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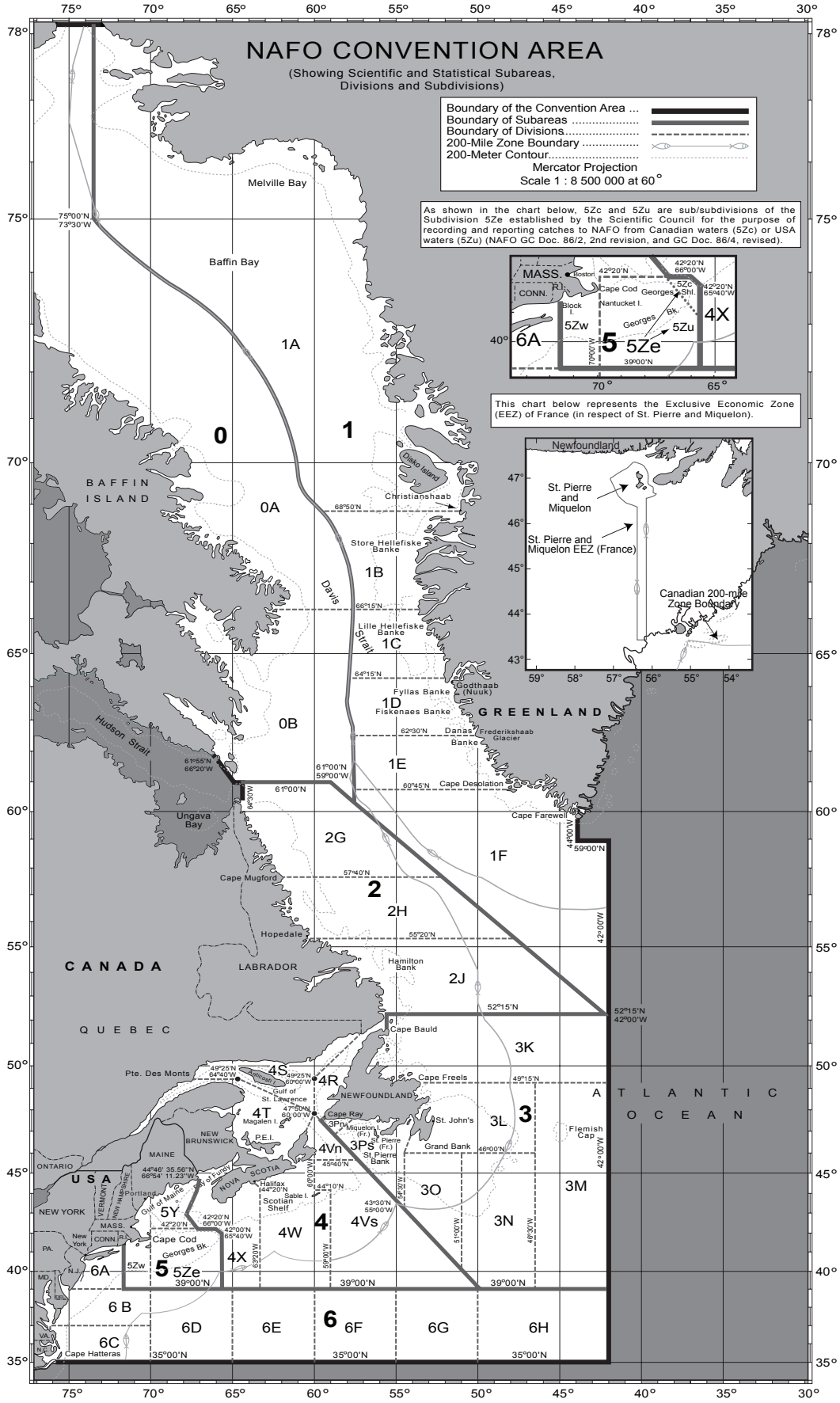
Scientific publications by ICNAF and NAFO have been in existence since ICNAF began in 1949 with the ICNAF Special Publication series dealing with proceedings of scientific symposia. The *ICNAF Research Bulletin* was started in 1964 to provide a means of publishing results of scientific research relevant to ICNAF. The ICNAF Research Bulletin was terminated in September 1979 after the issue of Number 14. The first volume of the NAFO *Journal of Northwest Atlantic Fishery Science* was published in December 1980, after NAFO came into force replacing ICNAF in 1979.

The Northwest Atlantic fisheries have a rich history, and a great deal of research has been sponsored and encouraged by NAFO and its predecessor ICNAF. NAFO has been a leader amongst international organizations in the application of science to fishery management and in the regulation of fisheries in areas beyond national jurisdiction. In accordance with its mandate to disseminate information on fisheries research to the scientific community, the Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fishery Science*, which contains peer-reviewed primary papers, and *NAFO Scientific Council Studies*, which contains unrefereed papers of topical interest and importance to the Scientific Council. Lists of these and other NAFO publications are given on the back of this issue.

Editorial Policy

The Journal provides an international forum for the primary publication of original research papers, with emphasis on environmental, biological, economic and social science aspects of fisheries and their interactions with marine habitats and ecosystems. While the Journal is intended to be regional in scope, papers of general applicability, and methodological and review papers, irrespective of region, are considered. Space is available for notes and letters to the editor to facilitate scientific discussion of published papers. Both practical and theoretical papers are eligible. All papers are peer-reviewed to determine their suitability for primary publication. Associate Editors arrange for the peer-reviews and ensure that the papers accepted for publication meet the high standards required for the Journal. Manuscripts approved for publication are accepted with the understanding that they are not copyrighted, published or submitted elsewhere except in abstract form. There are no page charges.

Editorial Board


NAFO CONVENTION AREA
(Showing Scientific and Statistical Subareas, Divisions and Subdivisions)
Boundary of the Convention Area ...
Boundary of Subareas .....
Boundary of Divisions.....
200-Mile Zone Boundary .....
200-Meter Contour.....
Mercator Projection
Scale 1 : 8 500 000 at 60°
As shown in the chart below, 5Zc and 5Zu are sub/subdivisions of the Subdivision 5Ze established by the Scientific Council for the purpose of recording and reporting catches to NAFO from Canadian waters (5Zc) or USA waters (5Zu) (NAFO GC Doc. 86/2, 2nd revision, and GC Doc. 86/4, revised).
This chart below represents the Exclusive Economic Zone (EEZ) of France (in respect of St. Pierre and Miquelon).
St. Pierre and Miquelon
St. Pierre and Miquelon EEZ (France)
Canadian 200-mile Zone Boundary
Newfoundland
Melville Bay
Baffin Bay
Davis Strait
Hudson Strait
BAFFIN ISLAND
GREENLAND
CANADA
QUEBEC
LABRADOR
NEWFOUNDLAND
ATLANTIC OCEAN
USA
Christianshaab
Store Hellefiske Banke
Lille Hellefiske Banke
Fyllas Banke
Fiskenaes Banke
Danas Banke
Godthaab (Nuuk)
Frederikshaab Glacier
Cape Desolation
Cape Farewell
Ungava Bay
Cape Mugford
Hopedale
Hamilton Bank
Cape Bauld
Pte. Des Monts
Gulf of St. Lawrence
Cape Freels
Cape Ray
St. John's
Grand Bank
St. Pierre Bank
Flemish Cap
Halifax
Scotian Shelf
Sable I.
Cape Cod
Georges Bk.
Nantucket I.
Block I.
Cape Hatteras
1A
0
1
0A
1B
1C
1D
0B
1E
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5Y
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5Zw
5Ze
4X
5Zc
5Zu
6A
6 B
6C
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6E
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6F
6G
6H

Foreword

The Scientific Council of NAFO publishes the *Journal of the Northwest Atlantic Fishery Science*, containing peer reviewed primary literature detailing original research of relevance to fisheries science and management in the Northwest Atlantic. Articles are published electronically under a Creative Commons 2.5 license and are freely available at http://journal.nafo.int. The Scientific Council has resolved to publish annual bound print volumes, and these represent a compilation of the web based articles published throughout the year. Additionally, the journal supports the use of digital object identifiers (doi) for electronic media and encourages others to support this initiative.

This issue contains a range of papers covering the broad spectrum of science being carried out in the Northwest Atlantic, and again, the effects of a warming planet upon marine resources are at the core of much of the research presented here. Some familiar issues are revisited, and we are pleased to publish works on the reproductive biology of Greenland halibut, selectivity in Redfish fisheries and structuring of deep-water fish communities.

I would like to take this opportunity to extend my thanks to all of the authors who submitted works during 2012, to the Associate Editors who make the administration of the Journal such a pleasure, and to Alexis Pacey, Publications Manager at the NAFO Secretariat, for her extensive support.

I hope you find this volume of JNAFS enjoyable and informative.

December 2012

Neil Campbell
General Editor,
Journal of Northwest Atlantic Fishery Science

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Understanding the Size Selectivity of Redfish (*Sebastes* spp.) in North Atlantic Trawl Codends

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Abstract

The majority of trawl selectivity studies for the three redfish species of particular commercial importance in North Atlantic fisheries: *Sebastes marinus*, *Sebastes mentella* and *Sebastes fasciatus,* are based on data collected from diamond mesh codends with mesh sizes ranging from 88 mm to 147 mm. We demonstrate how results from these studies can be understood by morphological characteristics of the species. We predict codend size selection based on morphological data collected from golden redfish (*S. marinus*) individuals. Further, consistent with previously reported morphological similarities between the three redfish species, we show the predictions for *S. marinus* may successfully be extrapolated to understand experimental codend size selectivity results reported for *S. mentella* and *S. fasciatus*. In addition to the comparison with previously reported data, we present new experimental results for a codend applied in Northeast Atlantic redfish trawl fishery.

Keywords: redfish, *Sebastes*, FISHSELECT, codend selectivity, mesh size

Introduction

Three of the many redfish species present in the North Atlantic are of major commercial significance: *Sebastes marinus*, *Sebastes mentella* and *Sebastes fasciatus*. These three species of the *Sebastes* genus are similar in shape and appearance especially at small sizes (Power and Ni, 1985; Pampoulie and Danielsdottir, 2008). In particular, *S. mentella* and *S. fasciatus* were grouped together as "beaked redfish" until only a few decades ago (Barsukov, 1968; Ni, 1981).

In the International Council for the Exploration of the Sea (ICES) subareas I and II (Norwegian Sea and Barents Sea), *S. marinus* and *S. mentella* are the two most commercially important redfish species. The two species have been continually exploited in these areas in the last decades but the ICES advice for 2012 for both of them recommends closing the directed fishery and limiting bycatch until "*a significant increase in the spawning-stock biomass (and a subsequent increase in the number of juveniles) has been verified*" (ICES, 2011a). Around Iceland and East Greenland (ICES Subareas V, VI, XII, and XIV), the situation is a bit better as ICES recommends that total allowable catches (TACs) for 2012 should not exceed 40 000 tons for *S. marinus* and 10 000 tons for *S. mentella* (ICES, 2011b). In the Northwest Atlantic (NAFO Subarea 3), the TAC for redfish (mainly *S. mentella* and *S. fasciatus*) in 2011 is set at 36 100 tons (NAFO, 2010).

