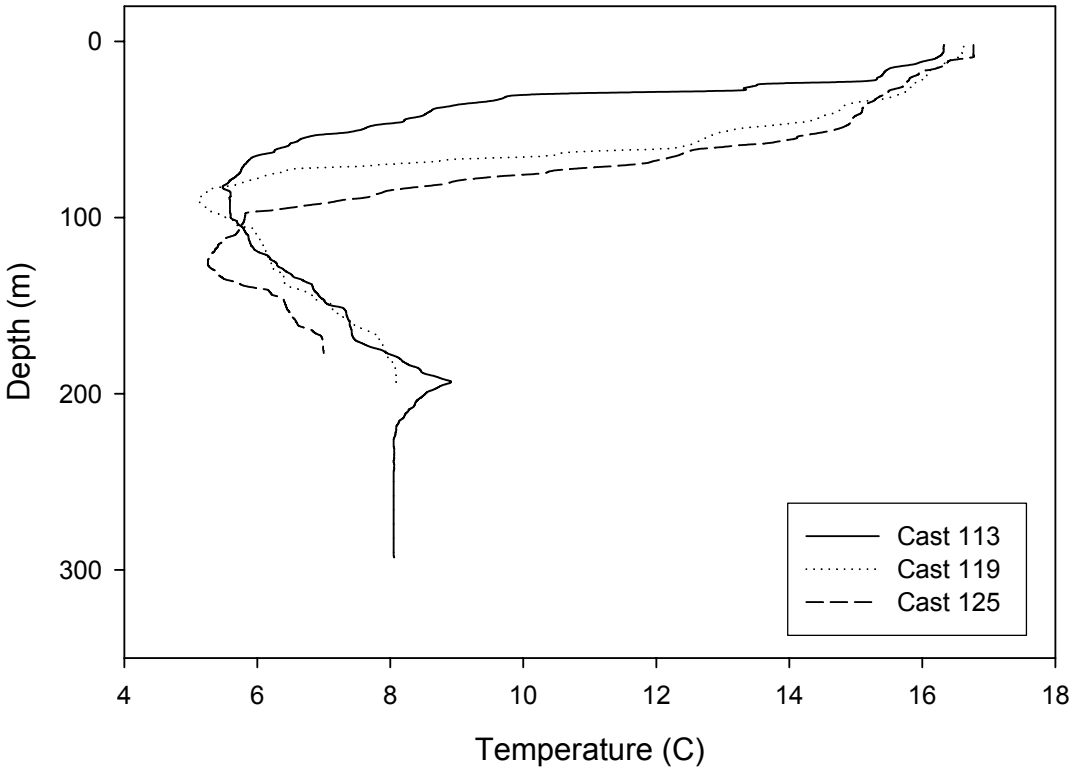


Figure 11. Temperature dynamics in three separate temperature casts showing an increase in temperature below the thermocline.

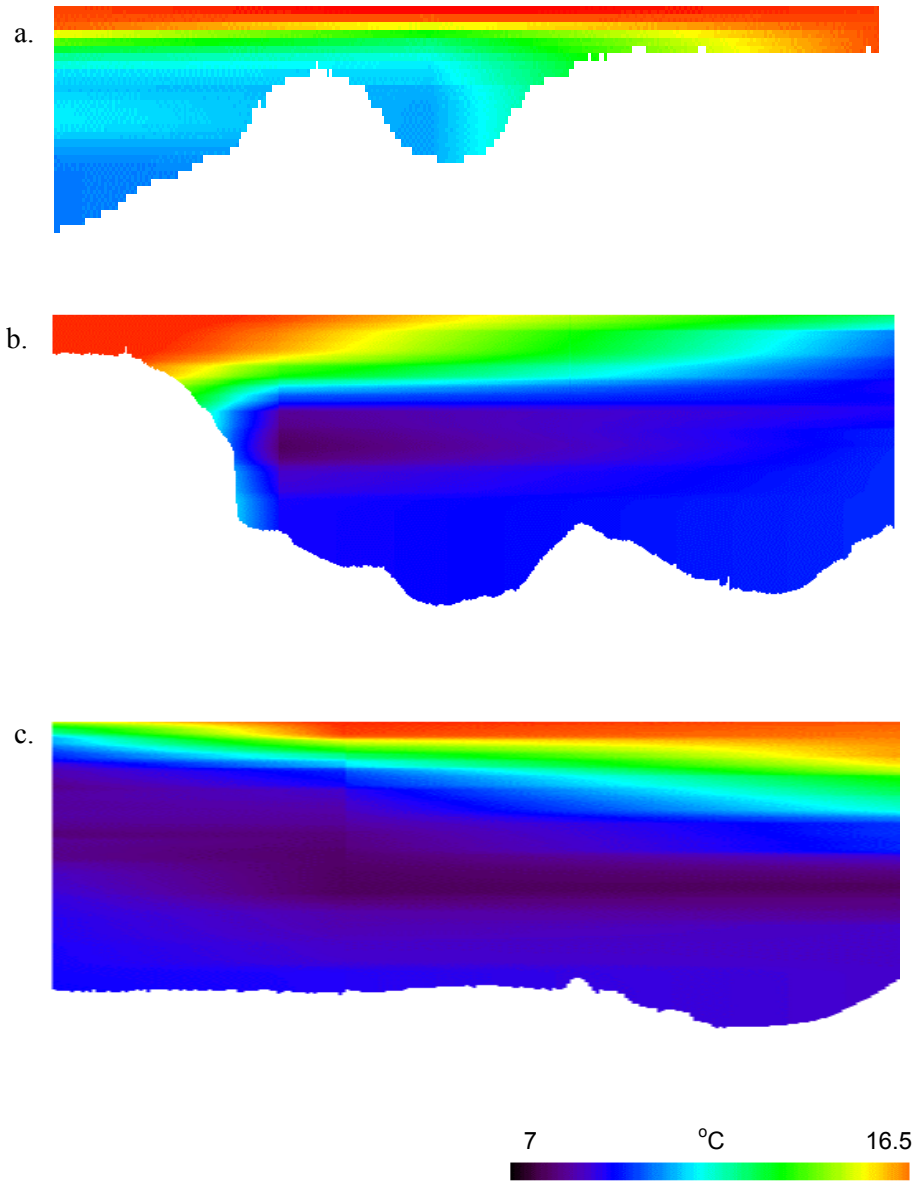


Figure 12. Temperature dynamics of three transects of 2000, 2001 and 2002. a) Transect 126 of 2000. b) Transect 99 of 2001. c) Transect 103 of 2002.

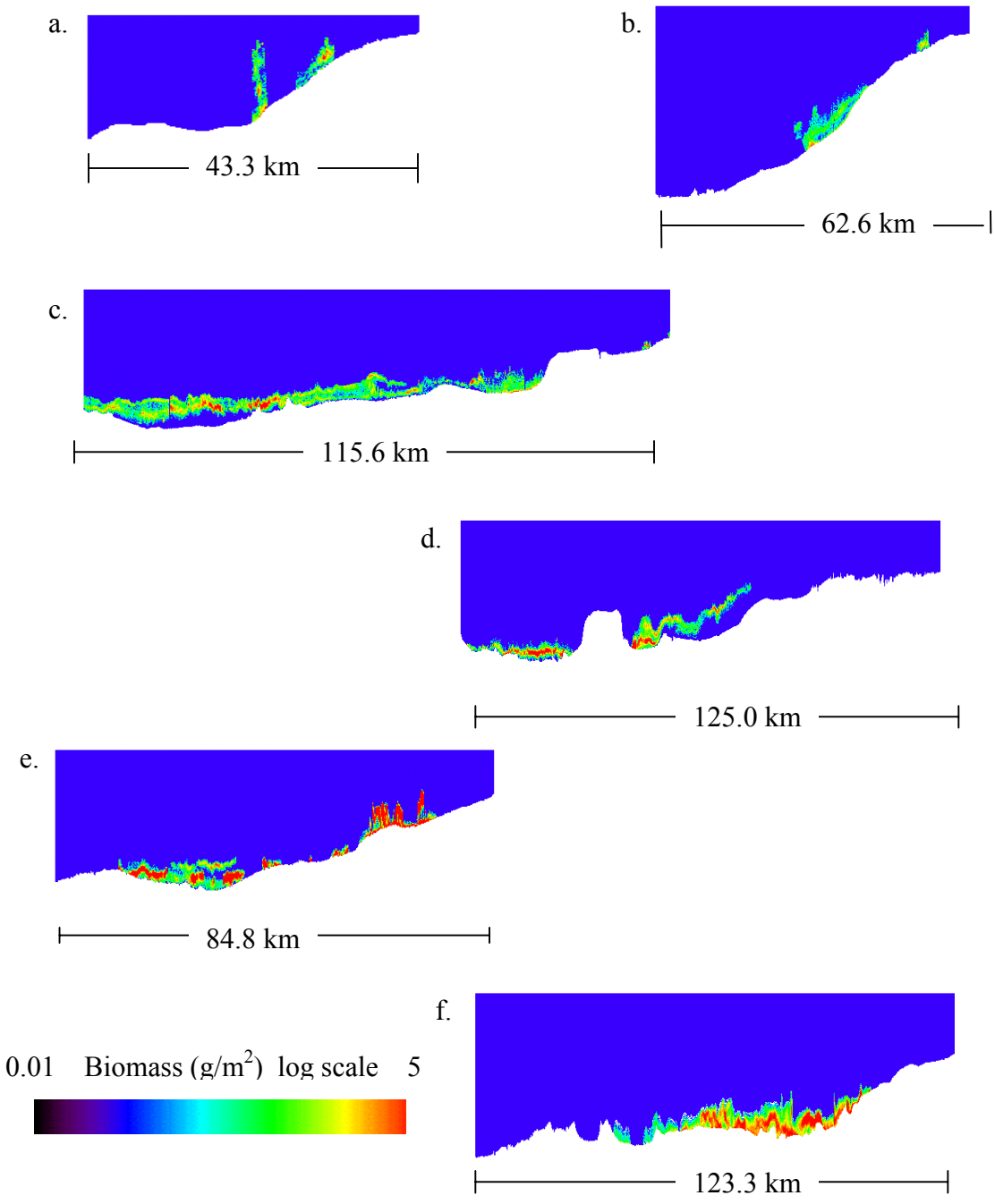


Figure 13. Biomass Map of Transects of region west of Georges Bank.
a.) Transect 106 b.) Transect 108 c.) Transect 110 d.) Transect 112
e.) Transect 114 f.) Transect 116

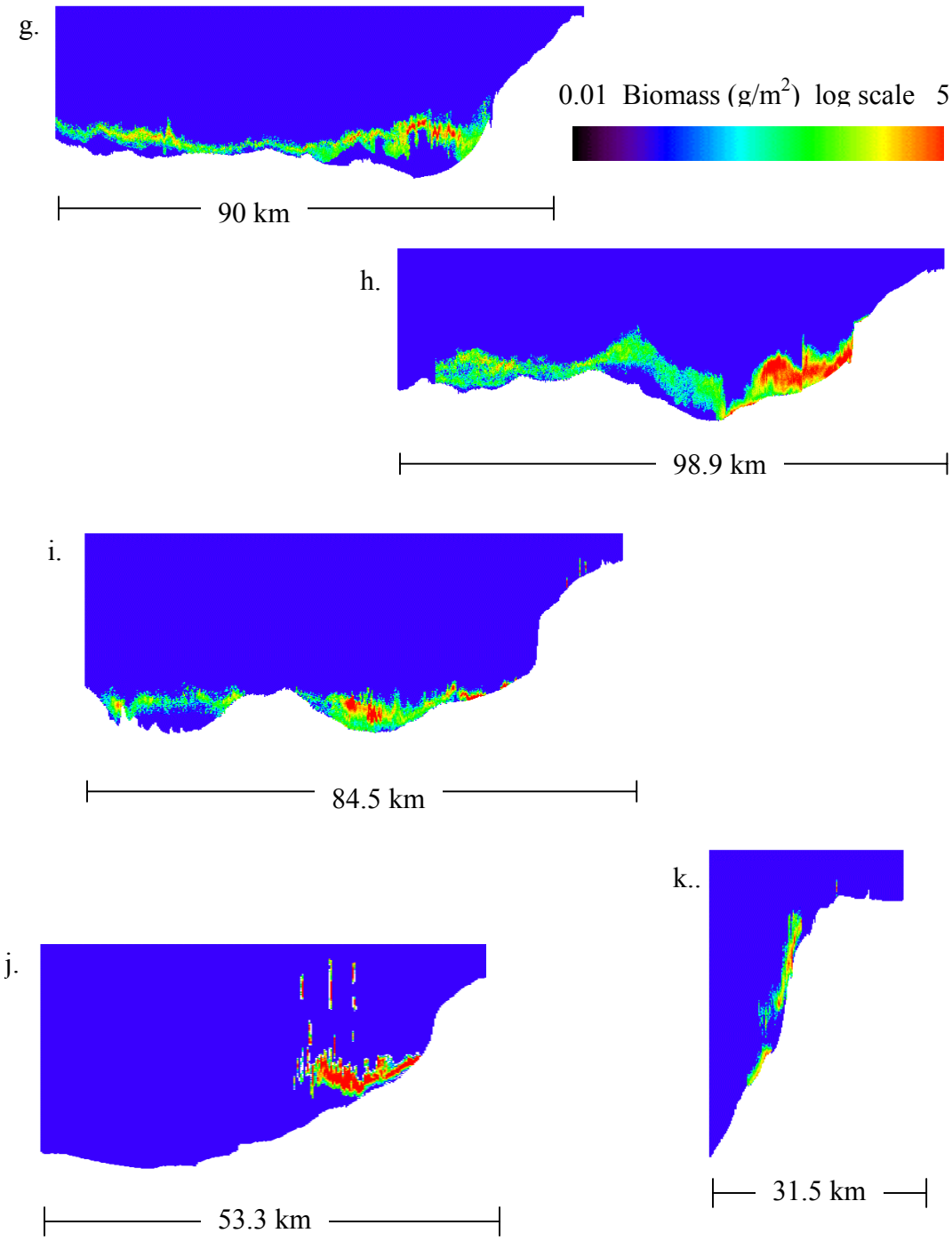


Figure13 (cont.) Map of Transects of central region of Georges Bank.
g.) Transect 118. h.) Transect 120. i.) Transect 122.
j.) Transect 124. k.) Transect 126