The incomplete stock differentiation and interspecific hybridization observed within the *Sebastes* spp. stocks in the North Atlantic evidences close connection between these stocks (Cadrin *et al*., 2010). Thus, because of the delicate situation of some of these stocks (especially in the Northeast Atlantic) the responsible management authorities are obliged to implement effective measures to maintain or restore stocks to MSY levels (*i.e.* the objective that UNCLOS (The United Nations Convention on the Law of the Sea) signatories in the 2002 Johannesburg Plan committed themselves to achieve by 2015 (Froese and Proelß, 2010)). Area closures and direct fishery bans can be applied in such situations but size selectivity focused on juvenile preservation is normally the least dramatic alternative for the fishing community. Constructing a size selective trawl requires a proper understanding of the behaviour and/or size selectivity of the fish that need to be selected and rejected.

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Today, redfish is mainly harvested with diamond mesh codends or combined systems using sorting grids together with diamond mesh codends (NAFO, 2011; Gunnarsson *et al*., 1998; Jørgensen *et al*., 2006). The few available published redfish size selectivity studies mainly involve diamond mesh codends; the results from such studies indicate that mesh size can affect size selectivity of this species (Lisovsky, 2001; Lisovsky *et al*., 2006). Most of the available *Sebastes* selectivity data have been collected by Russian research institutes and are summarized by Lisovsky (2001), Lisovsky *et al*. (1995; 2006) and Pavlenko (2009). German and Icelandic data, presented by Bohl (1961) and Thorsteinsson *et al*., (1979) respectively, are also available in the literature. A study carried out by Hickey *et al*. (1995) in Canada that examined the effect of lastridge ropes on the selectivity properties on redfish for three different mesh size codends completes the list of studies that to our knowledge are available on redfish diamond mesh codend selectivity (Table 1).

FISHSELECT is a fish morphology data- and simulation-based methodology that can be applied to investigate the basic size selective properties of meshes of different shape and size for individual fish species (Herrmann *et al.*, 2009). The methodology has been successfully applied for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the North Atlantic (Herrmann *et al*., 2009; Krag *et al*., 2011; Sistiaga *et al*., 2011). However, cod and haddock belong to a different fish family (Gadidae) than the redfish (Sebastidae). This difference has potential implications for selectivity studies as the general body shape of the Sebastidae species in question differs substantially from that of the Gadidae species mentioned.

In the present study we applied the FISHSELECT methodology to investigate the size selective properties of diamond mesh codends on redfish. The main objective of the investigation was to improve understanding of redfish diamond mesh codend size selectivity by integrating the available published data for redfish with new sea trial data and FISHSELECT predictions into a single comprehensive quantitative framework. Because of the morphometric differences between redfish and the other species previously investigated using FISHSELECT, the methodology was further developed during this study.

Material and Methods

Existing data for codend size selection of redfish in diamond mesh codends

Most of the size selectivity data available for *Sebastes* spp. in the North Atlantic have been collected using diamond mesh codends (*e.g.* Bohl, 1961; Thorsteinsson *et al*., 1979; Konstantinov *et al*., 1982; Gorchinsky *et al*., 1993; Hickey *et al*., 1995; Lisovsky *et al*., 1995; Lisovsky *et al*., 2006) and have recently been reviewed by an ICES Topic Group (ICES, 2011c). Data are available from the early 1960s and onwards for *S. marinus*, *S. mentella* and *S. fasciatus* (Table 1). The types of trawls and the codend constructions used for data collection differed among these studies. Besides mesh size, other design factors such as twine thickness and the number of meshes in the codend circumference are known to also potentially affect size selection in diamond mesh codends (Herrmann and O'Neill, 2006; O'Neill and Herrmann, 2007; Sala *et al*., 2007; O'Neill *et al*., 2008) and these factors likely differed as well between the reported redfish size selectivity studies. Nevertheless, the common focus on mesh size in these studies allows for compilation and integrated analysis of their data in order to determine possible trends in the effect of mesh size on the selection properties of *Sebastes* species in codends commonly used in trawl fisheries throughout the North Atlantic.

New size selection data from sea trials

Collection of new codend size selectivity data

Codend selectivity data collection took place aboard the RV *Jan Mayen* (63.8 m LOA and 4080 HP) off the Norwegian coast between the 10th and the 19th of March 2009 using the covered codend method. The trawl used was an Alfredo No. 5 trawl constructed from 155 mm mesh (the top front panel and the wings were built from 200 mm mesh). The selection system installed in the trawl was a Sort-V sorting grid (see Jørgensen *et al*., 2006) combined with a 135 mm codend. The codend was built with 8 mm braided polyethylene twine (called "Euroline premium"), was 70 meshes long and 70 meshes around. The codend cover was 13 m long and was constructed entirely of 60 mm square meshes (2.2 mm PE twine) based on the design in Grimaldo *et al*. (2008). Thus, the fish necessary to evaluate the selective properties of the codend used were collected from the fish retained by the codend and the fish retained by the codend cover. Redfish of the species *S. marinus* were captured during 11 hauls and the individuals collected respectively in the codend and in the cover were for each haul sorted into 1 cm wide length classes for the subsequently data analysis.

Data analysis

To model the size selectivity of *S. marinus* in the 135 mm codend we used a logistic curve described by the parameters L_{50}(the length of fish having 50% likelihood of being retained by codend given it enters it) and SR

Table 1: Redfish (*Sebastes* spp.) codend selectivity data for the north Atlantic region for the past 50 years.

Species	Research area	Codend mesh size (mm)	L_{50} (cm)	SR (cm)	Source
Sebastes marinus	Greenland	122	35.3	10	Bohl, 1961
Sebastes marinus	Greenland	131	33.5	14.5	Bohl, 1961
Sebastes marinus	Iceland	132	29.9	2.3	Thorsteinsson *et al*., 1979
Sebastes marinus	Greenland	139	37.2	13	Bohl, 1961
Sebastes marinus	Greenland	146	41.2	14.5	Bohl, 1961
Sebastes marinus	Greenland	147	38.4	15	Bohl, 1961
Sebastes mentella	NAFO 3N	88	24.6	4.4	Lisovsky *et al*., 1995
Sebastes mentella	NAFO 3Ps	90	27.2	5.9	Hickey *et al*., 1995
Sebastes mentella	NAFO 3Ps	90*	26.9	3.3	Hickey *et al*., 1995
Sebastes mentella	NAFO 3Ps	110	26.8	6.5	Hickey *et al*., 1995
Sebastes mentella	NAFO 3Ps	110*	32.1	3.3	Hickey *et al*., 1995
Sebastes mentella	NAFO 3Ps	115	31.5	5	Hickey *et al*., 1995
Sebastes mentella	NAFO 3Ps	115*	33.2	3	Hickey *et al*., 1995
Sebastes mentella	NAFO 3N	118	29.5	6.6	Lisovsky *et al*., 1995
Sebastes mentella	NAFO 3M/3N	124	29.8	8.4	Konstantinov *et al*., 1982
Sebastes mentella	NAFO 3M	126	36.5	5.6	Gorchinsky *et al*., 1993
Sebastes mentella	NAFO 3N	132	34.3	6.6	Lisovsky *et al*., 1995
Sebastes mentella	NAFO 3M	137	39.7	4.3	Gorchinsky *et al*., 1993
Sebastes mentellal/fasciatus	NAFO 30	96	25.0	5.4	Lisovsky *et al*., 2006
Sebastes mentellal/fasciatus	NAFO 30	100	26.0	4.1	Lisovsky *et al*., 2006
Sebastes mentellal/fasciatus	NAFO 30	106	27.6	5.5	Lisovsky *et al*., 2006

*Lastridge ropes were used in the codend.

– the selection range (= L_{75}–L_{25}). This type of curve has often proved to be appropriate for modelling the length-dependent retention likelihood in diamond mesh codends for many fish species (Wileman *et al*., 1996). Traditionally, the parameter estimation would follow a two-step procedure. The first step would involve the estimation of L_{50} and SR and their covariance matrix for individual hauls using the maximum likelihood estimation procedure. The second step would follow an approach described by Fryer (1991) to estimate the mean selection parameters, where both the estimated parameter values and their covariance matrix for the single hauls are used, assuming that the estimated parameter values are observations from a bivariate normal distribution. This method considers both the within- and between-haul variation in the parameter values. However, an initial inspection of the collected haul data revealed that the abundance of *S. marinus* was very low in at least one of the two compartments (codend or codend cover) in many of the individual hauls. For the majority of hauls it would therefore not be possible to estimate the size selection of the redfish on a single haul basis. Thus, we had to employ another approach to estimate the size selection of *S. marinus* in the codend. Our approach involves pooling the data for all hauls to estimate the average L_{50} and SR for the codend based on fitting a single logistic curve to the average data collected over the hauls, while using bootstrapping to estimate the confidence limits for the average parameter values. This approach avoids underestimation of the confidence limits of the average selection parameters L_{50} and SR, which according to Fryer (1991) would otherwise occur from simply estimating the average L_{50} and SR values from pooled data without using bootstrapping to account simultaneously for both within- and between-haul variation in the selection process. The bootstrapping method used is similar to the method described in Sistiaga *et al*. (2010) except that the model fitted to our data is much simpler. As in Sistiaga *et al*. (2010), the data analysis was carried out with the software tool SELNET (developed by the first author of this study). Further information on SELNET can be found in Frandsen *et al*. (2011), Wienbeck *et al*.

(2011) and Sistiaga *et al*. (2010) or can be obtained by contacting the corresponding author. To be able to estimate the 95% confidence bands for the retention likelihood along the entire selection curve, SELNET was further developed as part of this study. The estimated L_{50} and SR values in each of the 10 000 bootstrap repetitions were used to estimate the predicted retention likelihood for each length class by inserting the parameter values in the formulas for the logistic curve. This innovation enabled the estimation of the "Efron percentile" 95% confidence limits (Efron, 1982; Chernick, 2007) for the entire average selection curve over hauls. One advantage of this approach is the possibility to estimate confidence bands for the curve without having to rely on the "delta theorem" approximation described by Lehmann (1983).

Selectivity estimation by means of FISHSELECT

The FISHSELECT methodology (Herrmann *et al*., 2009), which includes procedures, tools and software, determines whether a fish is capable of passing through a certain mesh based on the morphology and compressibility of the fish, and shape and size of the mesh. By means of computer simulation, the method is ultimately used to predict the selective properties of diverse fishing gears. The method has already been applied in a number of studies to estimate the selective properties of towed fishing gears for both round-fish (Herrmann *et al*., 2009; Krag *et al*., 2011; Sistiaga *et al*., 2011) and crayfish (Frandsen *et al*., 2010). This section describes the different steps needed to apply the methodology to study the selectivity of *S. marinus* (see Herrmann *et al*. (2009) for more detailed information)).

Data collection

The FISHSELECT methodology was applied to *S. marinus* collected on a cruise carried out in the Barents Sea. The data collection took place once again on board R/V *Jan Mayen* from the 1st to the 10th of December 2008. The application of FISHSELECT requires: measuring the total length for each fish included; determining whether or not each fish can pass through a certain number of mesh templates (fall-through experiments); measuring the shape of the fish at a number of perpendicular cross-sections (CS) using a mechanical sensing tool (Morphometer). During the cruise the methodology was applied to 100 *S. marinus* individuals. The individuals were selected and handpicked from a continuous trawl fishing operation in order to cover the widest possible size range.

Measurement of fish shape and application of the fall-through procedure

For *S. marinus*, three cross-sections were carefully identified and chosen by inspection of the shape of the fish as well as by previous experience with the method. The cross-sections were chosen by their potential to determine fish passage through a mesh (Fig. 1): CS1, located at the end of the head and a spiny structure located in the middle of the opercula; CS2, located at the end of the opercula and the foremost point of the spiny dorsal fin; CS3, located at the point of the maximum transverse perimeter.