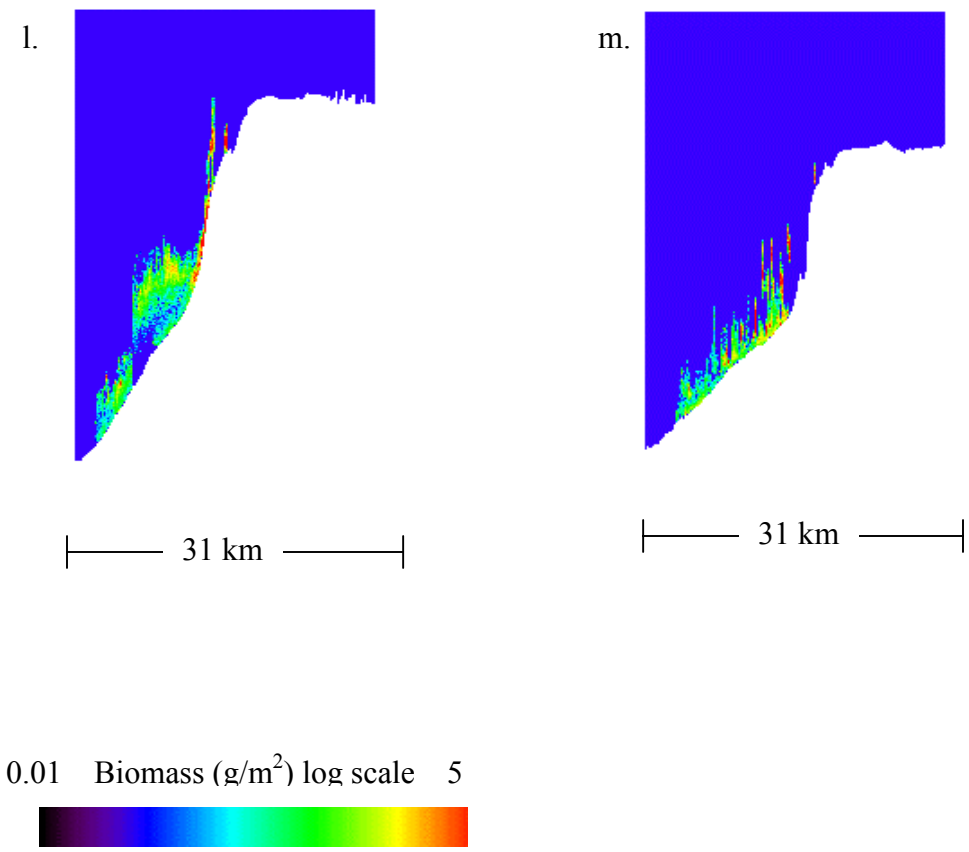


Figure13 (cont.) Biomass Map of Transects of east region of Georges Bank.
l.) Transect 128 m.) Transect 130

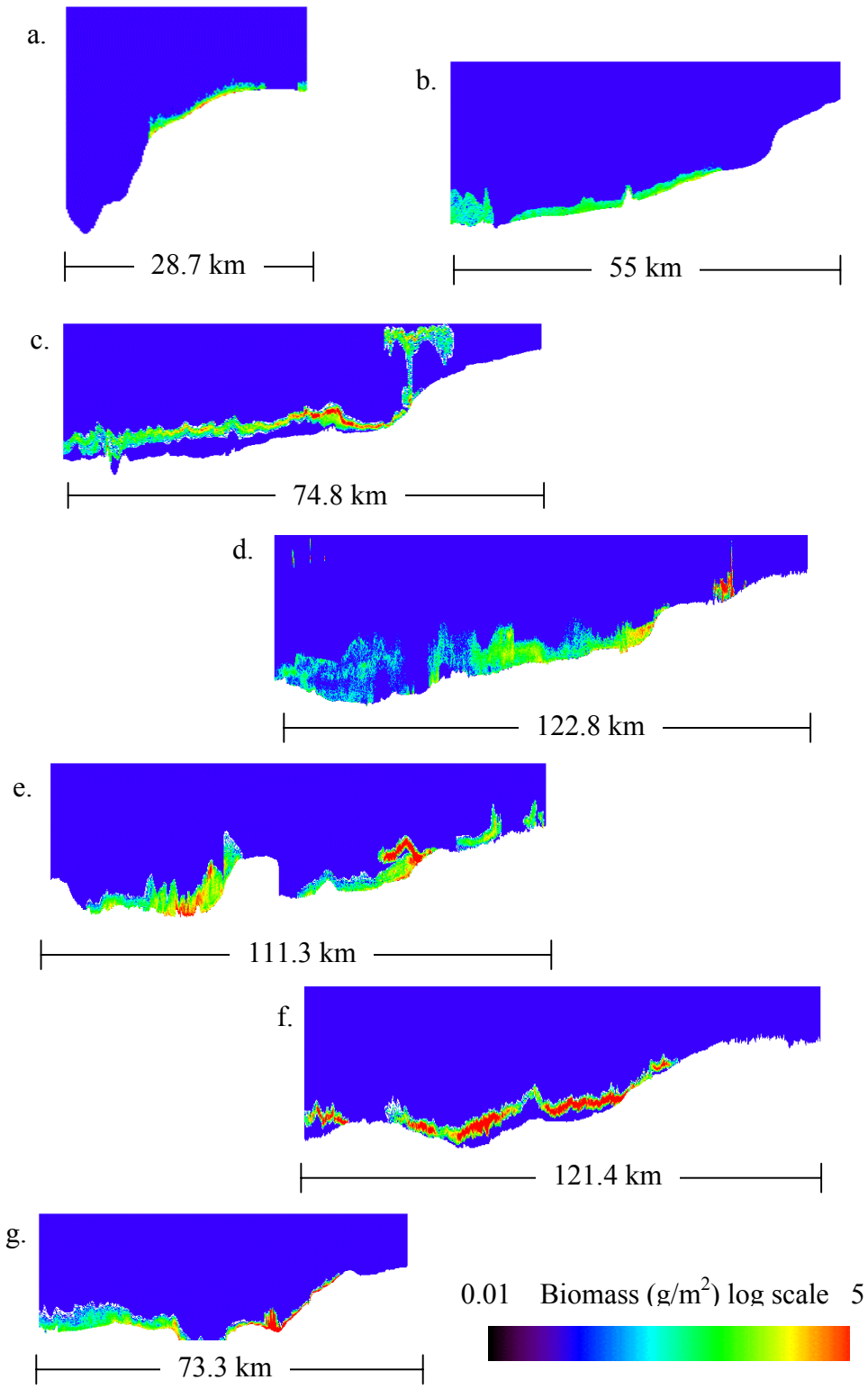


Figure 14. Biomass Map of 2001 Transects of region west of Georges Bank. a.) Transect 081 b.) Transect 083 c.) Transect 085 d.) Transect 087 e.) Transect 089 f.) Transect 091 g.) Transect 093

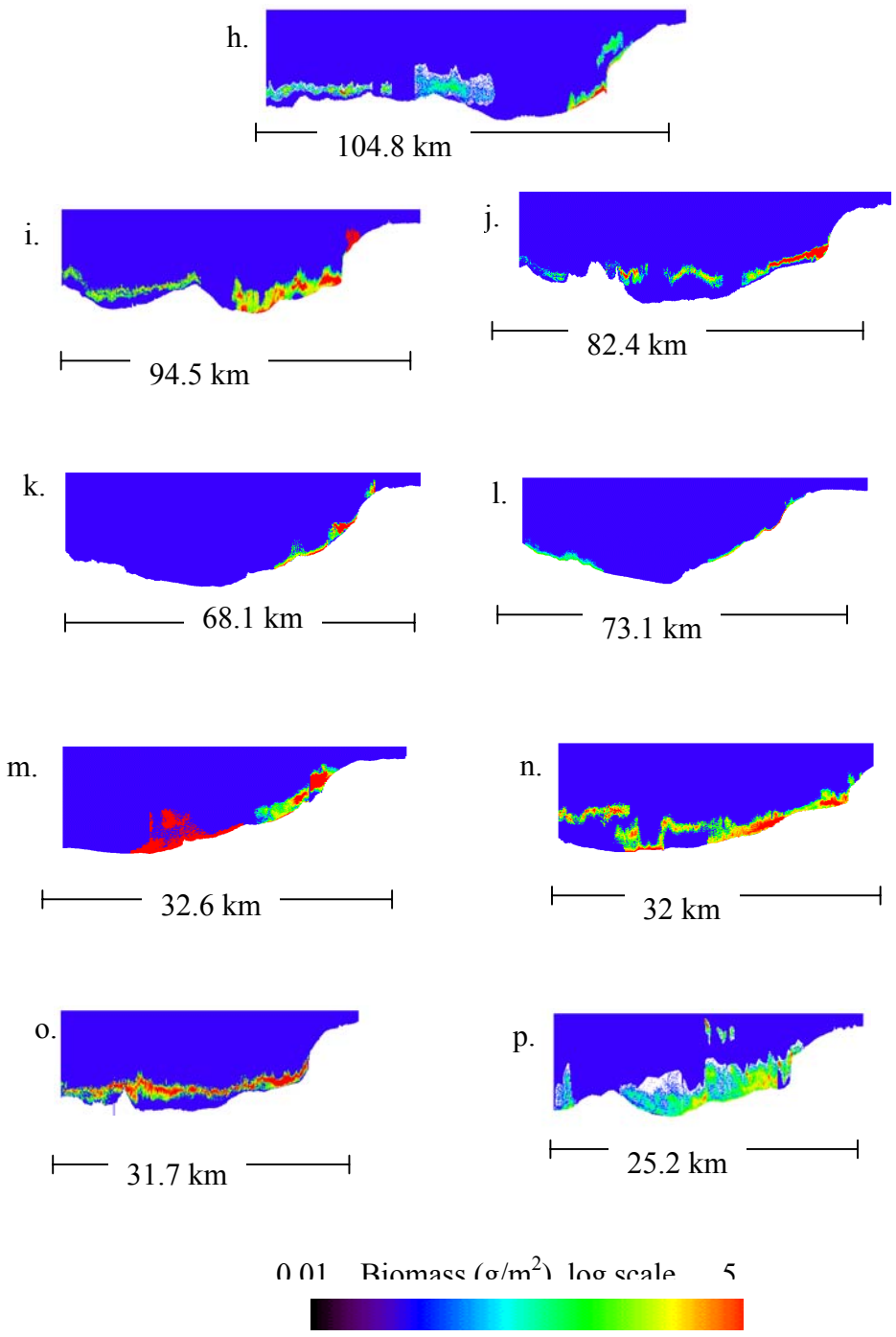


Figure 14 (cont.). Map of 2001 Transects of central region of Georges Bank. h.) Transect 099 i.) Transect 099 j.) Transect 101 k.) Transect 103 l.) Transect 105 m.) Transect 129 n.) Transect 131 o.) Transect 133 p.) Transect 135

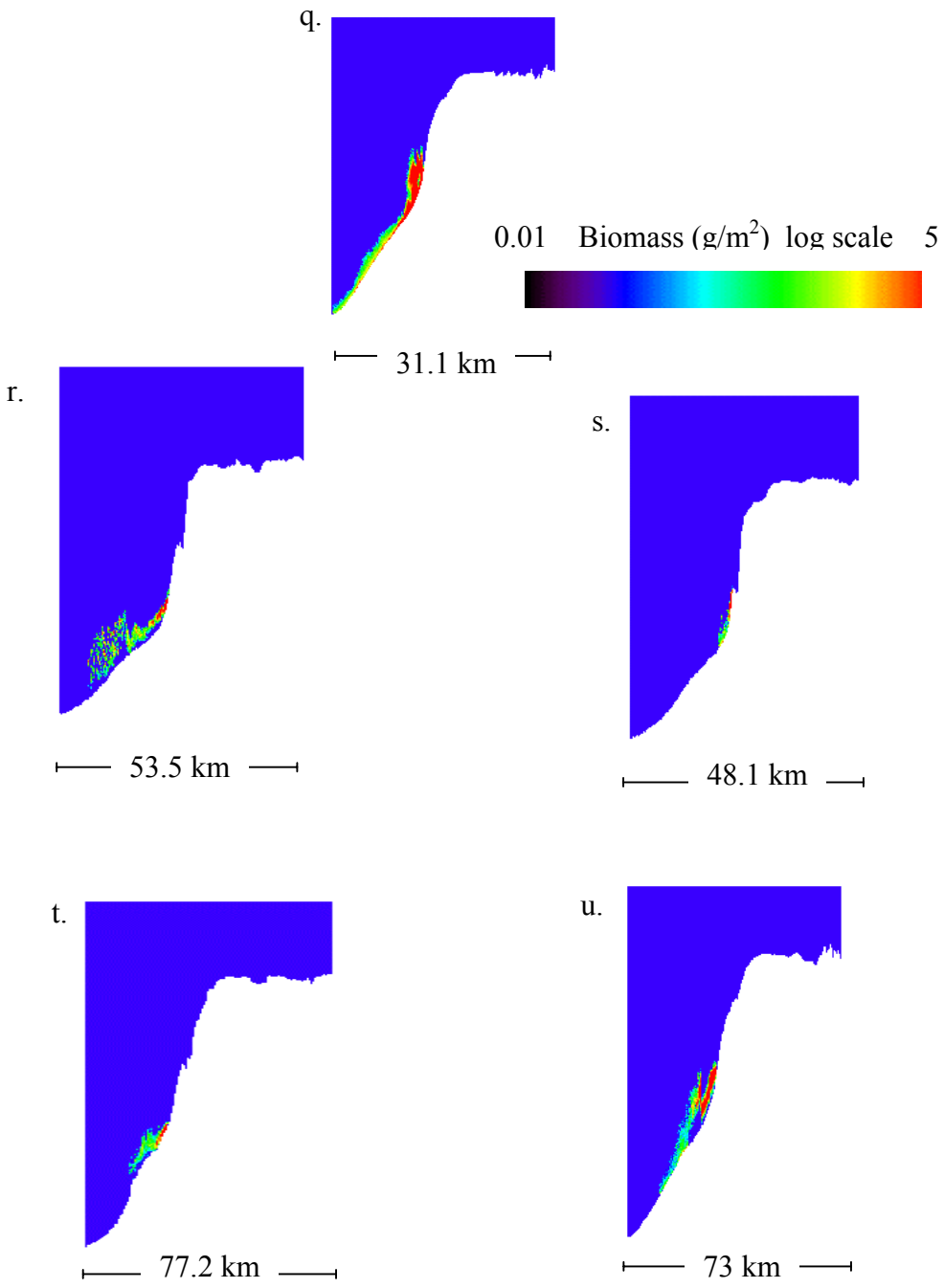


Figure 14 (cont.). Map of 2001 Transects of east region of Georges Bank.
q.) Transect 107 r.) Transect 111 s.) Transect 123
t.) Transect 125 u.) Transect 127