The three cross-sections were measured for each fish using a Morphometer (Fig. 2a–c) and the shapes formed in the Morphometer were scanned and converted into digital images using a flatbed scanner (Fig. 2d–f). The outlines of each digital image were modelled with different defined geometrical shapes that were chosen to describe the contours registered for each of the cross-sections as well as possible.

The three cross-sections of the 100 fish individuals included in the study were compared to six different shapes (Fig. 3). The differences between the individual shapes, all belonging to the *drop-shape* family, are quantified by the value of a fixed factor *d* in the mathematical description of the shape. If the factor *d* is exactly 0.0, then the shape will simplify to a perfect ellipse. An ellipse can therefore be interpreted as a borderline case belonging to the drop-shape family. The more *d* differs from 0.0, the more the shape deviates from an ellipse towards a rain-drop shape (Fig. 3). In the same manner as for the description of an ellipse, only two free parameters (c_1 and c_2) are required

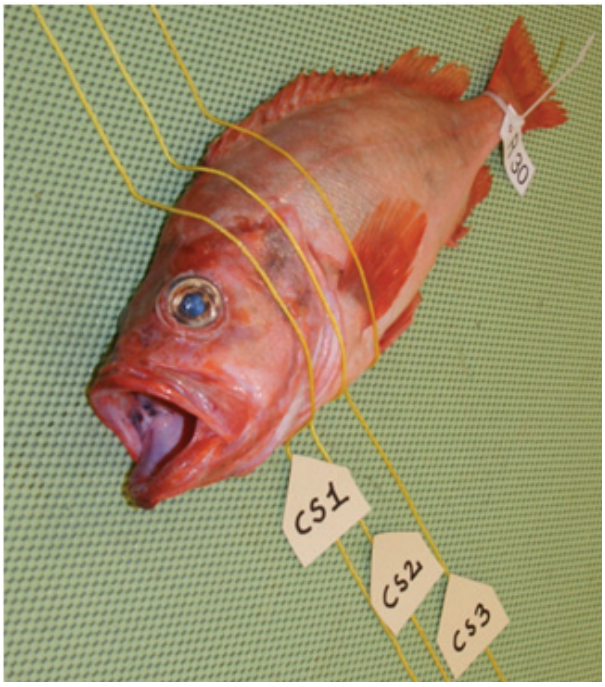


Fig. 1. Three cross-sections (CS1, CS2 and CS3) measured on *S. marinus*.

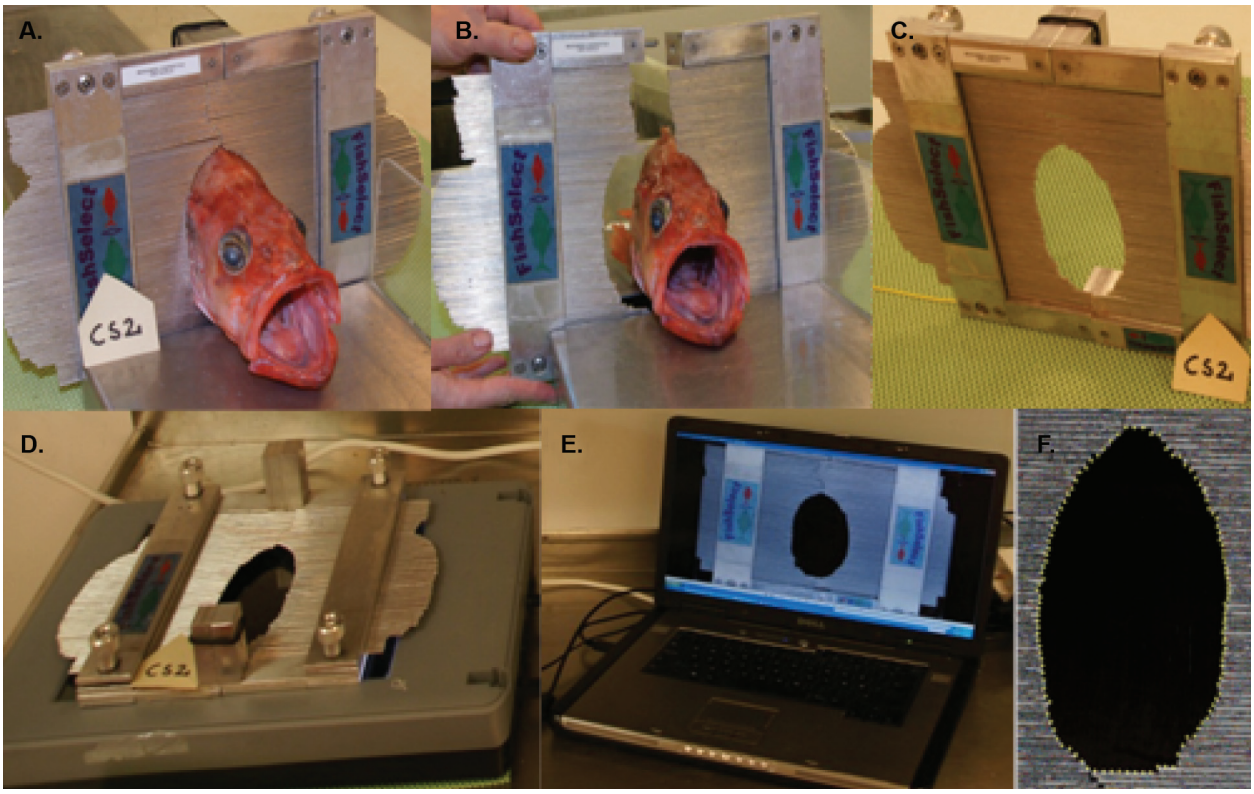


Fig. 2. Cross-section estimation process for a randomly selected fish and cross-section. The measurement of the cross-section shape of a *S. marinus* using a Morphometer (**A–C**) and the digitalization of the contour using a flatbed scanner (**D–F**) are shown.

to describe the individual members of *drop-shape* family (the Appendix outlines the mathematical description of the shapes belonging to the *drop-shape* family).

Using the measurements from the 100 fish, the average r^2-value was calculated for each of the six models for CS1, CS2 and CS3 (see appendix for details on the calculation method). The shape model with the highest average r^2-value was chosen to represent each cross-section further in the methodology.

The relationship between total length and cross-section shape parameters (c_1 and c_2) was assessed for the most suitable shapes found for CS1, CS2 and CS3. Using the morphometric data obtained from the 100 individuals included in the study, we modelled total length vs. c_1 and total length vs. c_2 considering the between-individual variability by the method described in Herrmann *et al.* (2009). The relationships total length vs. c_1 and total length vs. c_2 allowed us to simulate populations of fish with defined CS1, CS2 and CS3 shapes. For the selectivity prediction

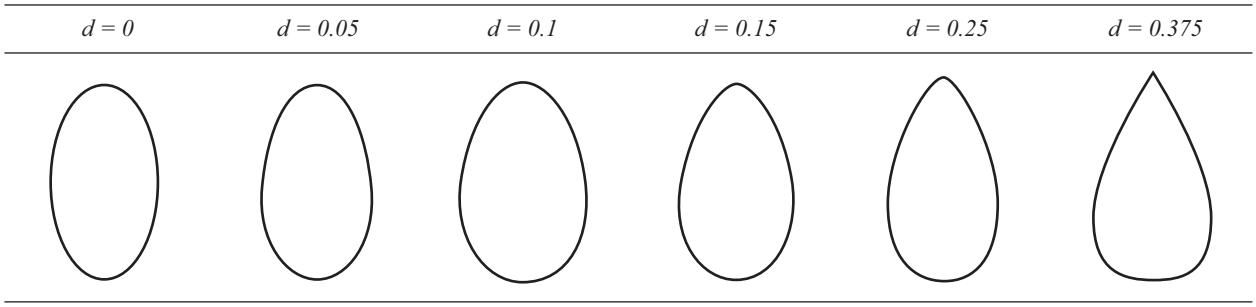


Fig. 3. Shapes belonging to the *drop-shape* family tested on the CS1, CS2 and CS3 contours of all *S. marinus* individuals included in the study. The value of the fixed factor *d* defines the exact shape.

analyses carried out at later stages of the methodology, a virtual population of 5 000 individuals uniformly distributed between 1 cm and 70 cm was generated based on the results from the regression analysis.

The fall-through experimental procedure examines whether or not a fish is able to physically pass through a rigid mesh template (Fig. 4). After being morphologically analysed, and using only the force of gravity, all 100 fish included in the study were tested on 191 different shapes (perforated in 5 mm thick solid nylon plates), including diamonds, hexagons and rectangles. The outcome for each of the 19 100 trials carried out (100 fish x 191 shapes) was registered as either "yes" (the fish was able to pass through the mesh template) or "no" (the fish was not able to pass through the mesh template). In the dubious cases we waited up to approximately one minute to see whether or not the fish slipped through the template. The perimeter of the shapes tested during the experiments varied from 140 to 420 mm for the diamonds, from 120 to 400 mm for the hexagons, and from 120 to 1000 mm for the rectangles (including some being square). For the diamond meshes the opening angle varied between 15° and 90° while it for the hexagons varied between 60° and 145°. The results from the fall-through experiments together with the modelled shapes CS1, CS2 and CS3 were used later in the FISHSELECT methodology to study the compressibility of the species and to predict the ability of individuals to pass through meshes of different size and shape.

Simulation of mesh penetration and selection of a penetration model

The shape and compressibility of a fish determines whether or not a fish will ultimately be able to pass through a mesh. The penetration models implemented in FISHSELECT simulate the lateral and vertical compressibility of the fish at each cross section. An initial investigation of the deformability of redfish carried out by simply squeezing the tissue by hand on a few individuals revealed that the dorsal and the ventral compressibility of the species are not symmetric. As previous penetration models implemented in FISHSELECT only considered symmetric vertical (dorsal-ventral) compression, a new model which takes the asymmetry observed for redfish into account had to be developed. This model included the estimation of three parameters, respectively representing the dorsal, lateral and ventral compressibility of the fish. The potential compressibility of the fish at an arbitrary angle around the fish cross-section was then modelled by linear interpolation between the potential compressibility (dorsally, laterally and ventrally) of the fish at each cross-section. We simulated the penetration of the modelled CS1, CS2 and CS3 shapes of each of the 100 fish through the 191 different shapes included in the fall-through trials using the FISHSELECT software. The purpose of these simulations was to estimate the exact compression potential of the cross-sections and to assess which cross-section combinations needed to be considered for estimation of the ability of redfish to pass through meshes of different size and shape. Models considering one cross-section at a time were created, where the dorsal, lateral and ventral compression independently were varied from 0 to 30% in 1% increment. This procedure resulted in 3 x 27 000 different penetration models. Using the FISHSELECT software we compared the results obtained from all of the different penetration models tested with the experimental fall-through results obtained in the lab. The penetration model which was best able to simulate the fall-through results was selected and used for further analysis in the FISHSELECT methodology. This evaluation was based on the DA-value (degree of agreement) for the different models. The DA-value expresses the percentage fraction of the fall-through results where the simulated results came up with the same result ("yes" or "no") as was obtained experimentally. A DA-value of for example 97.0% for a specific penetration model would mean that for 0.97 x 19 100 = 18 527 out of the 19 100 fall-through results was the model predicting the same result ("yes" or "no") as obtained during the experiment (see Herrmann *et al*. (2009) for further information on the DA-value). For completeness, penetration models considering combinations of the single cross-section models (that is, multiple cross-section models) were also tested in accordance with the FISHSELECT methodology.

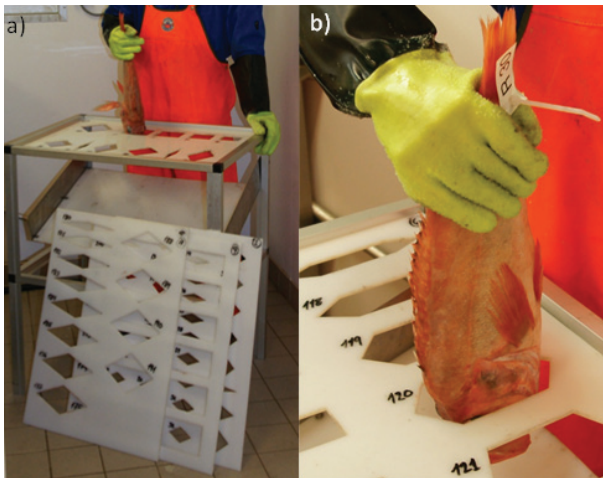


Fig. 4. Equipment (**A**) and procedure (**B**) used in the fall-through experiments.

Modelling of mesh shapes for diamond mesh codends used in the North Atlantic region

To predict size selection of *Sebastes* species in diamond mesh codends relevant to the North Atlantic region

trawl fishery using the FISHSELECT methodology, we developed an appropriate description of the shapes of the codend meshes during the trawling operation. This description is also necessary in order to enable comparisons of our predictions with previously published data from experimental fishing. In the Northeast Atlantic bottom trawl fishery, where the new experimental size selectivity data for *S. marinus* reported in this study were collected, it is common practice to use diamond mesh netting made of thick single twine netting. The codend used in the present experiment was built using the same material (8 mm PE twine) and design as the codends used for the experiments presented by Sistiaga *et al*. (2011). Sistiaga *et al*. (2011) demonstrated that the actual mesh shape in these types of codends, because of the presence of the knot, is better described by hexagons (Fig. 5) rather than by perfect diamonds. Hexagonal meshes are described by the length of the bars in the meshes (*B*), the size of the knot (*K*) and the opening angle (*OA*) of the mesh. *K* for the meshes built with this material and twine thickness was estimated to be constant at 27.2 mm by Sistiaga *et al*. (2011), meaning that *B* and *OA* are variables when modelling codend meshes with different size and shape. From underwater recordings performed for the same study, the meshes in these codends were estimated to have an *OA* of ~ 50°–90° while fishing. Nettings based on a thinner double twine (up to 6 mm) are also often used for diamond mesh codends in the North Atlantic region trawl fisheries harvesting *Sebastes* species (ICES, 2011c). However, since the meshes in these codends will also have knots of considerable size leading to a hexagonal model description too, we assume that the characteristics of the codends described by Sistiaga *et al*. (2011) are relevant as a model when investigating the selective properties of codends harvesting *Sebastes* species in most of the North Atlantic trawl fisheries. We therefore used this description and the mesh opening range 50°–90° to simulate the size selection of *Sebastes* species for a large range of different diamond mesh codends with mesh sizes from 50 mm to 200 mm. We predicted L_{50}s using the FISHSELECT methodology for meshes with *OA*s from 50° to 90° in 5° steps for each mesh size between 50 mm and 200 mm in steps by 10 mm. For each mesh size we selected the minimum and maximum predicted L_{50} value obtained with *OA*s between 50° to 90° and assumed that this interval represented the expected range of values that would occur during fishing.

To fully explore the selective properties for the diamond netting investigated we further extrapolated the use of the above described hexagonal model of the diamond mesh netting by investigating its expected size selective properties over a much broader range of *OA*s. This was done by simulating the expected L_{50} values for each mesh *OA* between 15° and 180° in steps by 5° for all the mesh sizes between 50 and 200 mm in steps by 10 mm. This modelling leads to a so called design guide (DG) consisting of L_{50} isoline curves showing the dependency of L_{50} on mesh size and *OA*. DGs are well suited to give a quick overview of how the size selective properties depend on the interaction between two parameters like mesh size and *OA* for a particular type of mesh and for a particular species (see Herrmann *et al*., 2009 for further description of DGs).

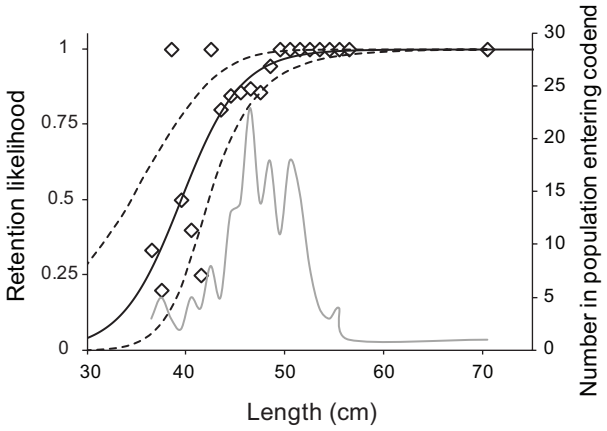


Fig. 5. A hexagon fitted to a random diamond mesh from the codends used in the experiment. The parameters "*B*", "*K*" and "*OA*", necessary to determine the shape of a hexagon, are also shown.

Results

Analysis of new selectivity data collected for codend applied in Northeast Atlantic

The data for the hauls belonging to the 135 mm diamond mesh codend were analysed to estimate the average size selectivity (Table 2). The estimated mean L_{50} value is 39.5 cm. Fit statistics revealed (*p*-value and DOF vs. deviance) no indications that compromised the use of the logistic curve to describe the size selection processes of *S. marinus* in the codend (see Wileman *et al*., 1996 for further information on how to interpret the values for the fit statistics).

The selection curve for the codend including its 95% confidence bands and the average experimental retention rate are plotted together (Fig. 6).

FISHSELECT results

Fish shape and cross-section analysis

The individual lengths of the 100 *S. marinus* included in the study for the FISHSELECT data collection ranged between 10 and 65 cm. The analysis of cross-section

scans in the FISHSELECT software-tool showed that the shape for all three cross-sections could be best modeled by employing parametric descriptions other than a standard elliptical shape. Based on the r^2-values obtained, the models belonging to the *drop-shape* family with $d > 0.0$ showed better performance than the perfect ellipse ($d = 0.0$) in describing the cross-sections of *S. marinus* (Table 3).

For CS1 a drop-shape with $d = 0.05$ yielded a mean r^2-value of 0.8941. For CS2 the best description was obtained with a shape having $d = 0.1$, resulting in a mean r^2-value of 0.9535. Finally, for CS3 a shape with $d = 0.15$ gave the best description with a mean r^2-value at 0.9479. These relatively high mean r^2-values demonstrate the ability of models belonging to the *drop-shape* family to reproduce the characteristics of the cross-section shapes critical for the escapement of this species through trawl meshes. For some of the tested models the difference in mean r^2-value based on the 100 measured redfish was so small that the specific model choice would in practice have little influence on the redfish cross-section description (Table 3). However, as these models all are equally complex, for consistency we for each CS chose to use the model having the highest mean r^2-value (Fig. 7).

Following the FISHSELECT methodology, the parameters describing how the different cross-sections (CS1 to CS3) depend on the length of the individual fish was modeled with regression models of the power type (see Herrmann *et al*. (2009) for description of this type of regression models). In the *drop-shape* family models, the dependency of the two free parameters c_1 and c_2 on length is estimated by a regression analysis for each cross-section (Table 4). The high r^2-values for the results for all the regressions (Table 4) demonstrate that power type models of the length dependencies are able to account for most of the variation in the collected data.

Table 2: Selectivity results from the 135 mm diamond mesh codend tested during the sea trials on board RV *Jan Mayen*. 95% confidence limits are shown in brackets.

Number of hauls	11
Number in codend	158
Number in codend cover	24
L_{50} (cm)	39.5 (34.5–42.3)
SR (cm)	6.7 (4.0–11.1)
p-value	0.56
DOF	20
Deviance	18.5

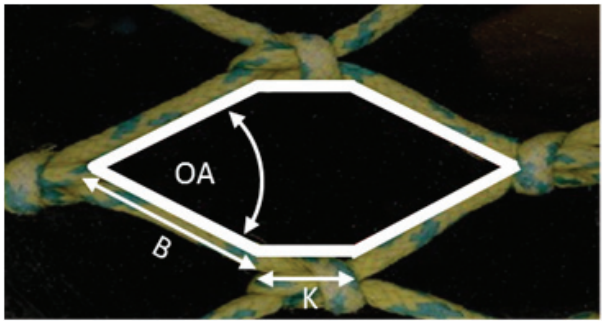
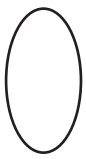


Fig. 6. Retention likelihood of *S. marinus* based on the population entering the 135 mm codend tested during the sea trials carried out on board RV *Jan Mayen*.

Degree of agreement (DA) and penetration model

For the penetration models based on only one cross-section (CS1, CS2 or CS3) the highest DA (97.9%) was found for a model based on CS2. This model had zero dorsal compression, 25% lateral compression and 6%

Table 3: Mean r^2-values for different shape descriptions. The highest r^2-value for each cross section is in bold.

						
d	0.0	0.05	0.1	0.15	0.25	0.375
CS1	0.8900	**0.8941**	0.8781	0.8429	0.7275	0.5153
CS2	0.9373	0.9531	**0.9535**	0.9397	0.8762	0.7542
CS3	0.8878	0.9224	0.9423	**0.9479**	0.9220	0.8437

ventral compression. Thus, this model predicted more lateral compression potential for *S. marinus* at CS2 (as the tissue at the side of the fish is soft) than ventral compression and no dorsal compression (where the tissue is hardest). These results support observations made on a few individual *S. marinus* that were manually compressed at different locations around the cross-sections. The models combining two cross-sections improved the DA very little (< 0.02%). Considering the gain in simplicity by using a single cross-section model and the high DA value obtained (97.9%), the model with the highest DA based on only CS2 was chosen for subsequent analysis.

Comparing FISHSELECT predictions with sea trial results for North Atlantic codends

The CS2 penetration model was applied to simulate the size selection of the virtual population of 5 000 *S. marinus* individuals through diamond mesh codends of different mesh sizes. The range of the predicted L_{50} results for the different codend mesh sizes was compared to the new result from sea trials with the 135 mm codend (including the confidence limits for the mean L_{50} value) and the previously published results for *S. marinus* (Table 1, Fig. 8).

The prediction of codend L_{50} based on the FISHSELECT analysis of data for *S. marinus* agreed well with previous results from similar sea trials (Fig. 8). Further, we compare the FISHSELECT predictions based on *S. marinus* with previous results collected from sea trials for *S. mentella* and *S. fasciatus* (Table 1; Fig. 8).