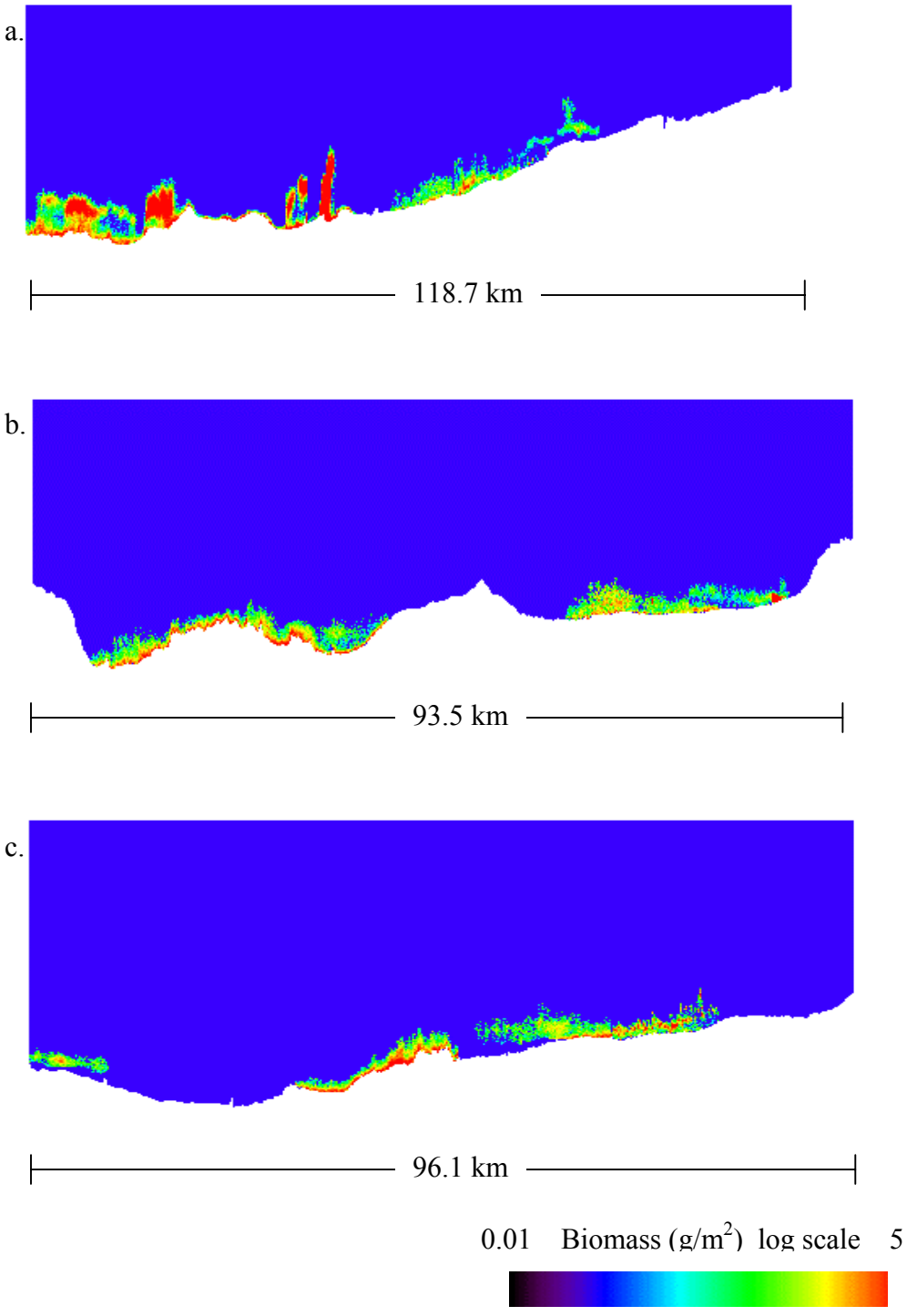


Figure 15. Biomass map of 2002 Transects of west region of Georges Bank. a.) Transect 109 b.) Transect 111 c.) Transect 113

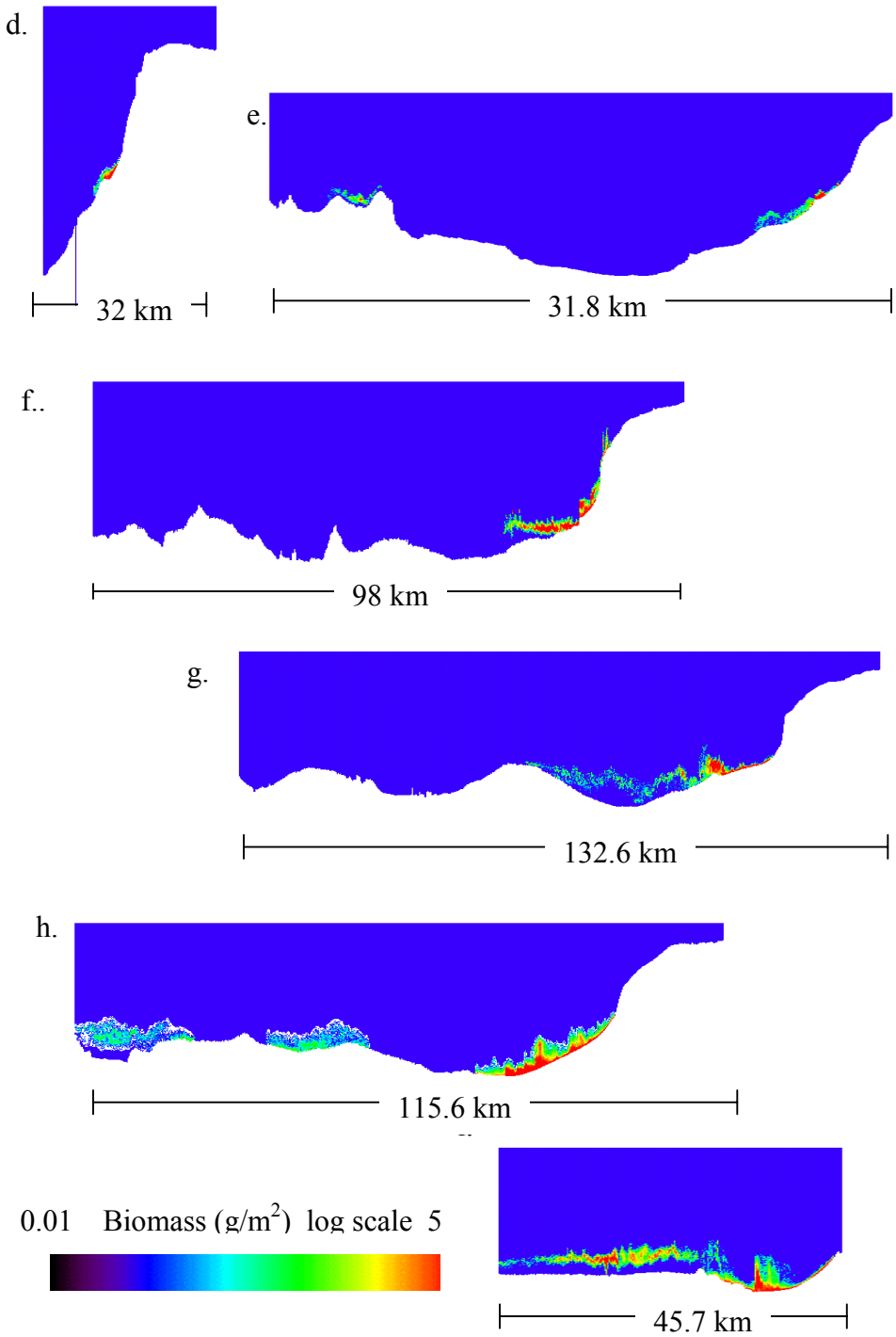


Figure 15(cont.) Map of 2002 Transects of central region of Georges Bank. d.) Transect 091 e.) Transect 093 f.) Transect 097 g.) Transect 099 h.) Transect 101 i.) Transect 103

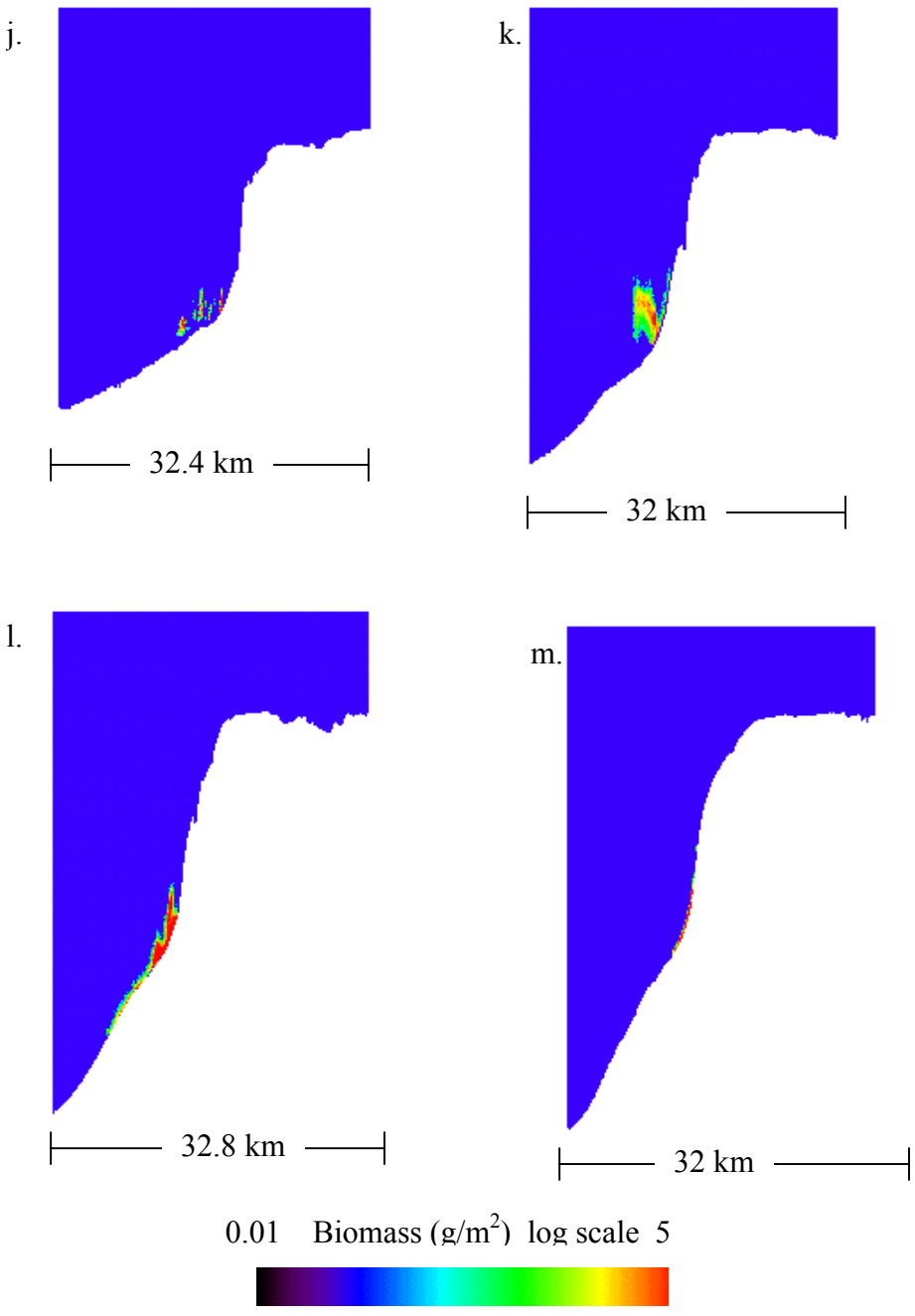


Figure 15 (cont.) Map of 2002 Transects of east region of Georges Bank.
j.) Transect 081 k.) Transect 083 l.) Transect 087
m.) Transect 089

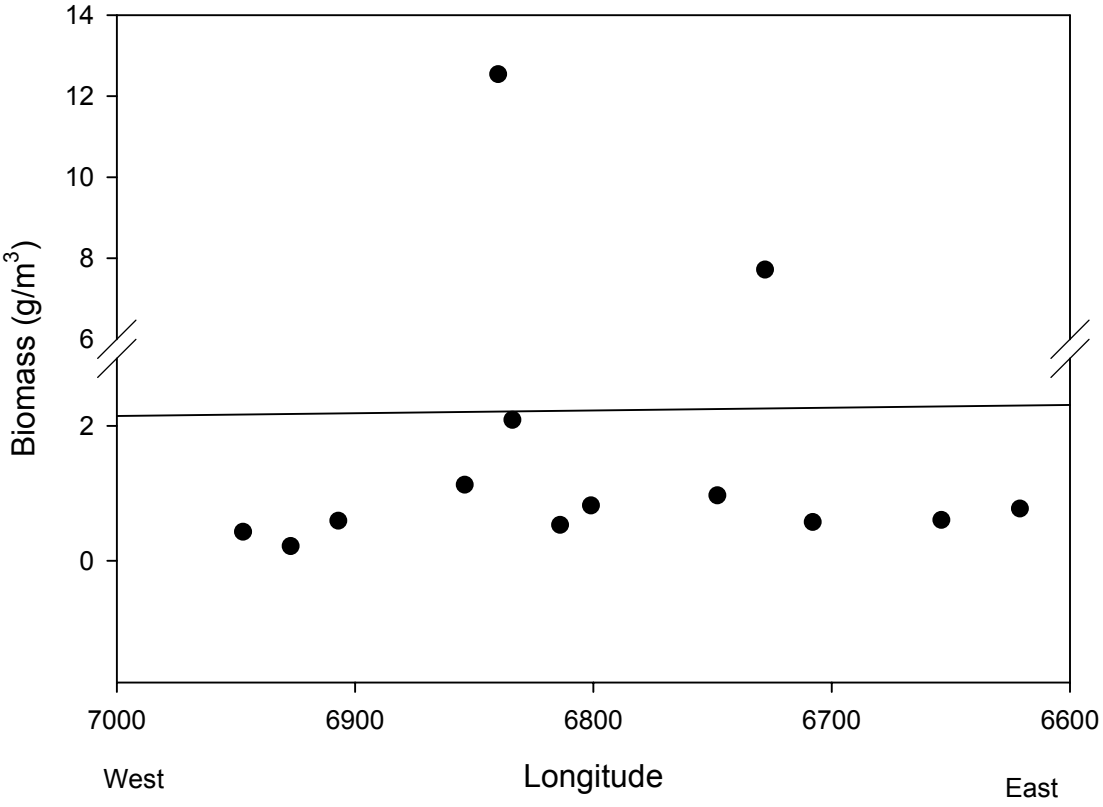


Figure 16. Biomass density values from west to east of Georges Bank for 2000. Trendline shows R^2=0.0001