The L_{50} predictions for mesh sizes between 50–200 mm and *OA*s between 15°–180° obtained from FISHSELECT were combined in a DG. This DG provides predicted L_{50} values for fixed combinations of mesh size (*x*-axis) and *OA* (*y*-axis). For example, for mesh sizes of 100 mm and L_{50} mm for an *OA* fixed at 50° L_{50}s are predicted to be 24 and 36 cm respectively. The results indicate that

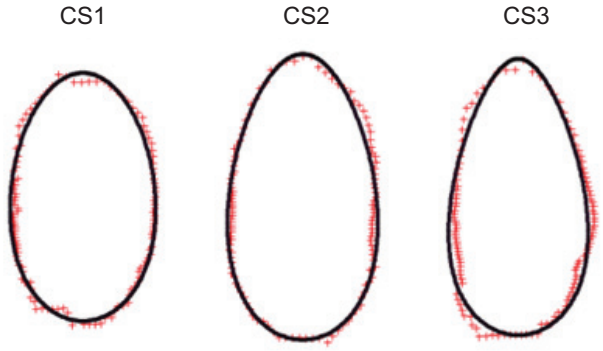


Fig. 7. Illustration of the fits of the models selected for CS1 (d = 0.05), CS2 (d = 0.1) and CS3 (d = 0.15) to the digitized cross-sections for a randomly selected *S. marinus* individual.

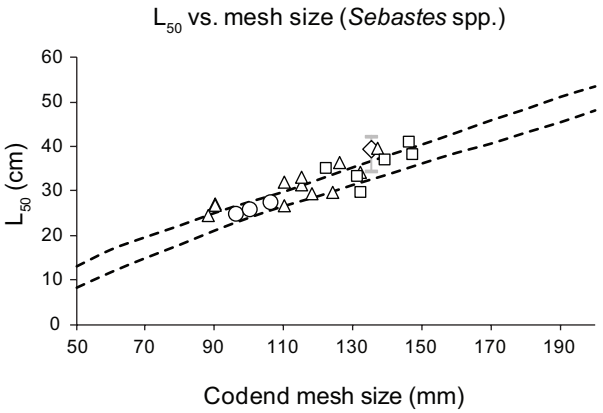


Fig. 8. Predicted (stippled curves – based on values for mesh size between 50 mm and 200 mm in steps by 10 mm) and observed (points) L_{50} vs. mesh size relationships for *Sebastes* spp. Predicted values are based on the FISHSELECT analysis of the data collected for *S. marinus*; diamond with error bars represents the new result from sea trials; previous results for *S. marinus* presented in Table 1 are squares; previous results for *S. mentella* are triangles and *S. mentella/fasciatus* circles.

Table 4: Values for regression coefficients and fit statistics for CS1, CS2, and CS3. All models are power models, as for example $c_1 = a$ x (Length)^b (See Herrmann *et al.* (2009) for details). Input for Length is in mm. Output for c_1 and c_2 are in mm. The value of fixed factor d defines which shape model was applied to describe the cross section (see appendix).

	d	Parameter	*a*	*b*	sd(*a*)	r^2
CS1	*0.05*	c_1	7.0749×10^{-2}	1.02	7.2800×10^{-3}	0.9140
		c_2	1.5903×10^{-1}	0.95	8.3335×10^{-3}	0.9779
CS2	*0.1*	c_1	5.5901×10^{-2}	1.06	6.1859×10^{-3}	0.9158
		c_2	1.8879×10^{-1}	0.94	1.0967×10^{-2}	0.9802
CS3	*0.15*	c_1	5.5324×10^{-2}	1.06	6.7863×10^{-3}	0.8995
		c^2	2.0181×10^{-1}	0.93	1.2580×10^{-2}	0.9764

for the diamond mesh types used in the North Atlantic, L_{50} increases with increasing mesh size for a given *OA*. For mesh size fixed at 150 mm for *OA* at respectively 50° and 90° the predicted L_{50}-values are 36 and 40 cm. The L_{50} result range for *OA*s between 50°–90° varied from ~10 cm for 50 mm meshes to ~53 cm for 200 mm meshes. The separation between the L_{50} isolines at the *OA*s observed while fishing (delimited by the stippled lines in Fig. 9) approaches the maximum separation between the lines, implying that large differences in L_{50} are achievable through changing mesh sizes. For diamond mesh codends the *OA*-value is not completely fixed as it can vary with location in the codend (Herrmann *et al*., 2007) and can potentially also be affected by the amount of catch (Herrmann (2005a; 2005b); Herrmann and O'Neill (2005)). The DG (Fig. 9) gives (through the dependency of L_{50} on *OA*) an impression of how this mechanism can lead to lack in determinism in the size selection process in the codend for individual fish. For the population of fish entering the codend during a trawl haul this *OA*-variation contributes to a bigger SR for the size selection process (Herrmann *et al*., 2009).

Discussion

Fish morphology affects the size selectivity of towed fishing gears. In the present study we further developed and applied the FISHSELECT methodology and tools (Herrmann *et al*., 2009) to assess the morphological component of the size selection process of *S. marinus* in diamond mesh codends. Our results indicate that using FISHSELECT we are able to understand and explain the results obtained from sea trials for *S. marinus* (Fig. 8). The previously published data for size selection of *S. mentella* and *S. fasciatus* also fall within the confidence band for L_{50} obtained from FISHSELECT for the *S. marinus* data (Fig. 8). This agreement is found for a very broad band of codend meshes sizes, which could indicate the validity of the extrapolation of our results to make predictions also for these two *Sebastes* species. The success in our attempt to extrapolate the FISHSELECT predictions for *S. marinus* to also explain and understand codend size selection of *S. mentella* and *S. fasciatus* indicates that the morphometric characteristics with respect to size selection in codends are similar for these species. This finding seems to be in good agreement with previously reported similarities between these species (Power and Ni, 1985; Pampoulie and Danielsdottir, 2008). But for future comparisons between the redfish species, it would be beneficial if comparable morphology data relevant for size selection are available for the different redfish species. Such morphometric data can be collected using the FISHSELECT tools.

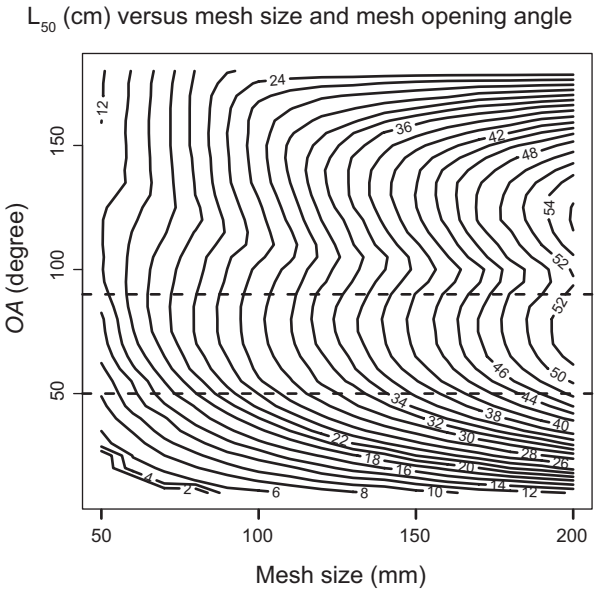


Fig. 9. Design guide showing L_{50} isolines for *S. marinus* with diamond codend mesh sizes between 50 mm and 200 mm and *OA*s between 15° and 180°. The stippled horizontal lines mark the range of *OA*s observed by Sistiaga *et al*. (2011) during underwater recordings carried out to observe the codends used in the Northeast Atlantic while fishing.

Fish behaviour can be important in the capture process of some fish, especially in the trawl mouth (Engås *et al*., 1998), but our method does not explicitly account for behavioral aspects of redfish. However the strong similarity found regarding the effect of codend mesh size between the FISHSELECT predictions and the different sea trial results (Fig. 8) indicates that the size selection of *S. marinus* in diamond mesh codends to a large extent can be explained by morphological characteristics of the species. Thus our results imply that the size selectivity of redfish in diamond mesh codend can be regarded as mostly a mechanical process without the need for considering behavioral aspects. In particular, selectivity appears dependent upon the girth and compressibility of a redfish at the cross section located at the end of the opercula and the foremost point of the dorsal fin.

The design guide as seen in Fig. 9, which predicts how L_{50} for *S. marinus* depends on mesh size and mesh opening angle (*OA*), demonstrates the importance of open codend meshes while fishing. This dependency on *OA* demonstrates that technical measures such as codend lastridge ropes can affect L_{50} due to a stable *OA* during the fishing process (Hickey *et al*., 1995). Diamond mesh codends with less number of open meshes on the around have also been reported to increase L_{50} for other fish

species (Sala *et al*., 2007; O'Neill *et al*., 2008) as reduced number of meshes implies increased *OA*s given a certain circumference. The method and data presented in this study could also form the base for investigating the size selection of redfish species in other fishing gear devices than diamond mesh codends. For example a design guide describing size selection of *S. marinus* in square mesh codends could be constructed based on the data described in this paper by using the method described in a case study for haddock in Krag *et al*. (2011).

The ability to reproduce the complex characteristics of the cross-section shapes of *S. marinus* using the mathematical description for the *drop-shape* family of models, which requires only two independent parameters to be estimated as function of fish length, highlights the power of this type of parametric description to model the cross-section shapes of fish. This type of mathematical description could in the future be applied to other fish species. Further, it could also be applied as a tool to categorize fish species morphologically according to their mathematical description. The selection of different models to describe the transversal contour of *S. marinus* at different positions along its length also represents a new way of quantifying how its shape changes along its length.

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References

BARSUKOV, V. V. 1968. The systematic relationship of redfishes of the genus *Sebastes* of the Northwest Atlantic Ocean. *DokladyAkad. Nauk. SSSR*, **183**: 479–482. [Trans. from Russian in *DokladyBioI. Sci.*, **183**: 734–737.]

BERS, L. and F. KARAL. 1976. Calculus, 2nd edition. Holt, Rinehart and Winston, New York, 783 p.

BOHL, H. 1961. German mesh selection experiments on redfish. Coun. Meet. *ICES, Comp. Fish. Comm.*, Doc. Nr. 88, 1991.

CADRIN, S. X., M. BERNREUTHER, A. K. DANÍELSDÓTTIR, E. HJÖRLEIFSSON, T. JOHANSEN, L. KERR, K. KRISTINSSON, S. MARIANI, K. NEDREAAS, C. PAMPOULIE, B. PLANQUE, J. REINERT, F. SABORIDO-REY, T. SIGURDSSON, and C. STRANSKY. 2010. Population structure of beaked redfish, *Sebastes mentella*: evidence of divergence associated with different habitats. *ICES J. Mar. Sci.*, **67**: 1617–1630. http://dx.doi.org/10.1093/icesjms/fsq046

CHERNICK, M. R. 2007. Bootstrap methods: a guide for practitioners and researchers. *In*: Wiley Series in Probability and Statistics, second edition. Wiley, New York.

EFRON, B. 1982. The jackknife, the bootstrap and other resampling plans. *SIAM Monograph* No. 38, CBSM-NSF. http://dx.doi.org/10.1137/1.9781611970319

ENGÅS, A., T. JØRGENSEN, and C. W. WEST. 1998. A species-selective trawl for demersal gadoid fisheries. *ICES J. Mar. Sci.*, **55(5)**: 835–845. http://dx.doi.org/10.1006/jmsc.1998.0352

FRANDSEN, R. P., B. HERRMANN, and N. MADSEN. 2010. A simulation-based attempt to quantify the morphological component of size selection of *Nephrops norvegicus* in trawl codends. *Fish. Res.*, **101**: 156–167. http://dx.doi.org/10.1016/j.fishres.2009.09.017

FRANDSEN, R. P., B. HERRMANN, N. MADSEN, and L. A. KRAG. 2011. Development of codend concept to improve size selectivity of *Nephrops* (*Nephrops norvegicus*) in a multi-species fishery. *Fish. Res.,* **111**: 116–126. http://dx.doi.org/10.1016/j.fishres.2011.07.003

FROESE, R., and A. PROELß. 2010. Rebuilding fish stocks no later than 2015: will Europe meet the deadline? *Fish Fish.*, **11**: 194–202. http://dx.doi.org/10.1111/j.1467-2979.2009.00349.x

FRYER, R. J. 1991. A model of between-haul variation in selectivity. *ICES J. Mar. Sci,*. **48**: 281–290. http://dx.doi.org/10.1093/icesjms/48.3.281

GORCHINSKY K. V., S. F. LISOVSKY, and M. K. SADOKHIN. MS 1993. Selectivity of Bottom Trawls during the Fishery for Redfish on the Flemish Cap Bank. *NAFO SCR Doc.*, 93/100, Serial No. N2293, 9 p.