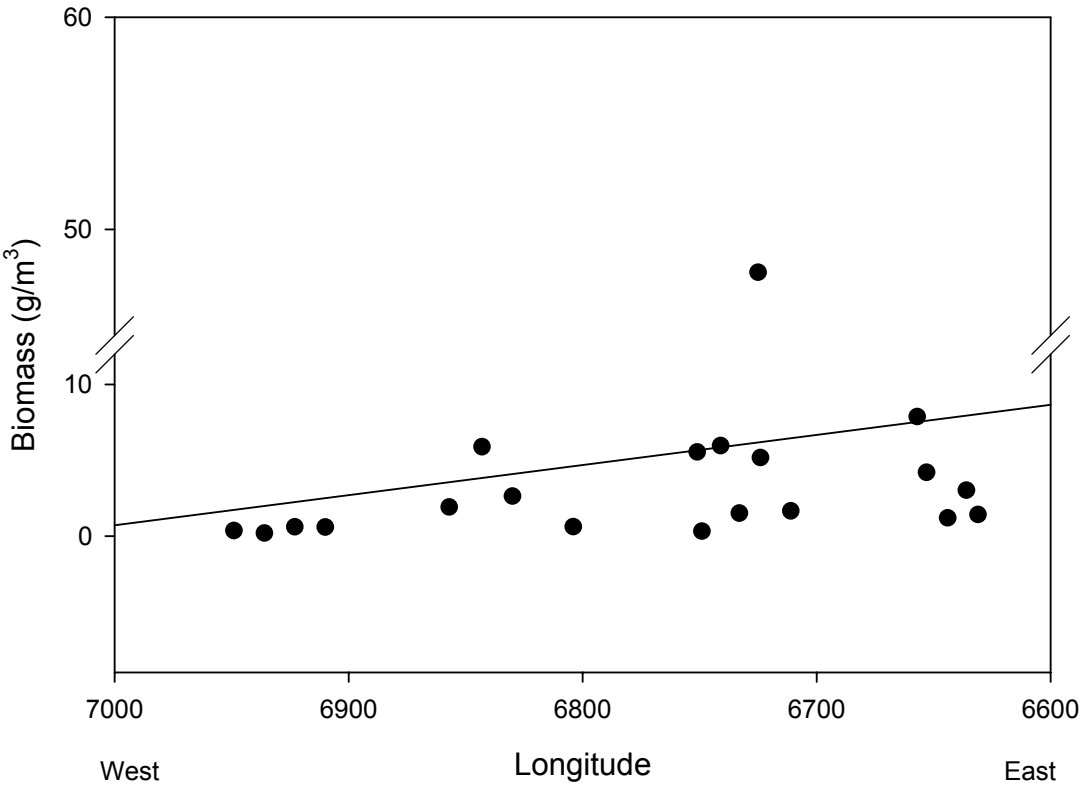


Figure 17. Biomass density values from west to east of Georges Bank for 2001. Increasing trendline shows R^2=0.04.

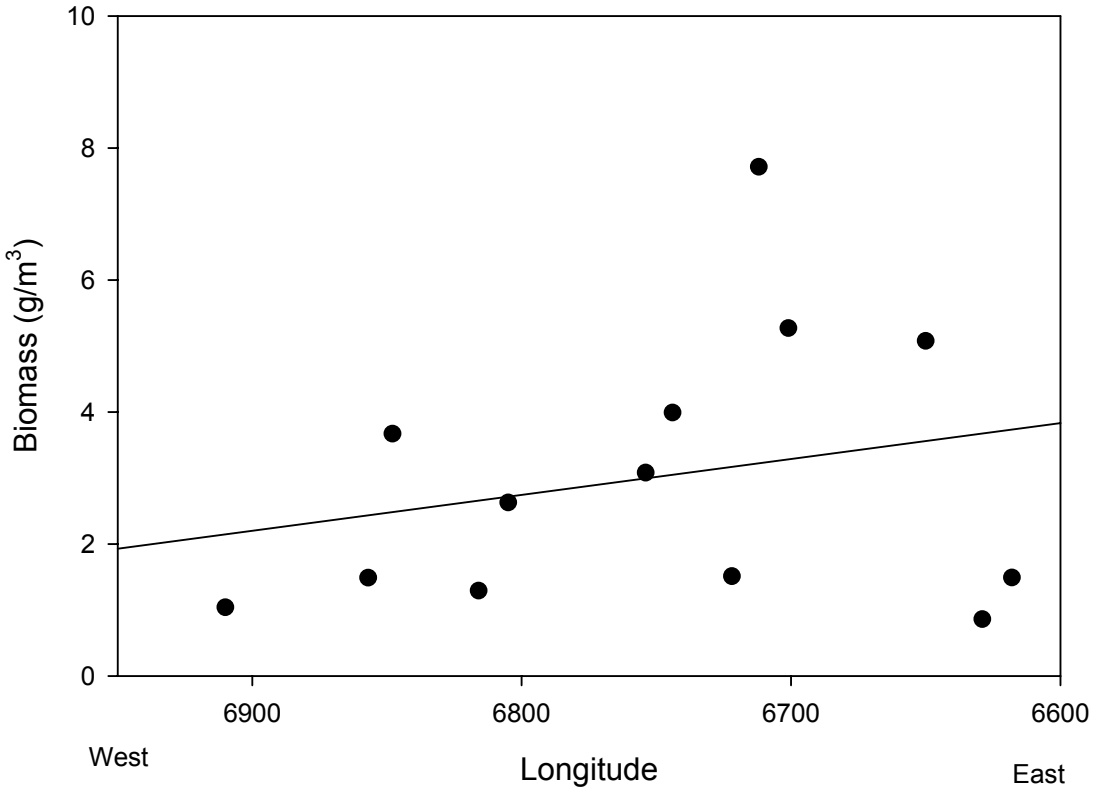


Figure 18. Biomass density values from west to east of Georges Bank for 2002. Increasing trendline shows R^2=0.06

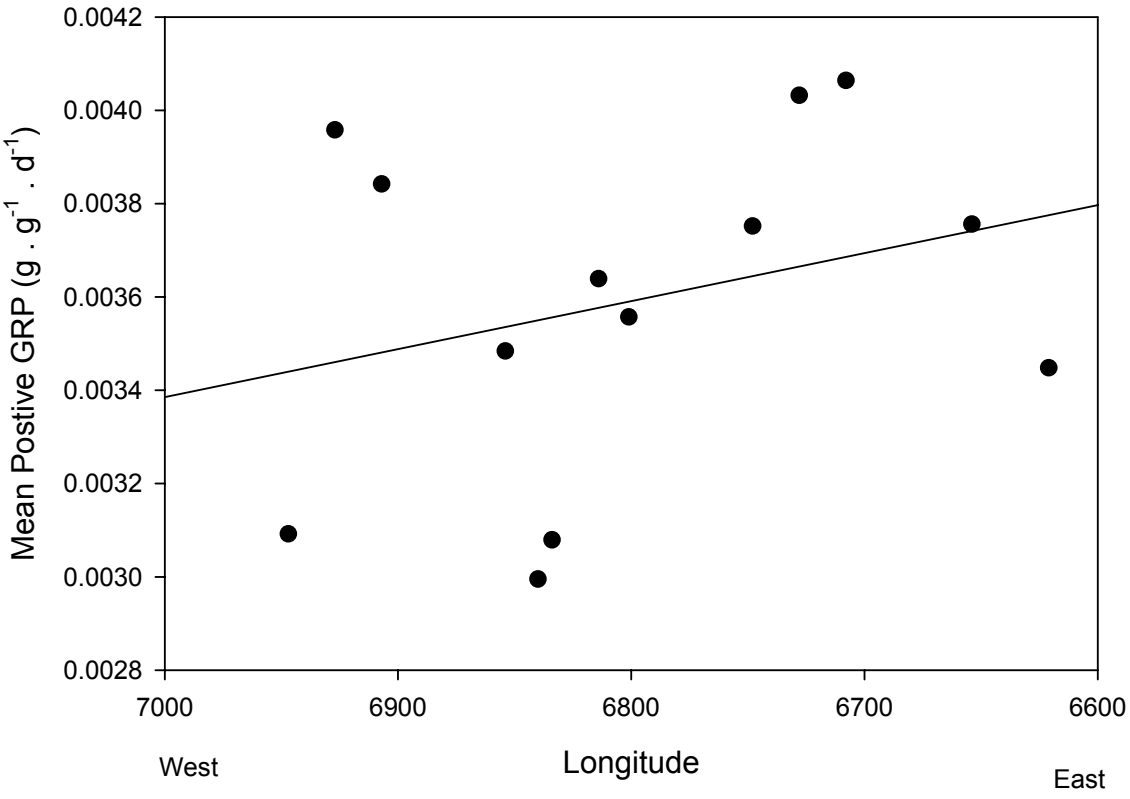


Figure 19. Mean positive GRP values from west to east for 2000. Increasing trendline shows R^2=0.08

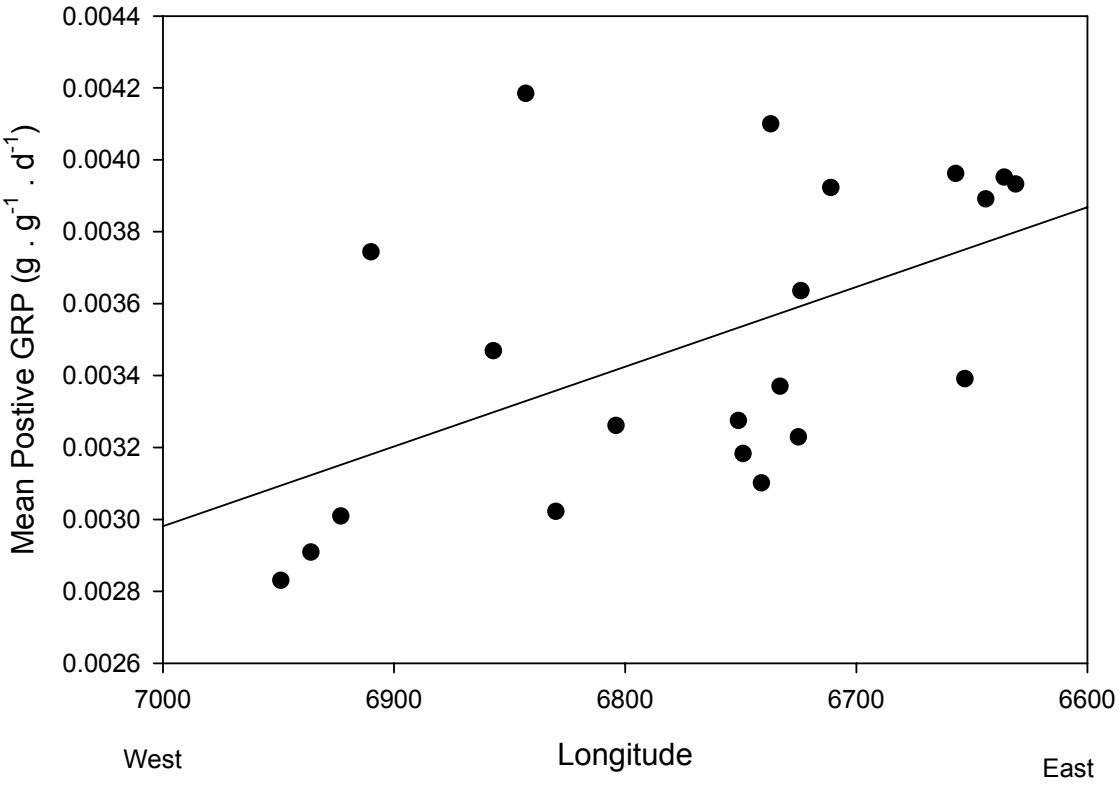


Figure 20. Mean positive GRP values from west to east of 2001. Increasing trendline shows R^2=0.3

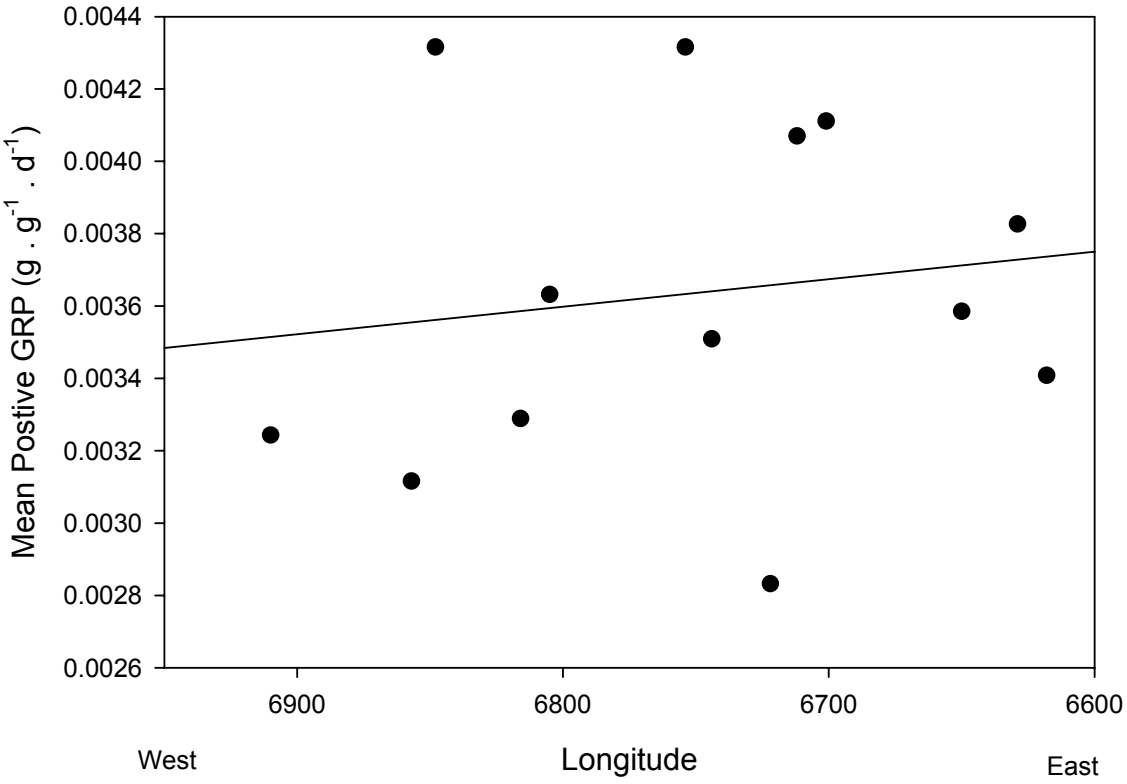


Figure 21. Mean positive GRP values from west to east for 2002. Increasing trendline has R^2=0.02

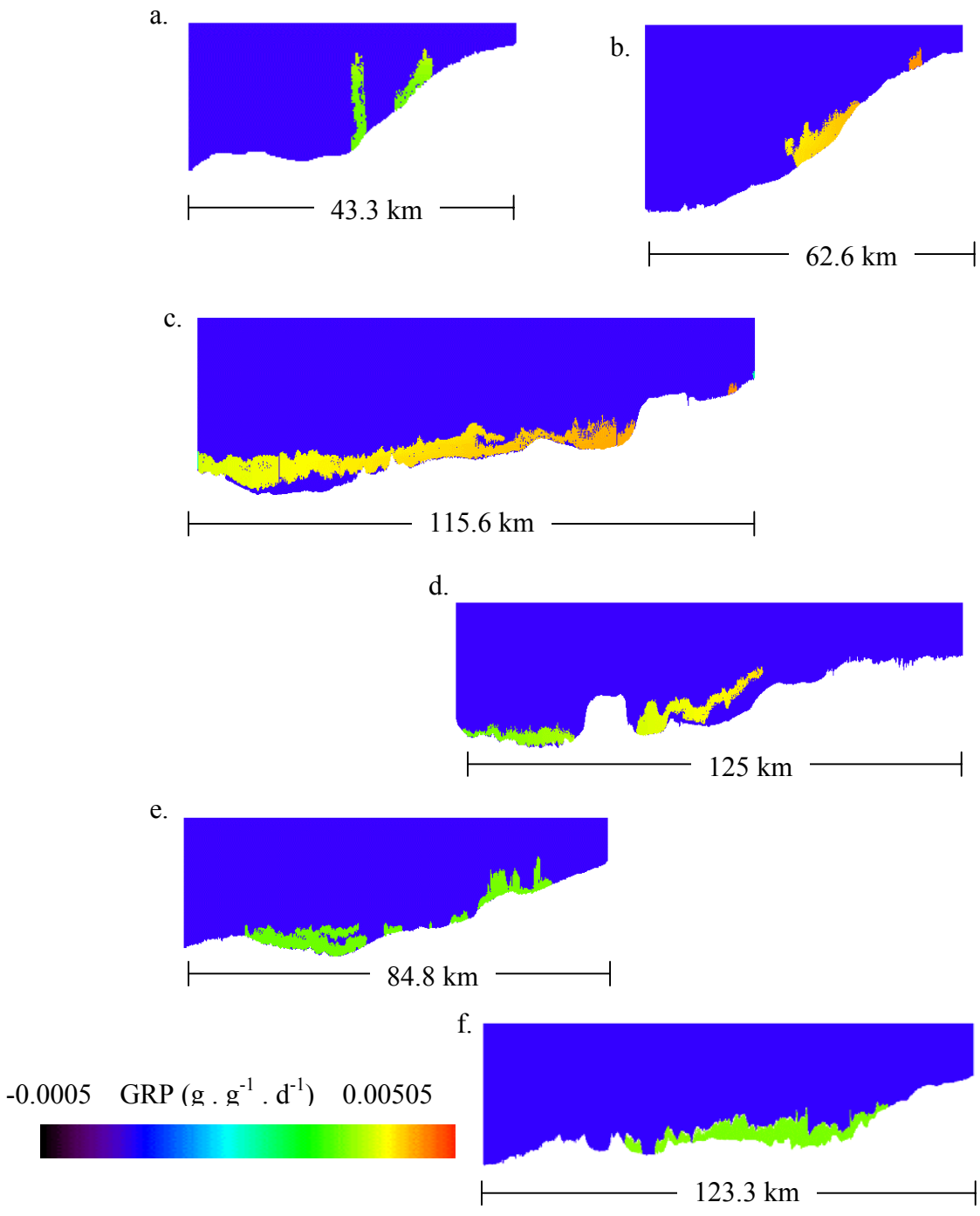


Figure 22. 2000 GRP Maps of Transects of west region of Georges Bank.
a.) Transect 106 b.) Transect 108 c.) Transect 110
d.) Transect 112 e.) Transect 114 f.) Transect 116

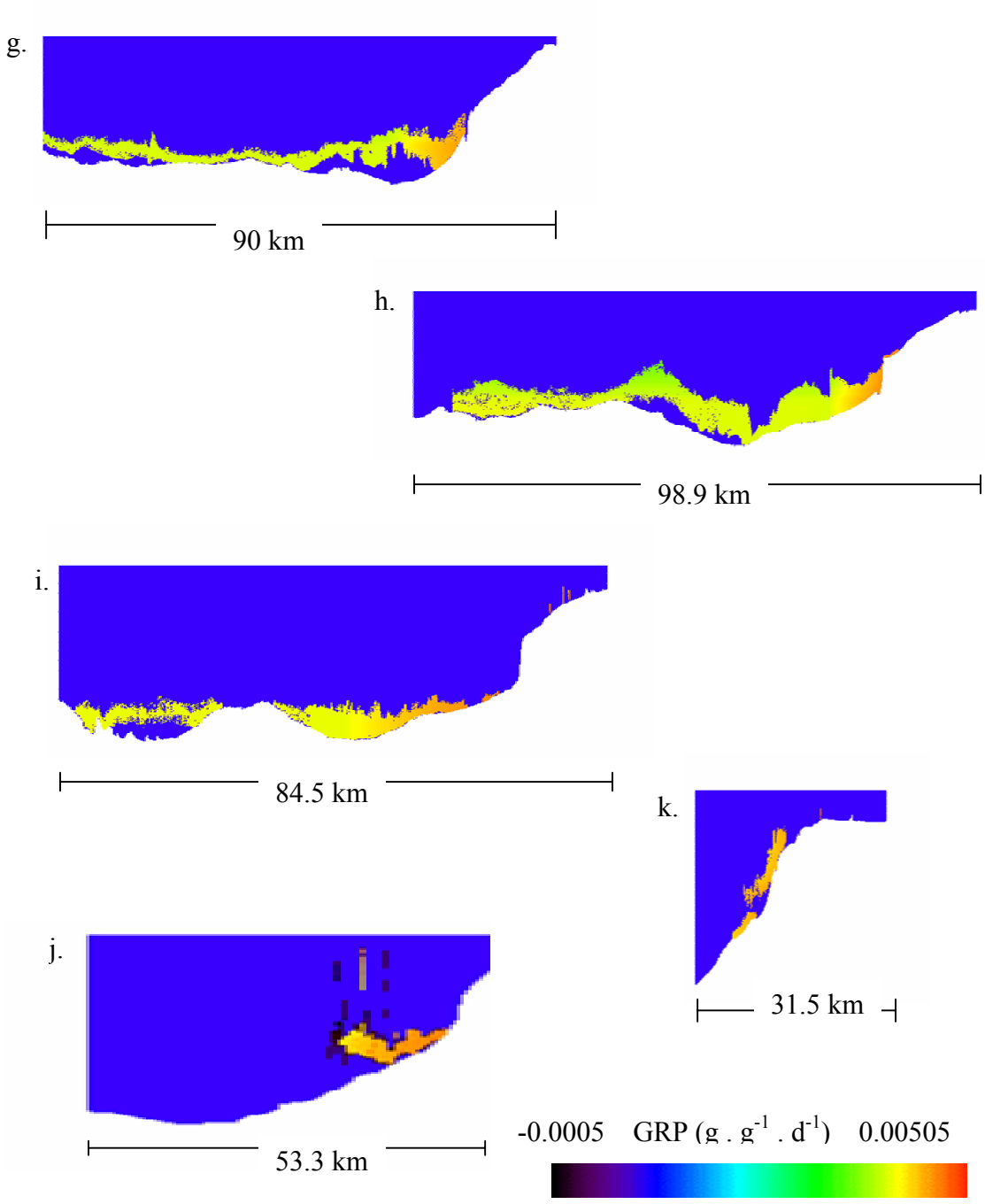


Figure 22 (cont.).2000 GRP Map of Transects of central region of Georges Bank. g.) Transect 118 h.) Transect 120 i.) Transect 122 j.) Transect 124 k.) Transect 126

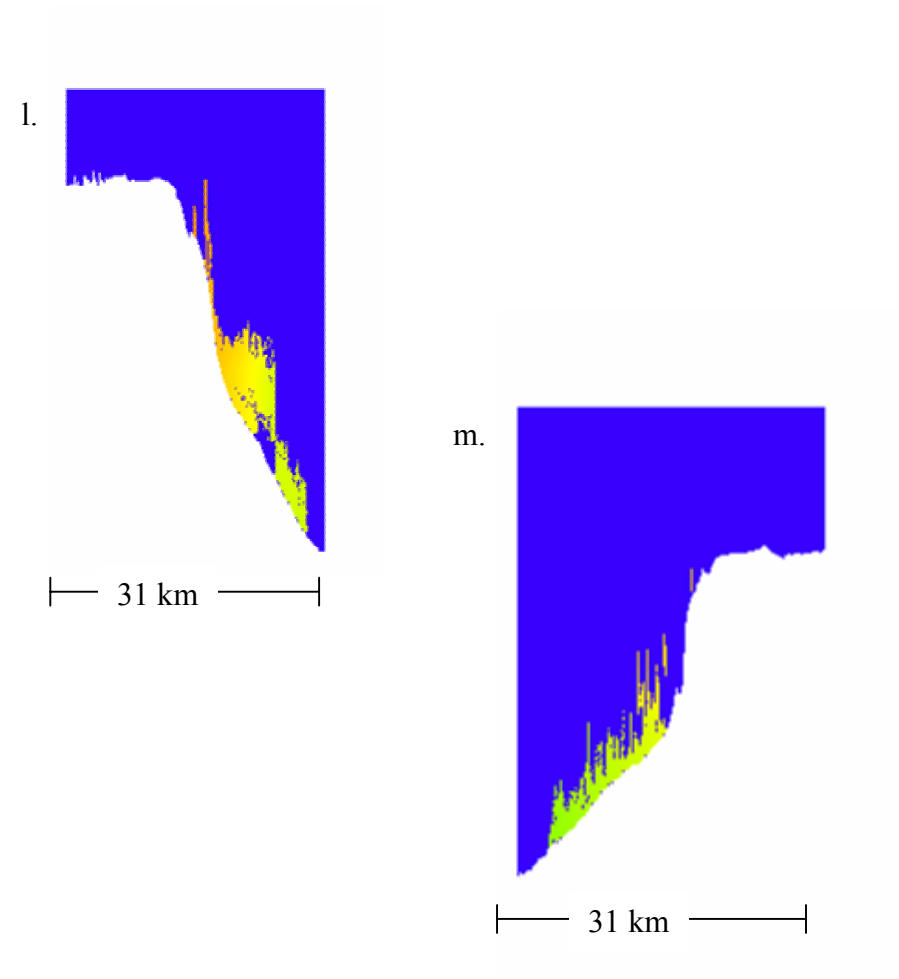


Figure 22 (cont.) 2000 GRP Map of Transects of east region of Georges Bank. l.) Transect 128 m.) Transect 130

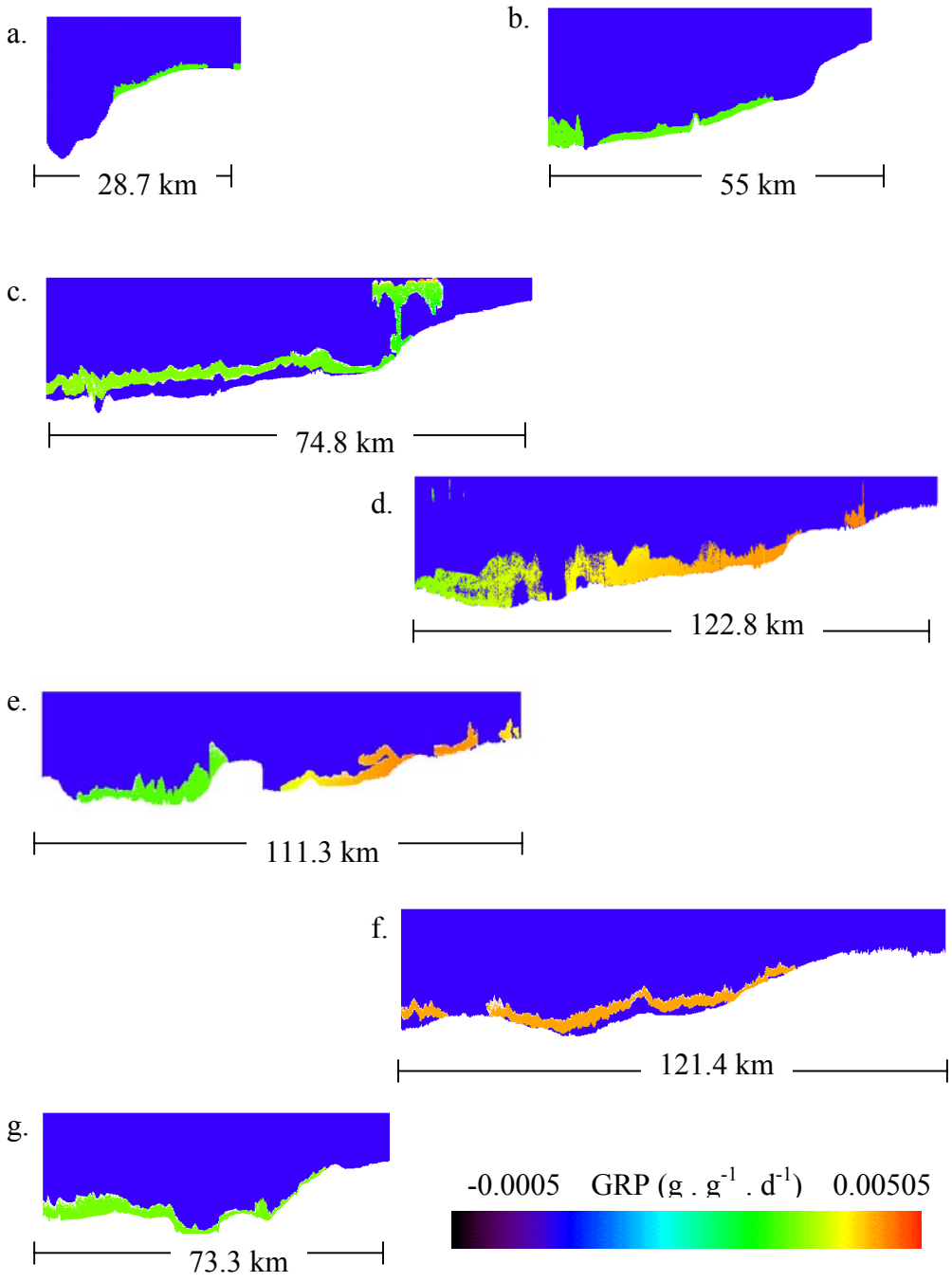


Figure 23. GRP Map of 2001 Transects of region west of Georges Bank.
a.) Transect 081 b.) Transect 083 c.) Transect 085 d.) Transect 087
e.) Transect 089 f.) Transect 091 g.) Transect 093