GRIMALDO, E., M. SISTIAGA, and R. B. LARSEN. 2008. Evaluation of codends with sorting grids, exit windows and diamond meshes: Size selection and fish behavior. *Fish. Res.,* **97**: 271–280. http://dx.doi.org/10.1016/j.fishres.2007.12.003

GUNNARSSON, K., G. JÓNSSON, and Ó. K. PÁLSSON. 1998. Sjávarnytjar við Ísland, Mál og menning, Reykjavík (1998), 280 p.

HERRMANN, B. 2005a. Effect of catch size and shape on the selectivity of diamond mesh cod-ends: I. Model development. *Fish. Res.,* **71**: 1–13. http://dx.doi.org/10.1016/j.fishres.2004.08.024

2005b. Effect of catch size and shape on the selectivity of diamond mesh cod-ends: II. Theoretical study of haddock selection. *Fish. Res.,* **71**: 15–26. http://dx.doi.org/10.1016/j.fishres.2004.08.021

HERRMANN, B. and F. G. O'NEILL. 2005. Theoretical study of the between-haul variation of haddock selectivity in a diamond mesh cod-end. *Fish. Res.*, **74**: 243–252. http://dx.doi.org/10.1016/j.fishres.2005.01.022

2006. Theoretical study of the influence of twine thickness on haddock selectivity in diamond mesh cod-ends. *Fish. Res.*, **80**: 221–229. http://dx.doi.org/10.1016/j.fishres.2006.04.008

HERRMANN, B., L. A. KRAG, R. P. FRANDSEN, N. MADSEN, B. LUNDGREN, and K. J. STÆHR. 2009. Prediction of

selectivity from morphological conditions: Methodology and a case study on cod (*Gadus morhua*). *Fish. Res.,* **97**: 59–71. http://dx.doi.org/10.1016/j.fishres.2009.01.002

HERRMANN, B., D. PRIOUR, and L. A. KRAG. 2007. Simulation-based study of the combined effect on cod-end size selection of turning meshes by 90° and reducing the number of meshes in the circumference for round fish. *Fish. Res.*, **84**: 222–232. http://dx.doi.org/10.1016/j.fishres.2006.10.020

HICKEY, W. M., D. L. BOULOS and G. BROTHERS. 1995. A Study of the Influence of Lastridge Ropes on Redfish Selectivity in a Bottom Trawler. *Can. Tech. Rep. Fish. Aquat. Sci*., **2076**: vii+25.

ICES 2011a. *ICES Advice 2011* (Book 3). Copenhagen.

2011b. *ICES Advice 2011* (Book 2). Copenhagen.

2011c. Report of the ICES-FAO Working Group on Fishing Technology and Fish Behaviour (WGFTFB), 9–13 May 2011. *ICES CM 2011/SSGESST*:11.

JØRGENSEN, T., O. A. INGÓLFSSON, N. GRAHAM, and B. ISAKSEN. 2006. Size selection of cod by rigid grids—is anything gained compared to diamond mesh codends only? *Fish. Res.,* **79**: 337–348. http://dx.doi.org/10.1016/j.fishres.2006.01.017

KONSTANTINOV, K. G., A. K. CHUMAKOV, K. N. NIKESHIN, and V. G. KOVALENKO. MS 1982. On Validity of Trawl Mesh Size used in Fishing Areas in the Northwest Atlantic. *NAFO SCR Doc.,* No. 14 Serial No. N502, 30 p.

KRAG, L., B. HERRMANN, N. MADSEN, and R. P. FRANDSEN. 2011. Size selection of haddock (*Melanogrammus aeglefinus*) in square mesh codends: A study based on assessment of decisive morphology for mesh penetration. *Fish. Res.*, **110**: 225–235. http://dx.doi.org/10.1016/j.fishres.2011.03.009

LEHMANN, E. L. 1983. Theory of Point Estimation. New York, John Wiley and Sons.

LISOVSKY, S. F. MS 2001. On Optimal Mesh Size When Fishing Redfish in the Atlantic. *NAFO SCR Doc*., 01/21, Serial No. N4389, 16 p.

LISOVSKY, S. F., V. L. TRETJAK, V. M. KISELEVA, and S. M. KOTLJAROV. MS 1995. On Minimum Mesh-size During Deepwater Redfish Fishery with Mid-water Trawl in NAFO Division 3NO, *NAFO SCR Doc.*, 95/25. Serial No. N2533, 9 p.

LISOVSKY, S. F., A. A. PAVLENKO, A. A. VASKOV. MS 2005. On the Minimal Trawl Codend Mesh Size in the Fishery of Redfish Species in Division 3O of the NAFO Regulation Area. *NAFO SCR Doc.*, 05/18, Serial No. N5099, 17 p.

NAFO. 2010. Northwest Atlantic Fisheries Organization, *Annual Report 2010* (www.nafo.int). ISSN-0704-4798, 16 p.

MS 2011. Northwest Atlantic Fisheries Organization Conservation and Enforcement Measures. *NAFO/FC Doc.*, 11/1. Serial No. N5867. 98 p.

NI, I-H. 1981. Separation of sharp-beaked redfishes, *Sebastes fasciatus* and *S. mentella* from northeastern Grand Bank by morphology of extrinsic gas bladder musculature. *J. Northw. Atl. Fish. Sci.*, **2**: 7–12. http://dx.doi.org/10.2960/J.v2.a1

O'NEILL, F. G. and B. HERRMANN. 2007. PRESEMO a predictive model of codend selectivity – a tool for fisheries managers. *ICES J. Mar. Sci.,* **64**: 1558–1568.

O'NEILL, F. G., N. GRAHAM, R. J. KYNOCH, R. S. T. FERRO, P. A. KUNZLIK, and R. J. FRYER. 2008. The effect of varying cod-end circumference, inserting a 'flexi-grid' or inserting a Bacoma type panel on the selectivity of North Sea haddock and saithe. *Fish. Res.,* **94**: 175–183. http://dx.doi.org/10.1016/j.fishres.2008.06.007

PAMPOULIE, C. and A. K. DANÍELSDÓTTIR. 2008. Resolving species identification problems in the genus *Sebastes* using nuclear genetic markers. *Fish. Res.,* **93**: 54–63. http://dx.doi.org/10.1016/j.fishres.2008.02.007

PAVLENKO, A. A. MS 2009. Optimum Mesh Size in Redfish Fisheries in the North Atlantic. *NAFO SCR Doc*., 09/52. Serial No. N5696, 6 p.

POWER, D. J. and I. H. NI. 1985. Morphometric differences between golden redfish (*Sebastes marinus*) and beaked redfishes (*S. mentella and S. fasciatus*). *J. Northw. Atl. Fish. Sci.*, **6**: 1–7.

SALA, A., A. LUCCHETTI, G. BUGLIONI. 2007. The influence of twine thickness on the size selectivity of polyamide codends in a Mediterranean bottom trawl. *Fish. Res.,* **83**: 192–203. http://dx.doi.org/10.1016/j.fishres.2006.09.013

SISTIAGA, M., B. HERRMANN, R. B. LARSEN, E. GRIMALDO. 2010. Assessment of dual selection in grid based selectivity systems. *Fish. Res.,* **105**, 187–199. http://dx.doi.org/10.1016/j.fishres.2010.05.006

SISTIAGA, M., B. HERRMANN, K. N. NIELSEN, and R. B. LARSEN. 2011. Understanding limits to cod and haddock separation using size selectivity in a multispecies trawl fishery: an application of FISHSELECT. *Can. J. Fish. Aquat. Sci.,* **68**: 927–940. http://dx.doi.org/10.1139/f2011-017

THORSTEINSSON, G., E. P. EINARSSON, H. VILHJÁLMSSON. 1979. Netfrædi, Hafrannsóknir - No 18. HAFRO, Reykjavik, Iceland,

WIENBECK, H., B. HERRMANN, W. MODERHAK, and D. STEPPUTTIS. 2011. Effect of netting direction and number of meshes around on size selection in the codend for Baltic cod (*Gadus morhua*). *Fish. Res.,* **109**: 80–88. http://dx.doi.org/10.1016/j.fishres.2011.01.019

WILEMAN, D., R. S. T. FERRO, R. FONTEYNE, and R. B. MILLAR. (eds.). 1996. Manual of methods of measuring the selectivity of towed fishing gears. *ICES Coop. Res. Rep.* No. 215.

Appendix

Describing the cross-section shapes of *S. marinus* in FISHSELECT requires a representation in polar coordinates (θ, r), where θ is the angle (0°–360°) and r is the corresponding radius (see appendix in Herrmann *et al*., 2009). A description that involves only a few parameters is preferred. One flexible method, which enables the modelling of a large family of different shapes by few parameters, is to use a parametric description in Cartesian coordinates of the following form (Bers and Karal, 1976):

$$x = f(t)$$

$$t \in [0, 360]$$

$$y = g(t)$$

The actual shape is then defined by the selected formulas for the two functions *f(t)* and *g(t)*.

The polar representation of the points on the cross-section surface is then calculated by:

$$r = \sqrt{x^2 + y^2}$$

$$\theta = \tan^{-1}(y, x)$$

where our representation returns the angle in the correct quadrant.

To represent the cross-sections of *S. marinus*, we needed to find mathematical descriptions for the two functions (*f(t)* and *g(t)*) with as few free parameters as possible but which are still able to describe the main characteristics of the cross-section shapes of the species. During initial experimentations with implementations and test of different new formulas based on trigonometric functions in the FISHSELECT software tool, we discovered that a certain type of description with only two free parameters would potentially be able to produce points which together generated shapes that looked like the shape of the different cross-sections of *S. marinus*. Besides the two free parameters c_1 and c_2, which roughly define the main dimensions of the shape (height and width) and should therefore be linked to the length of the individual fish, this description also contains an additional fixed factor *d*. The value of this fixed factor is able to give the shape quite different characteristics spanning from an ellipse towards a shape looking like a rain drop. Therefore we named the descriptions resulting from these models as the *drop-shape* family. Due to this versatility we decided to base the modelling of the cross-sections of *S. marinus* on this mathematical description. For the *drop-shape family* of contours the functions *f(t)* and *g(t)* are given by:

$$f(t) = c_1 \times \sin\left(\pi \frac{t}{180}\right) + d \times c_1 \times \sin\left(\pi \frac{t}{90}\right)$$

$$g(t) = -c_2 \times \cos\left(\pi \frac{t}{180}\right)$$

Quantification of the ability of a particular shape to describe the experimental collected data for a cross section on a fish can be based on calculation of the r^2-value for the fit of the model to the data. The r^2-value expresses the fraction of the variation in the in the data accounted for by the model to the total variation in the data. By using the polar expression (Θ,*r*) for the points along the cross section shape the r^2-value for the shape fit can be calculated by for each angle Θ to compare the radius values *r* based on the model against *r* based on the experimental data. The total variation in the data is calculated as the variance in the *r*-values from the experimental data.

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Oocyte Development and Vitellogenin Production in Northwest Atlantic Greenland Halibut *Reinhardtius hippoglossoides*

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Abstract

Histological data presented here supports the notion of an uncommon oocyte development pattern for Greenland halibut, with two simultaneous groups of developing oocytes in the ovary, the larger group developing for the upcoming spawning season and the smaller group developing for next year (*i.e.* the duration of vitellogenesis is > 1 yr.). We analyzed blood samples collected from wild fish as well as fish that were part of the first documented study of Greenland halibut reproductive development in captivity in order to explore the annual cycle of vitellogenin production for this species. Despite the unusual oocyte development strategy there were no obvious differences in seasonal vitellogenin profiles versus fish with more traditional oocyte development strategies. Blood plasma vitellogenin levels generally peaked prior to or during spawning for those fish that successfully spawned, while patterns were highly variable for fish that did not spawn. Maximum plasma vitellogenin levels observed were 25 mg/ml and within the range of values observed for other fish species. Continued refinements in husbandry and experimental protocols for the study of Greenland halibut in captivity will provide a valuable tool for examining aspects of the species' biology that are difficult to ascertain based on sampling of only wild fish.

Keywords: Greenland halibut, reproduction, spawning, vitellogenesis, oogenesis

Introduction

Greenland halibut *Reinhardtius hippoglossoides* is a deepwater flatfish with a circumpolar distribution. It is an important commercial species in the Newfoundland and Labrador region with a fishery that is executed primarily on immature fish (NAFO, 2011). This species has many intriguing features that are atypical of flatfish, including a highly active and migratory lifestyle and reduced association with the substrate (de Groot, 1970; Bowering, 1984; Bowering and Lilly, 1992; Boje, 2002; Vollen and Albert, 2008; Dennard *et al.*, 2009).

Aspects of Greenland halibut reproductive biology are equally intriguing. For example, early tagging data suggested that Greenland halibut around Newfoundland and Labrador migrated northward to the Davis Strait to spawn (Templeman, 1973) but as surveys and fisheries extended effort to depths exceeding 1000 m, it became apparent that some degree of spawning also occurs in areas along the Newfoundland and Labrador Shelf (Junquera and Zamarro, MS 1992). There have also been longstanding questions regarding the pattern of oocyte development in this species. Fish species examined to date have been categorized within one of three well-described patterns of oocyte development: synchronous, group synchronous, and asynchronous (Wallace and Selman, 1981; Tyler and Sumpter, 1996; Murua and Saborido-Rey, 2003). Synchronous species (*e.g.* Pacific salmons) exhibit the synchronous development of all oocytes within the ovary, leaving no 'reserve' oocytes for spawning in subsequent years. Group synchronous species (*e.g.* Atlantic cod *Gadus morhua*) contain a distinct mode of developing oocytes that will be spawned in the current year as well as a reserve of immature oocytes that will form the basis for spawning in subsequent years.

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Asynchronous species contain all potential oocyte stages and sizes at the same time with no obvious modes. They are characterized by continuous recruitment of oocytes into vitellogenesis. Greenland halibut ovaries are typical of a group synchronous species in that they contain both a mode of developing (*i.e.* vitellogenic) oocytes as well as immature oocytes. Unlike a typical group synchronous species, a second mode of oocytes begins to develop as development of the first mode proceeds, such that the ovaries contain two distinct modes of vitellogenic oocytes. The difficulty in categorizing the oocyte development pattern of Greenland halibut has come as a result of trying to fit this species into one of the current categories by speculating as to the fate of the second group of developing oocytes. Among the suggestions for this second group of developing oocytes were the idea that they were (1) residual (Junquera and Saborido-Rey, MS 1995) and eventually resorbed (Fedorov, 1968) or, (2) the basis for a second spawning episode later in the summer (Fedorov, 1968), or (3) quickly promoted through vitellogenesis in order to increase the current year's reproductive output (Rideout *et al.*, 1999). These suggestions were highly driven by the assumption that vitellogenesis in Greenland halibut was an annual phenomenon as seen in other well studied fish, like Atlantic cod. More recently it was suggested that Greenland halibut of the Northeast Arctic stock are characterized by the simultaneous development of oocytes for this year and next year (Kennedy *et al.*, 2011). This strategy enables annual spawning despite the fact that vitellogenesis requires greater than one year to complete (Junquera *et al.*, 2003) and was suggested to be a unique strategy among fishes described to date (Kennedy *et al.*, 2011).

The physiological processes involved in controlling vitellogenesis in fishes with traditional oocyte development patterns (*e.g.* group synchronous) have been studied in detail (Wallace, 1985; Specker and Sullivan, 1994; Tyler *et al.*, 2000). Basically, surges in pituitary and gonadal hormones stimulate the production of vitellogenin by hepatocytes. The vitellogenin enters the bloodstream, is actively sequestered by developing oocytes, and is cleaved to form yolk proteins. The accumulation of these yolk proteins results in a major period of oocyte growth, and upon fertilization provides the primary nutritional source for developing embryos and yolk-sac larvae. Most fishes have seasonal reproductive patterns and hence the production of vitellogenin occurs on a seasonal basis (*e.g.* Methven *et al.*, 1992; Mosconi *et al.*, 1998; Sun and Pankhurst, 2003; Mandich *et al.*, 2004; Guzmán *et al.*, 2008). The proposed pattern of reproductive development for Greenland halibut (*i.e.* the simultaneous development of vitellogenic oocytes for two consecutive years), however, suggests that mature fish will always possess vitellogenic oocytes. The pattern of vitellogenin production for such a strategy has never been demonstrated but could potentially be quite different than the previously demonstrated cycles for fish with only a seasonal occurrence of vitellogenic oocytes.

The objectives of the current study were to evaluate the unusual oocyte development strategy proposed for Greenland halibut based on fish from the Northwest Atlantic stock and to examine the annual vitellogenin production cycle in relation to fish with more typical oocyte development patterns. Analyses are based on samples collected from wild fish as well as the first reported reproductive work on Greenland halibut in captivity.

Materials and Methods

Wild Fish: Sample collection and histology

A sample of ovarian tissue was taken from Greenland halibut ($n = 301$) collected during Canadian multi-species groundfish surveys and from commercial gillnets in 2006 and 2007 (Fig. 1, Table 1) and fixed in 10% neutral buffered formalin. Blood was collected from the caudal peduncle using a heparinized syringe and centrifuged at 1 200 x g for one min. The supernatant was removed and frozen (-20°C at sea for up to two weeks, followed by -80°C in the lab) until analyzed for vitellogenin.

Thin (~5 mm) cross-sections were removed from each of the formalin-fixed ovary samples, run through a dehydration series (Leica TP1020) and embedded in Paraffin (Leica EG1160). Sections were cut at 5–7 µm using an automated rotary microtome (Leica RM2265) and stained with Haematoxylin and Eosin (Leica Auto Stainer XL).

Histological maturity status was assigned based on the criteria of Federov (1968). This scale is based on the cytoplasmic characteristics of the oocytes present in the ovary (Table 2). Digital images of each ovary section were captured using a compound microscope (Leica DM 1000) equipped with a digital camera (Leica DFC490). Using the freeware ImageJ (http://rsb.info.nih.gov/ij/) and a drawing tablet (Wacom Cintiq® 21UX), the outline of individual oocytes was traced and the cross-sectional area calculated. Only those oocytes that were sectioned through the nucleus were included.

Oocyte diameter was calculated based on the formula for the area of a circle and the mean vitellogenic oocyte

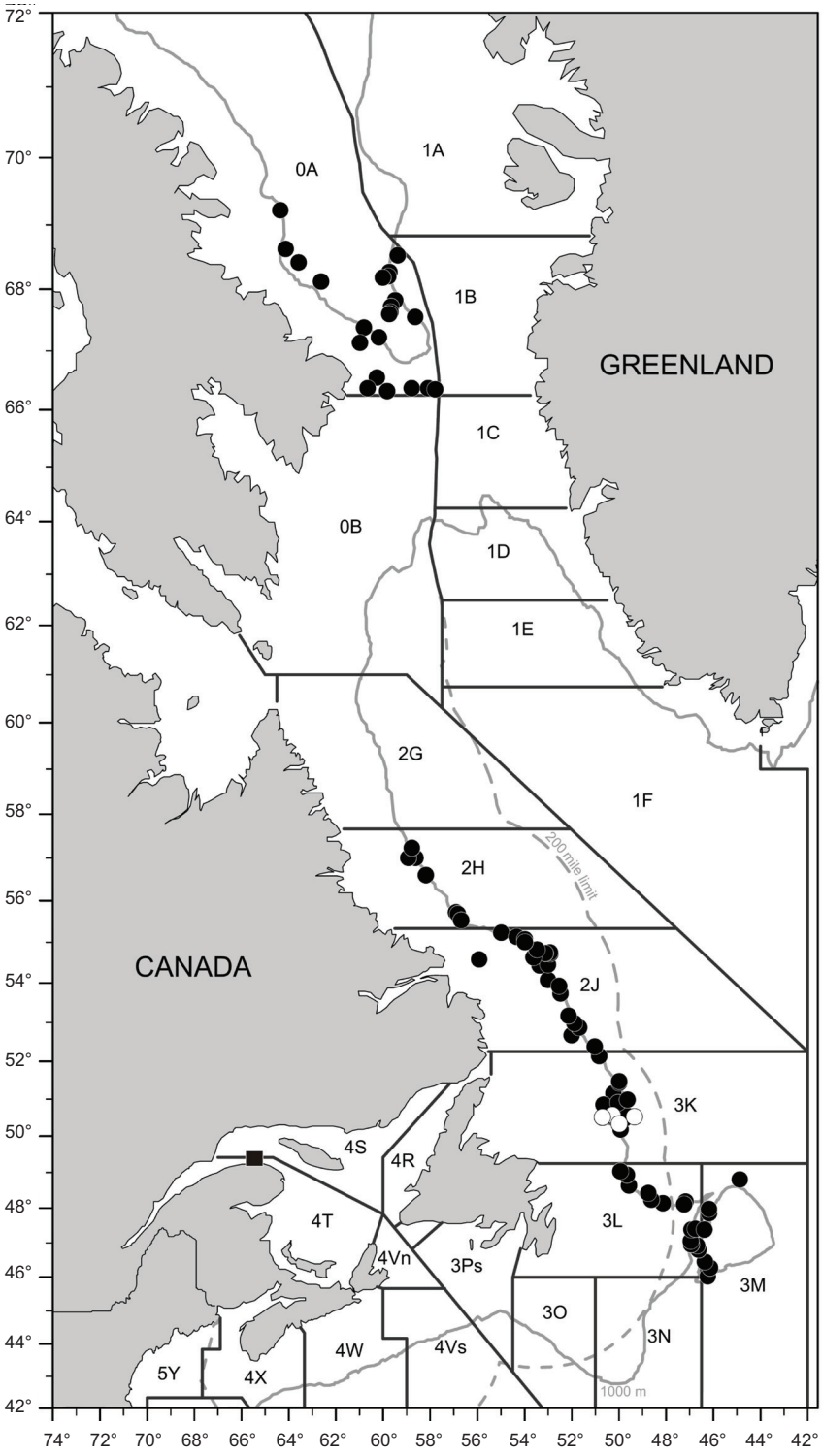

Fig. 1. Map of northwest Atlantic demonstrating areas where Greenland halibut were sampled by bottom trawl (solid circles) and deepwater gillnets (open circles) as well as the collection site for fish that were transferred to the laboratory for captive studies (solid square). Northwest Atlantic Fisheries Organization (NAFO) management Divisions are demonstrated along with the Canadian 200 mile limit (dashed grey line) and the 1 000 m depth contour (solid grey line).