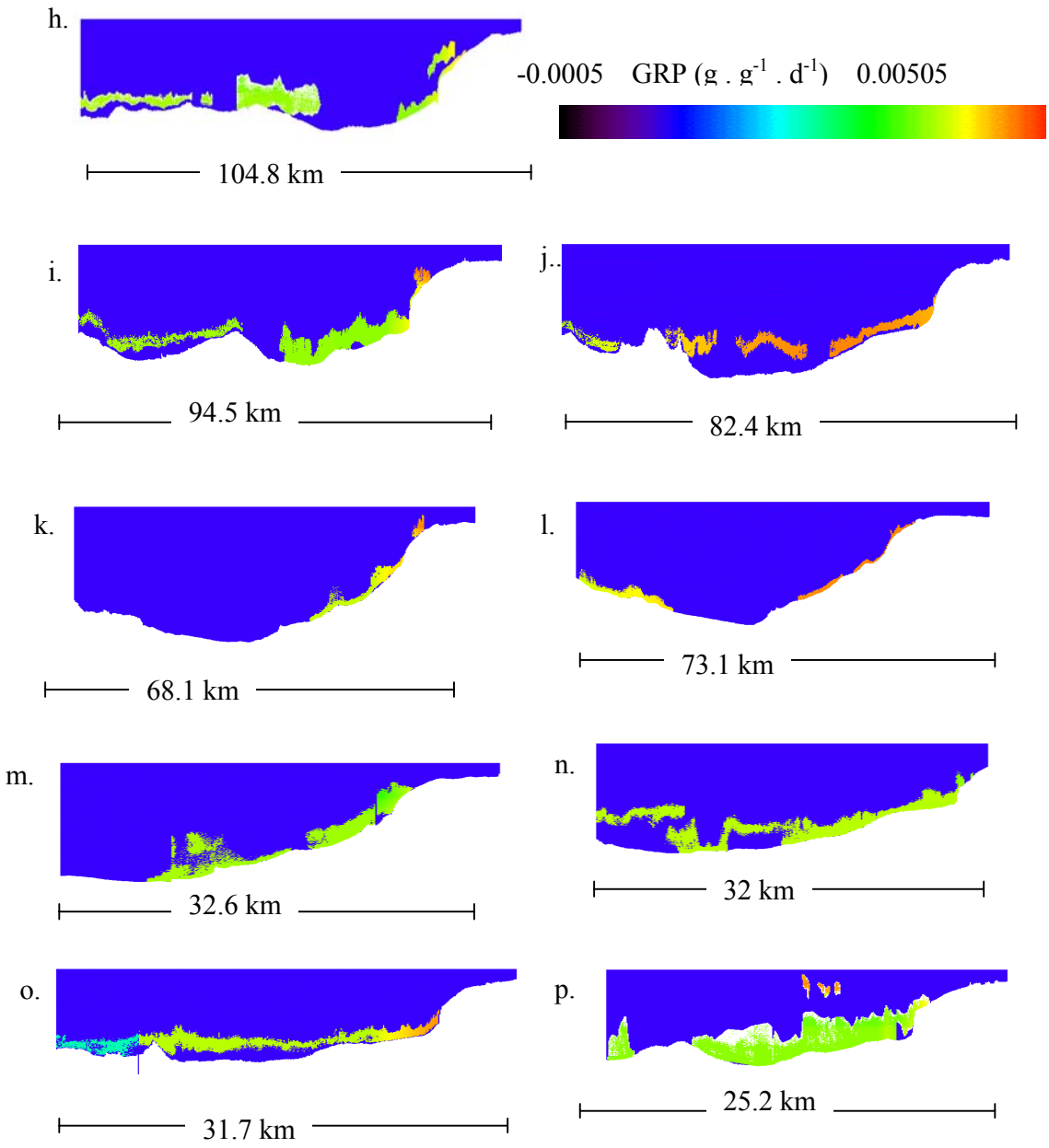


Figure 23 (cont.). GRP Map of 2001 Transects of central region of Georges Bank. h.) Transect 097 i.) Transect 099 j.) Transect 101 k.) Transect 103 l.) Transect 105 m.) Transect 129 n.) Transect 131 o.) Transect 133 p.) Transect 135

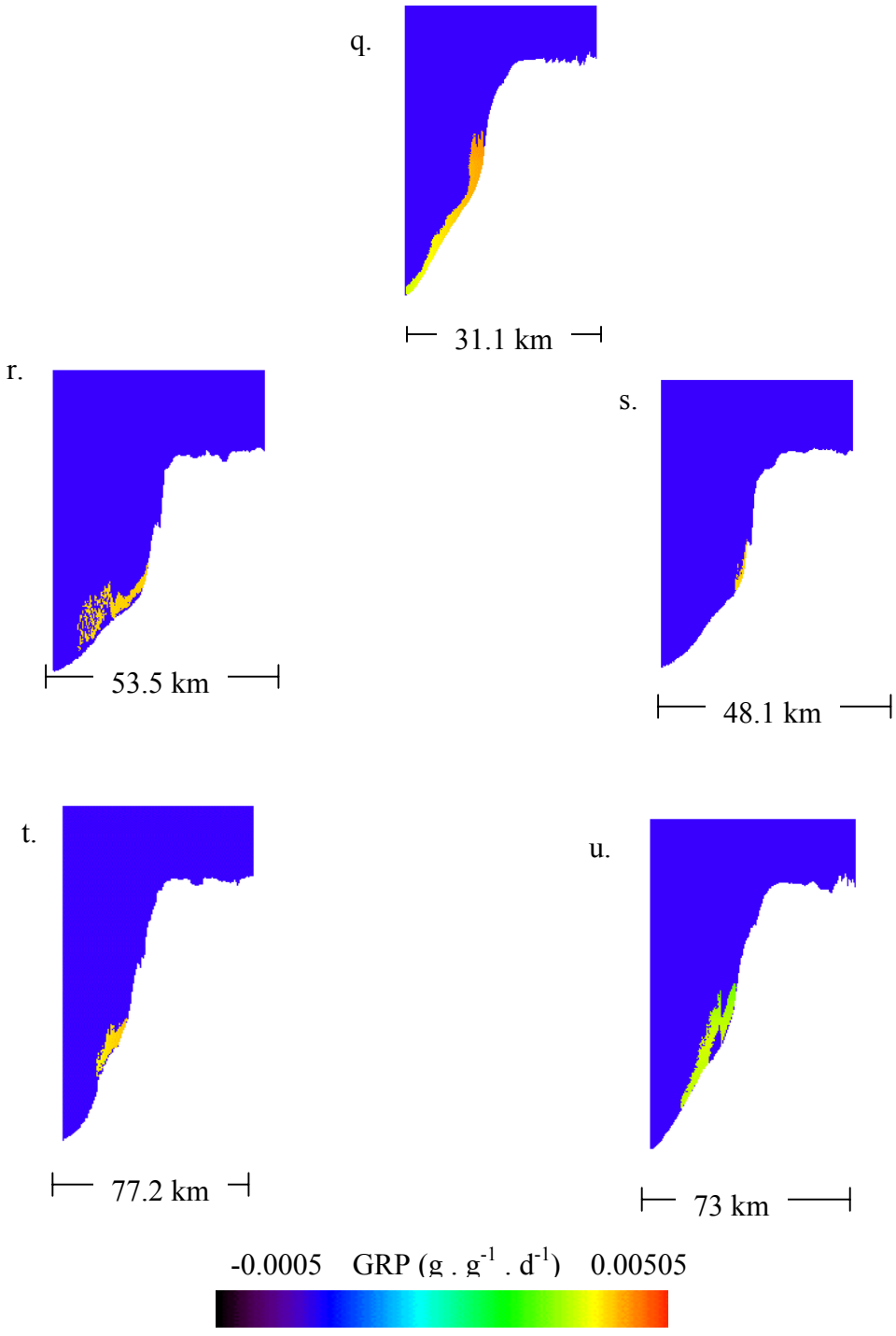


Figure 23 (cont.). GRP Map of 2001 Transects of east region of Georges Bank. q.) Transect 109 r.) Transect 111 s.) Transect 123 t.) Transect 125 u.) Transect 127

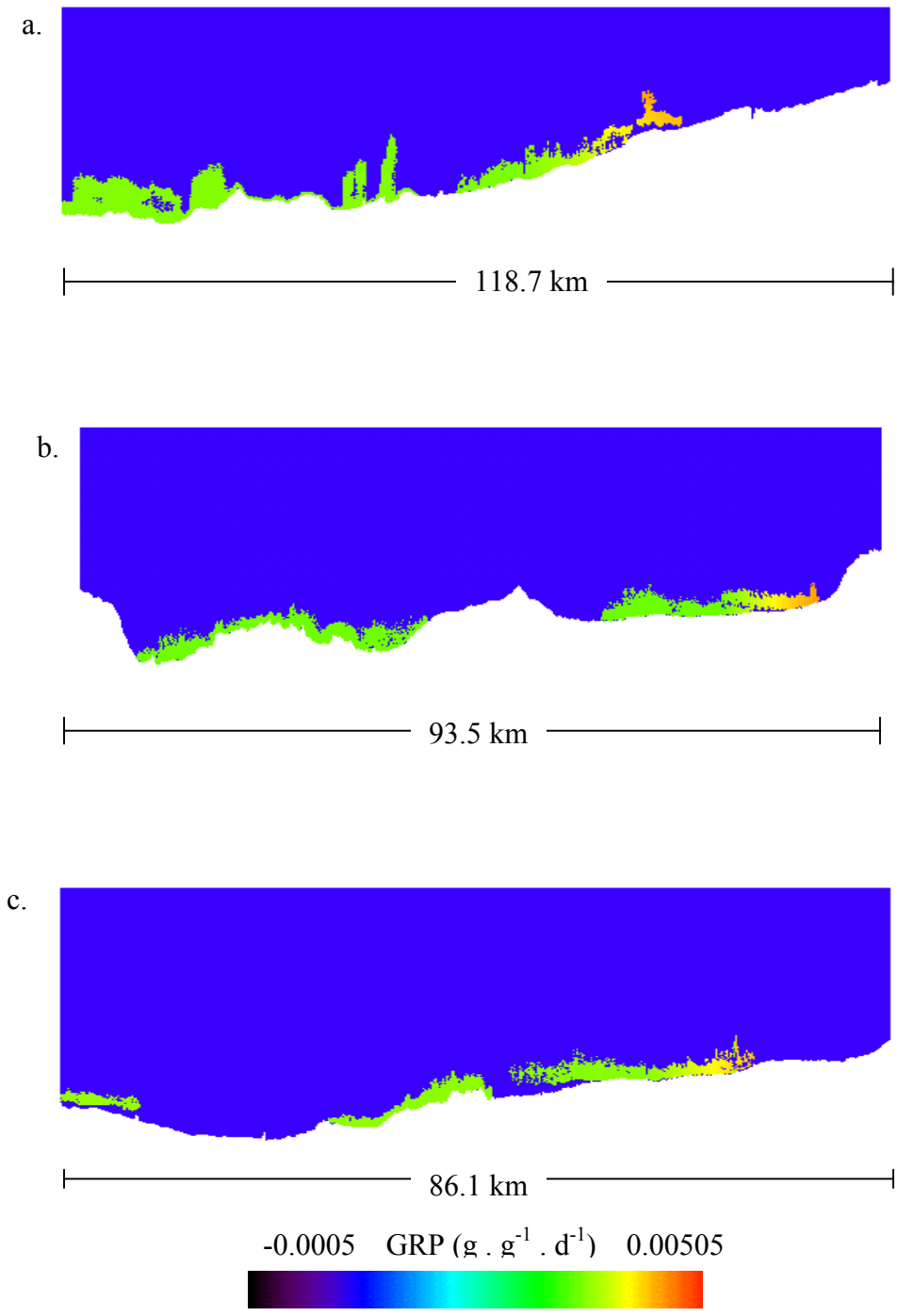


Figure 24. GRP Map of 2002 Transects of west region of Georges Bank. a.) Transect 109 b.) Transect 111 c.) Transect 113

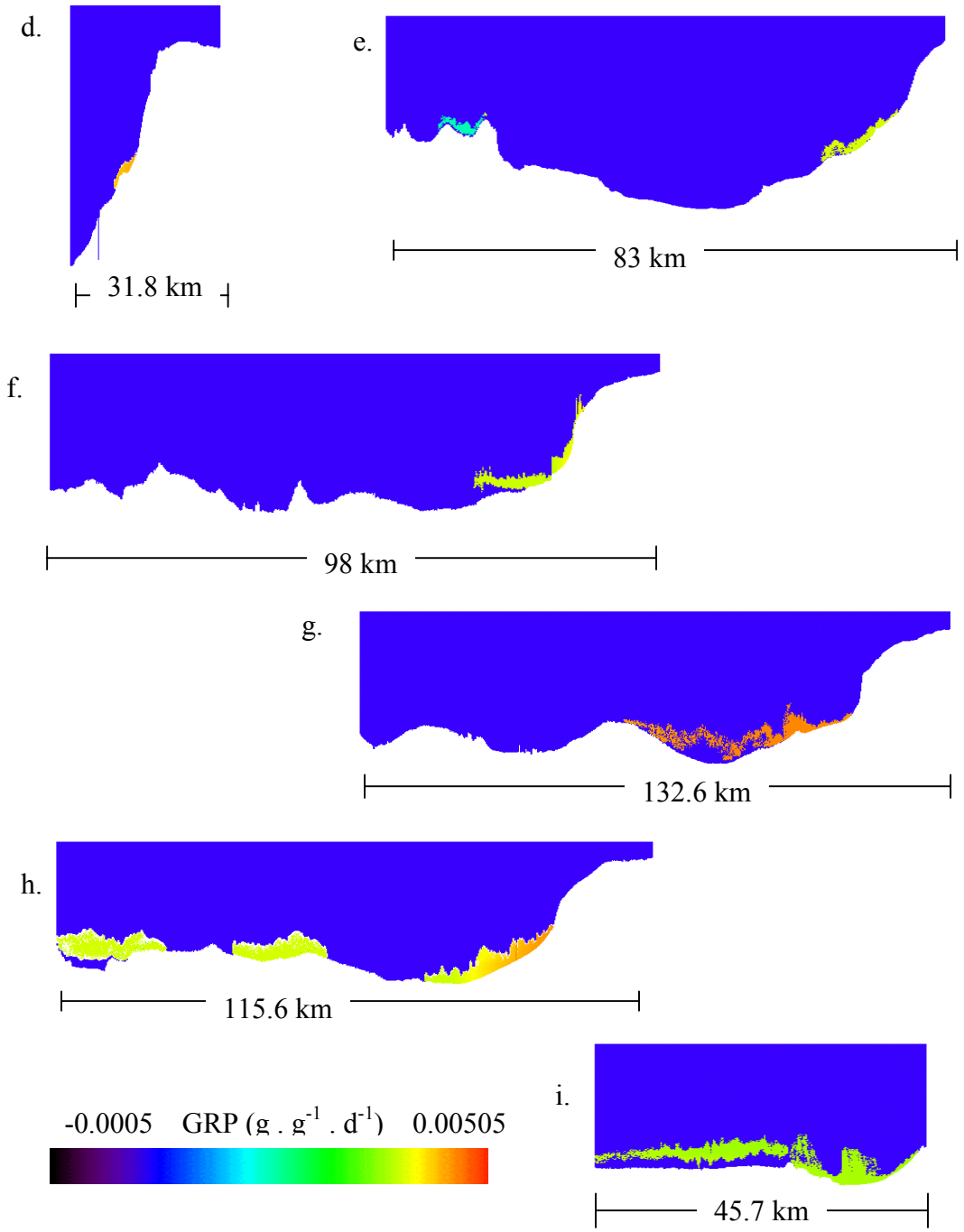


Figure 24 (cont.). GRP Map of 2002 Transects of central region of Georges Bank. d.) Transect 091 e.) Transect 093 f.) Transect 097 g.) Transect 099 h.) Transect 101 i.) Transect 103

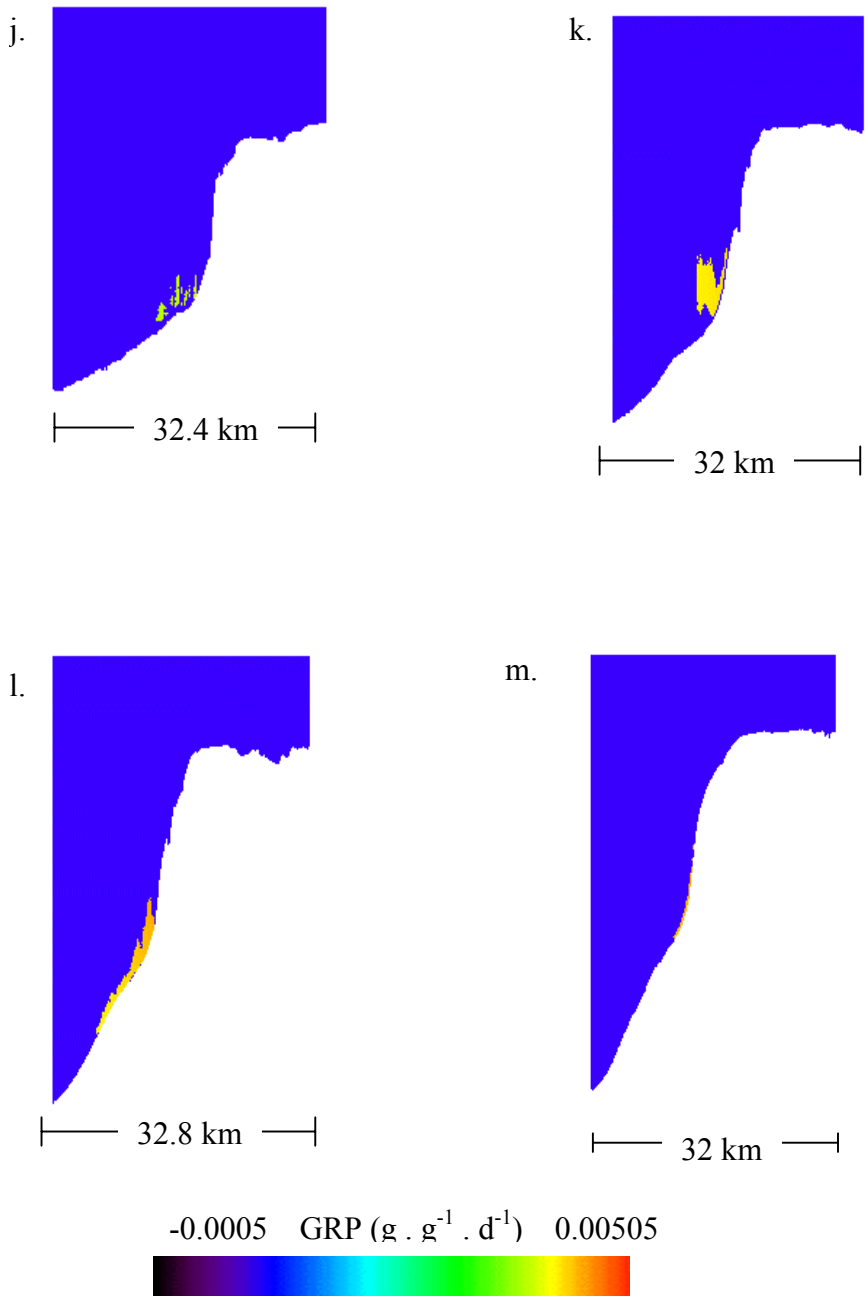


Figure 24 (cont.). GRP Map of 2002 Transects of east region of Georges Bank. j.) Transect 081 k.) Transect 083 l.) Transect 087 m.) Transect 089

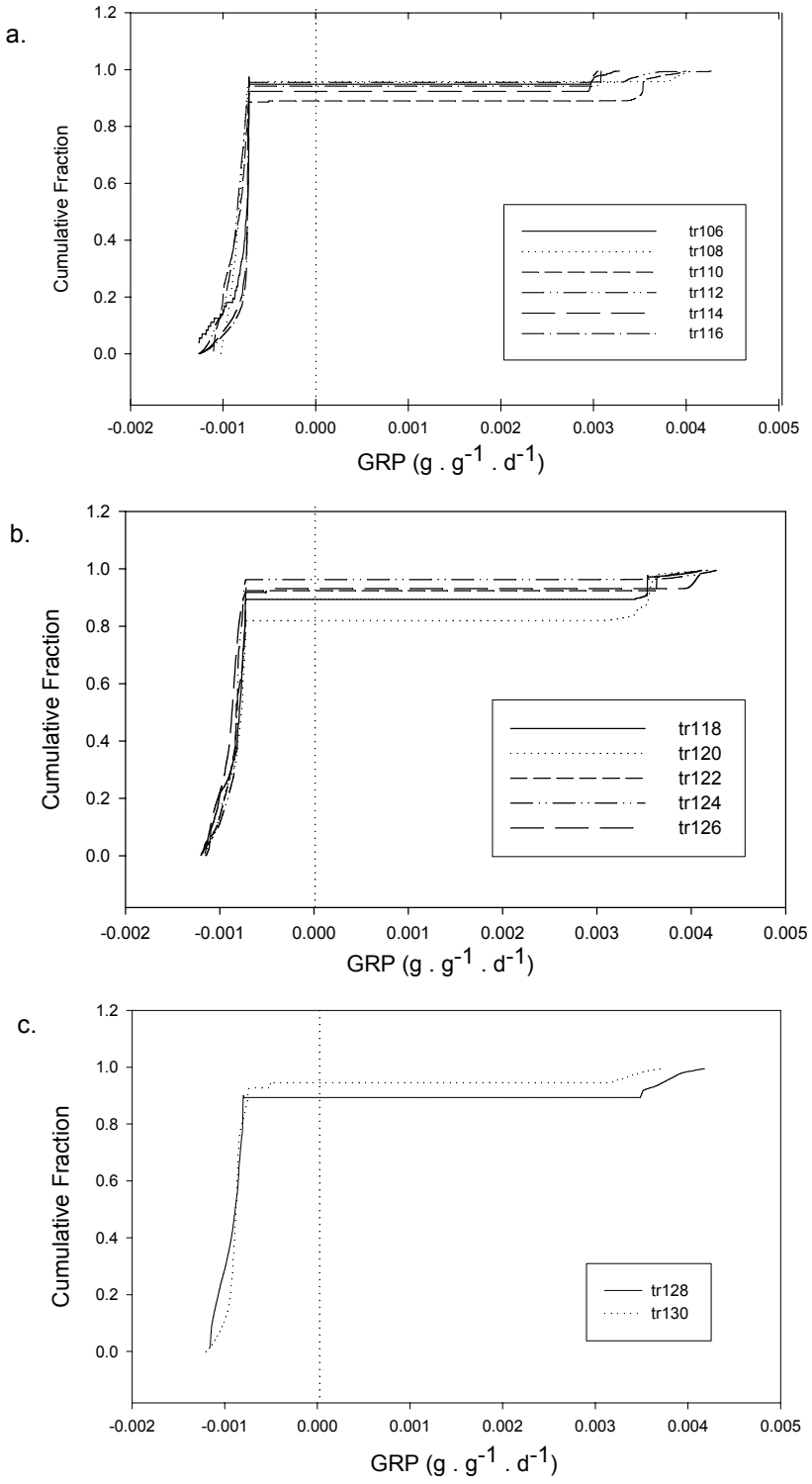


Figure 25. Cumulative fractions of 2000 GRP values for a.) west of Georges Bank b.) central region of Georges Bank c.) east of Georges Bank. Dotted line depicts the zero GRP value.

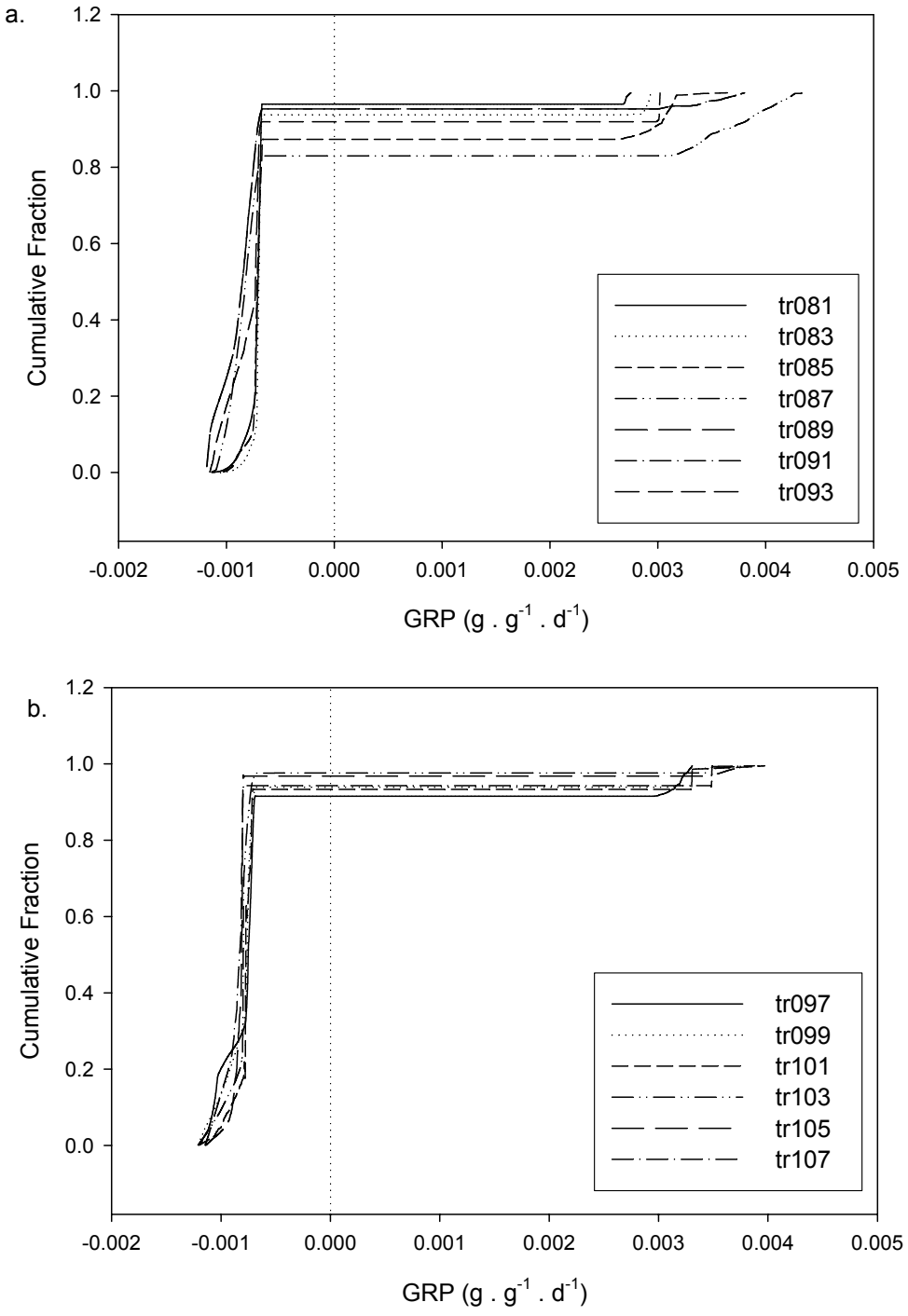
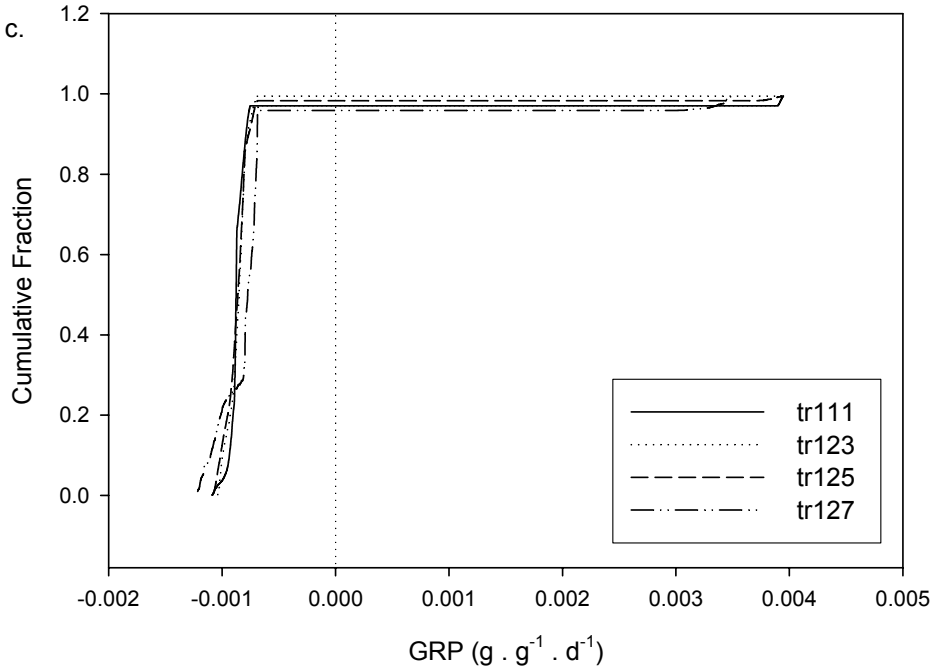


Figure 26. Cumulative fractions of 2001 mean GRP values for a.)west region of Georges Bank. b.) Central region of Georges Bank. Dotted line depicts zero GRP line.



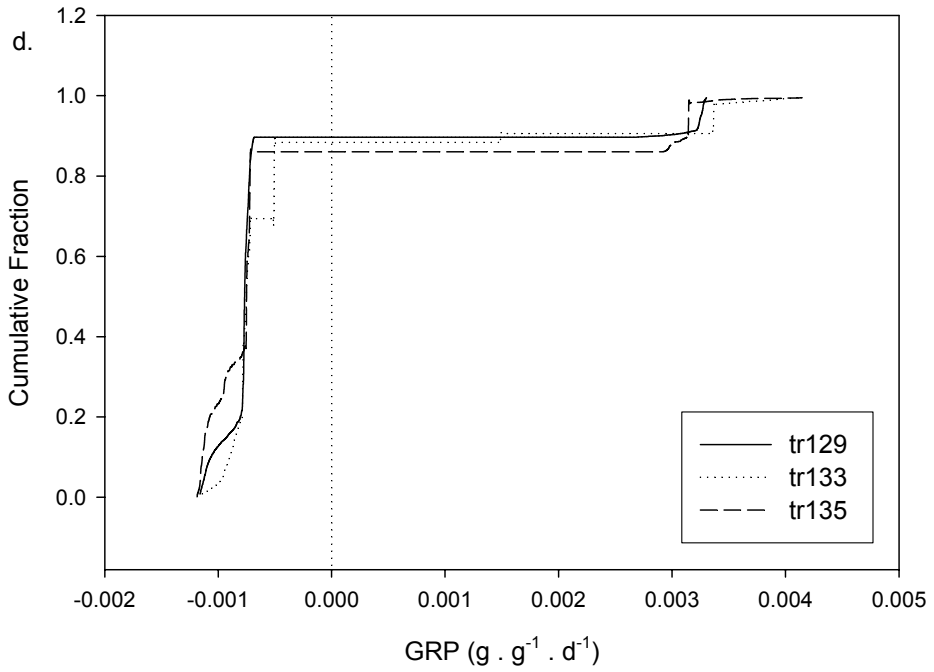


Figure 26 (cont.). Cumulative fractions of 2001 mean GRP values for c.) east t region of Georges Bank. d.) Central region of Georges Bank. Dotted line depicts zero GRP line.

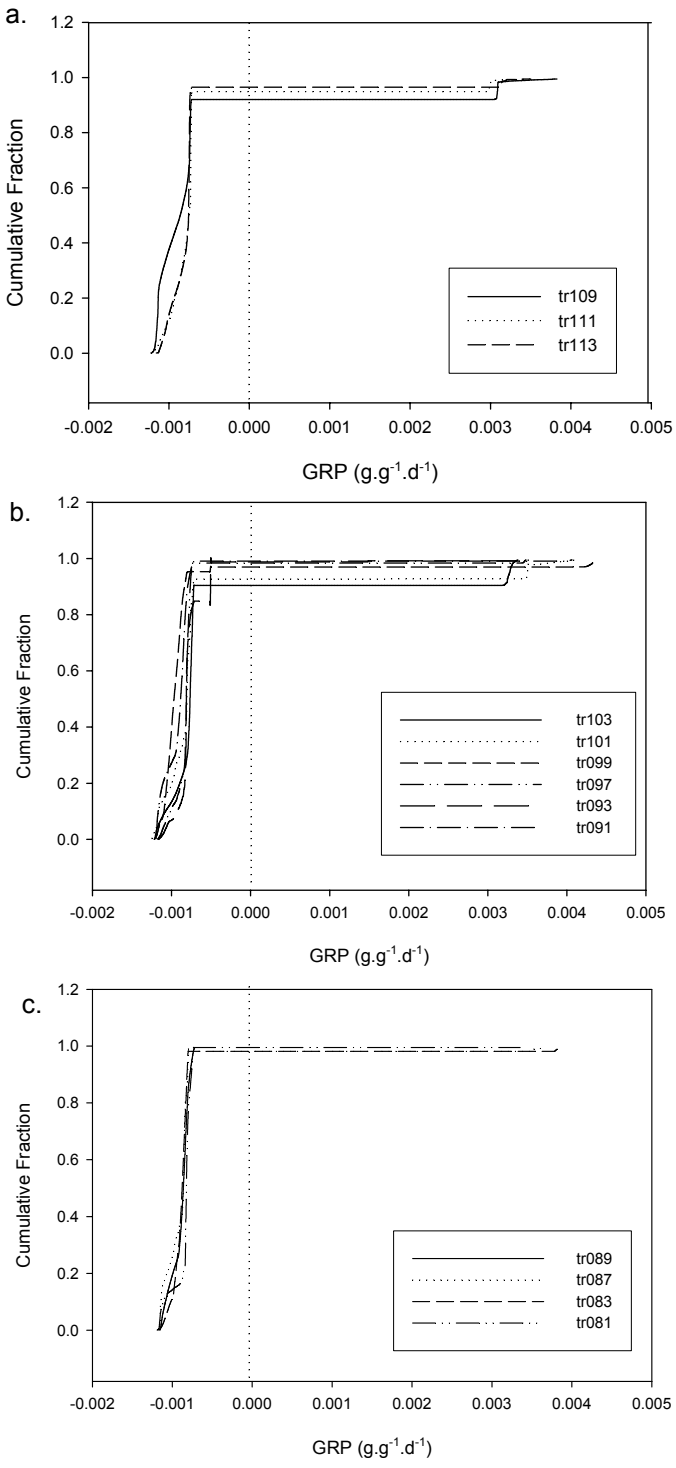


Figure 27. Cumulative fractions of 2002 mean GRP values for: a.) west region of George Bank. b.) Central region of Georges Bank. c.) East region of Georges Bank. Dotted line depicts zero GRP line.

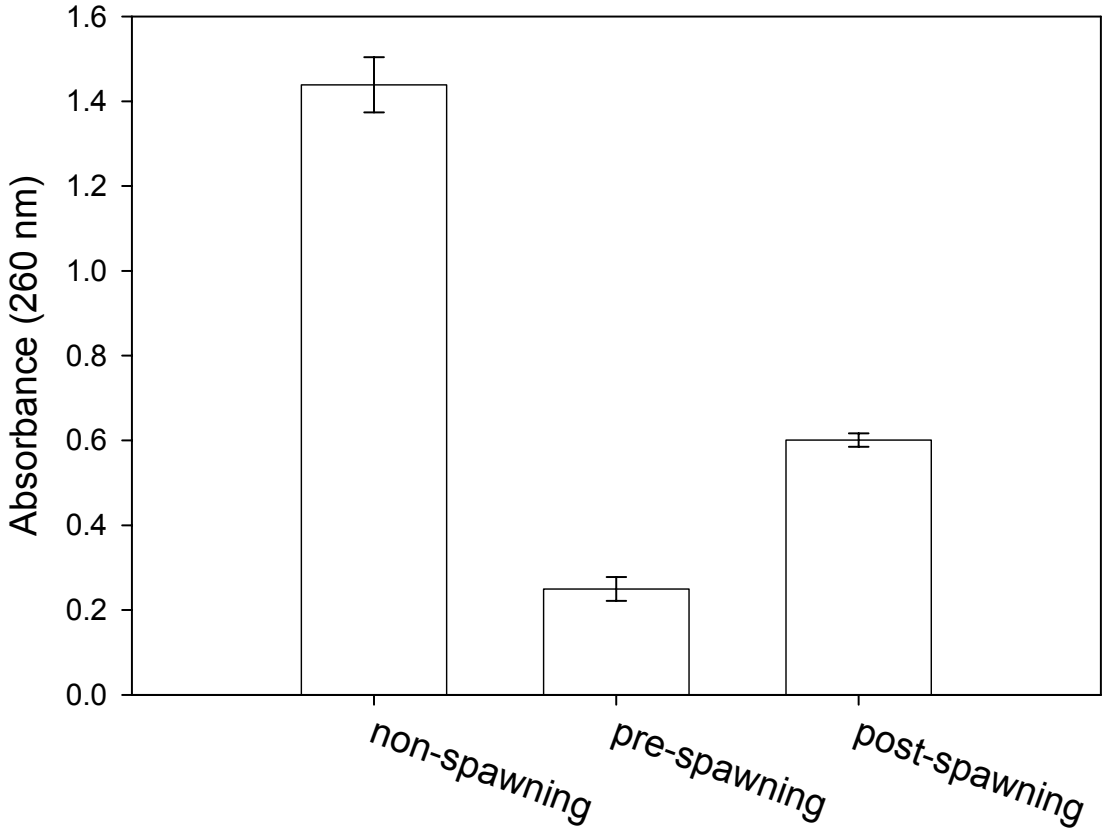


Figure 28. Mean spectrophotometric absorbance readings at a wavelength of 260 nm for non-, pre-, and post-spawning groups

Appendix A.

ATLANTIC HERRING LENGTHS AND WEIGHTS.

Fall 2002 Hydroacoustic Survey (post-spawn)
Trawl Length and weight data

Trawl #	Fish I.D.	Length (mm)	Weight (g)
138	1	260	182
	2	247	148
	3	236	114
	4	236	142
	5	268	172
	6	240	134
	7	248	156
	8	231	128
	9	236	134
	10	235	142
	11	267	194
	12	275	216
	13	268	188
	14	239	138
	15	265	202
	16	275	172
	17	241	134
	18	246	154
	19	245	140
	20	247	144

Fall 2002 Hydroacoustic Survey (pre-spawn)
Trawl Length and weight data

Trawl #	Fish ID	Length (mm)	Weight (g)
48	1	260	218
	2	275	180
	3	235	142
	4	235	130
	5	255	160
	6	255	170
	7	245	154
	8	232	106
	9	255	184
	10	275	226
	11	255	180
	12	260	184
	13	230	134
	14	210	96

	15	270	180
	16	275	224
	17	260	192
	18	225	116
	19	255	150
	20	265	152
52	21	235	125
	22	238	126
	23	255	150
	24	296	222
	25	246	140
	26	247	156
	27	251	156
	28	286	206
	29	260	170
	30	270	174
	31	282	198
	32	255	174
	33	265	152
	34	267	196
	35	239	136
	36	264	184
	37	242	158
	38	236	132
	39	244	152
	40	232	122
60	41	245	148
	42	274	236
	43	236	134
	44	239	140
	45	248	146
	46	267	200
	47	240	138
	48	253	158
	49	280	206
	50	239	144
	51	242	154
	52	251	158
	53	269	136
	54	244	148
	55	238	148
	56	247	172
	57	250	170
	58	229	160
	59	234	126
	60	236	138
69	61	245	156
	62	250	138

	63	240	140
	64	251	136
	65	260	154
	66	236	116
	67	244	118
	68	245	154
	69	280	168
	70	250	126
	71	270	162
	72	265	166
	73	250	150
	74	265	158
	75	260	190
	76	260	152
	77	240	140
	78	245	154
	79	240	148
	80	280	202
80	81	275	188
	82	250	168
	83	245	142
	84	260	152
	85	250	146
	86	260	172
	87	235	134
	88	230	128
	89	245	142
	90	275	206
	91	245	188
	92	235	128
	93	260	154
	94	265	160
	95	270	242
	96	235	146
	97	240	132
	98	225	122
	99	235	146
	100	290	258

Summer Cruise 06/26/02 (non-spawning)		
Atlantic Herring - Gulf of Maine		
Fish I.D.	**Fork length (mm)**	**full length (mm)**
1	245	275
2	260	295
3	265	300

4	265	300
5	260	295
6	225	250
7	235	265
8	275	305
9	240	265
10	240	270
11	245	275
12	230	260
13	270	305
14	245	280
15	240	270
16	240	270
17	270	300
18	275	305
19	225	255
20	255	285
21	235	270
22	265	295
23	220	245
24	215	245
25	265	300
26	265	300
27	230	255
28	270	305
29	240	270
30	270	305
31	230	260
32	280	310
33	260	295
34	240	270
35	270	295
36	240	265
37	270	305
38	255	285
39	240	265
40	260	290
41	245	275
42	260	295
43	260	290
44	230	260
45	280	310
46	215	240
47	255	285
48	215	240
49	260	290
50	240	270