Table 1. Collection details for female Northwest Atlantic Greenland halibut.

Date	NAFO area	Gear type	n	Fish size (cm) mean (range)
Jul 2006	3K	GN	76	69.2 (46–93)
Oct 2006	0A	OT	58	55.7 (41–73)
Oct–Nov 2006	2HJ3KLM	OT	99	58.7 (46–85)
Sep 2007	3K	GN	49	63.4 (42–91)
Oct–Dec 2007	2J3KL	OT	19	70.5 (50–85)
Total			301	62.3 (41–93)

GN: commercial deepwater gillnet
OT: research vessel otter trawl

diameter (minimum of n = 15 oocytes) was calculated. In more advanced fish, a hiatus in oocyte size frequency distribution appeared at approximately 750–900 µm, which agrees with previous reports (*e.g.* Kennedy *et al.*, 2011). In such cases the vitellogenic oocytes on each side of the hiatus were considered as distinct modes and we calculated the average diameter for each group. Vitellogenic modes to the right of the hiatus were referred to as the leading cohort (LC; equivalent to the G1 of Gundersen *et al.*, 2010) and always had a mean diameter > 1000 µm. The mode of vitellogenic oocytes to the left of the hiatus (or when only a single mode was present, *i.e.* no hiatus) was referred to as the developing cohort (DC; equivalent to the G2 of Gundersen *et al.*, 2010) and always had a mean diameter of < 950 µm. No distinction was made here between early vitellogenic and cortical alveoli stage oocytes (*i.e.* both were considered part of the DC). This approach is supported by the fact that there is no hiatus in size distribution between cortical alveoli and early stage vitellogenic oocytes (Kennedy *et al.*, 2011).

Captive Fish: Husbandry, experimental design and sample collection

The work done here to monitor the growth and reproductive development of Greenland halibut in captivity would

Table 2. Histological maturity stages for Greenland halibut based upon the stages from Federov (1968).

Stage	Characteristics
H1 Immature	Only previtellogenic (PV) oocytes present.
H2 Corticol alveoli	Oocytes have started developing. A band of cortical alveoli can be seen in the peripheral part of the oocyte. There is only 1 group of developing oocytes.
H3 Vitellogenesis 1	Two groups of oocytes present in addition to PV oocytes. In the oocytes of the most developed group, yolk granules have developed and start to fill the cytoplasm between the nucleus and zona radiata. In these oocytes, corticol alveoli appear as an external ring or even mixed with the yolk granules. The less developed oocyte group is characterised by a band of corticol alveoli in the periphery of the oocyte.
H4 Vitellogenesis 2	In the most developed group, yolk globules fill the cytoplasm between the nucleus and zona radiata. Yolk globules closer to the nucleus are larger than those farther away, forming a gradient of decreasing size outwards from the nucleus.
H5 Vitellogenesis 3	In the most developed oocytes the largest yolk globules are now seen in the peripheral part of the oocyte, reversing the gradient.
H6 Vitellogenesis 4	Fusion between yolk globules may be seen. The nucleus starts moving towards the pole of the oocyte.
H7 Spawning	Oocytes are characterised by large fused yolk globules and hydration.
H8 Spent	The ovaries are dominated by postovulatory follicles

appear to be the first published report of its kind so some text dedicated to describing the methods used to collect and maintain Greenland halibut in captivity is provided prior to the details of the experimental design.

Greenland halibut used for the experiment were caught with longlines in the St. Lawrence Estuary in October 2005. Fishing activities were conducted at depths between 200 and 350 m in areas around Matane (48° 59' N, 67° 25' W) and Mont-Louis, Québec (49° 14' N, 65° 44' W). Soaking time was normally between 12 and 24 h. Live specimens lifted aboard were placed in 1 m³ tanks with aerated seawater at ~ 5°C. Individuals with wounds, broken jaws or that appeared thin and moribund were not kept. Live fish were brought ashore every day and placed in land based 1 m³ tanks with aerated seawater at densities not exceeding ~ 30–40 fish per m³. Within 12 to 48 h following capture, fish were transported via truck in tanks with aerated seawater to the Maurice Lamontagne Institute (Fisheries and Oceans Canada, Mont-Joli, QC) located at a distance of 100–350 km. Mortality during transport was very low (~1%). In the lab, fish were kept in two 24 m³ tanks (4 m x 4 m x 1.5 m depth) at temperatures between 3 and 5°C and salinities between 28 and 32 ppm under natural photoperiod. Fish resumed feeding after an acclimation period of 2 to 4 weeks. They were then fed to satiation with capelin *Mallotus villosus*, three times a week until the beginning of the experiment in June 2006.

The maturation experiment was conducted in 2 semi-squared (2m x 2m) tanks. Seawater flow to each tank was ~ 10–15 $L \cdot min^{-1}$ through a semi-recirculated system equipped with a head tank, a sand filter and a thermo pump to regulate water temperature. Seawater temperature was kept constant at 5°C under conditions of natural photoperiod (latitude 49°45' N) and salinity (28–32 ppm) for the duration of the experiment.

At the beginning of the experiment, 30 fish were randomly distributed in the two experimental tanks. Fish were anaesthetized in a 5mg $\cdot L^{-1}$ metomidate solution (Mattson and Riple, 1989), measured (fork length ± 1mm), weighed (± 0.1g), and individually identified with a passive integrated transponder (PIT) tag injected in the muscle below the dorsal fin. Fish were fed to satiation three times weekly with capelin for the duration of the experiment. Feeding was stopped three days before each sampling period to ensure that fish had empty stomachs when manipulated.

The two groups of 15 fish were monitored on a two month interval in order to examine reproductive development in captivity. The first group of fish was examined in months 7, 9, 11, 1, 3, 5, 7 (where 1 is January), while the second group was examined in months 8, 10, 12, 2, 4, 6, 8. At each examination period, fish were anaesthetized, measured, weighed, and observations on maturity status were recorded. Maturity was estimated based on a combination of the fish's external features and observations on gonad size and the presence/absence of hydrated oocytes using ultrasound (Table 3). During each examination period a blood sample was collected from the caudal peduncle and frozen for the determination of plasma vitellogenin concentration as described previously for samples from the wild fish. All fish were euthanized at the end of the study. Once killed, information was collected as per previous sampling dates along with ovary and liver weight. Reproductive status was determined by macroscopic examination of the gonads.

Identification and quantification of vitellogenin

Greenland halibut blood samples were analyzed by high performance liquid chromatography coupled to electrospray ionization tandem mass spectrometry

Table 3. Characteristics used to monitor reproductive development in experimental Greenland halibut.

	Distinguishing characteristics	
Maturity stage	External	Ultrasound
Immature	flat abdomen	no clear definition of gonad
Developing	swollen abdomen	clear identification of gonad due to higher density of developing oocytes vs. other tissue
Spawning	swollen abdomen and extrusion of hydrated oocytes	large gonad size with clearly visible hydrated eggs
Spent	flat abdomen	smaller gonad size and some residual hydrated oocytes

(HPLC-ESI-MS/MS), according to Cohen *et al.* (2009). This technique for protein quantification was adopted due to the absence of commercial antibodies targeting vitellogenin for this particular species. Briefly, plasma samples were subjected to an overnight trypsin digestion and later analyzed by HPLC-ESI-MS/MS operated in Selective Reaction Monitoring (SRM) mode. The SRM method monitored two diagnostic MS/MS transitions (*m/z* 750.0→1020.4 and 750.0→1205.4) of a characteristic vitellogenin 'signature' peptide (sequence: FFGQEIAFANIDK). The concentrations of vitellogenin were calculated from calibration curves of this peptide obtained by chemical synthesis according to the following equation:

$$C_{Vt} = \frac{(C_S \cdot A_P \cdot V_R \cdot MW_{Vt})}{(A_S \cdot V_{Pl} \cdot MW_S)} \cdot 1000$$

where

A_P = integrated area of peptide

A_S = average integrated area of peptide standard

V_R = final reaction volume in µl

V_{Pl} = plasma volume in µl

MW_{Vt} = molecular weight of Greenland halibut vitellogenin in g/mol or Da

MW_S = molecular weight of the peptide standard in g/mol or Da

The concentration of peptide standard used here was C_S = 1 µg/ml. The average integrated area of the 1 µg/ml peptide standard was A_S = 14 427. The final reaction volume was V_R = 110 µl. The volume of plasma used was V_{Pl} = 1 µl. The sequence of Greenland halibut vitellogenin is not known but the molecular weight has been estimated at 185 000 Da according to SDS-PAGE analysis (Cohen *et al.*, 2009). The molecular weight of the peptide standard was 1499 Da.

Seasonal vitellogenin profiles were examined for individual fish in captivity and compared to vitellogenin data obtained from wild fish. For wild fish, data points that were one or more standard errors from the mean were considered outliers and were removed.

Results

Oocyte development strategy

Histological analyses (Fig. 2) confirmed that Greenland halibut ovaries in the early stages of development contained small vitellogenic and cortical alveoli stage oocytes. Later in development a hiatus in oocyte size frequency distribution appears, resulting in a mode of large (LC) and smaller (DC) vitellogenic oocytes (Fig. 2). Comparison of mean oocyte diameter between LC and DC oocytes within the same fish showed that DC oocytes are growing simultaneously with LC oocytes but at a much slower rate of development (Fig. 3).

Growth and reproductive development in captivity

Four fish died during the study. Another eight fish demonstrated fin erosion and/or substantial negative growth in weight and were excluded from the analyses. Therefore data on growth and reproductive development were collected from a total of 18 females.

Growth in length ranged from 0.2 to 6.0 cm per year (Table 4). Growth was significantly reduced in fish that spawned in comparison to fish that did not spawn (t-test, p = 0.01).

Eight fish spawned successfully in captivity (Table 4, Fig. 4). Five of these were actually observed to have clear, running eggs during regular sampling or on the final sampling day when fish were killed. The other three were never observed in spawning condition but upon the final (lethal) sampling were observed to have spent ovaries containing residual hydrated oocytes. This was taken as evidence that the fish had recently spawned. Five of the fish that spawned also demonstrated a sharp decline in weight (Fig. 4), representing the weight loss from the release of oocytes during spawning.

An additional 10 fish that were transferred to the laboratory did not spawn and showed no evidence of residual hydrated oocytes when killed at the end of the experiment. Despite their failure to spawn, these fish appeared otherwise healthy (no significant lesions or fin rot and no period of dramatic negative growth). These fish did have a tendency for an initial increase in body weight followed by a period of reduced weight gain or even slight weight loss (Fig. 5) but not to the extent experienced by spawners.

Vitellogenin production

Wild fish

Plasma vitellogenin levels in wild Greenland halibut at the time of capture were strongly related to the fish's stage of reproductive development (Fig. 6). When the most advanced oocyte size in the ovary was less than ~ 500 µm in diameter blood plasma vitellogenin levels were

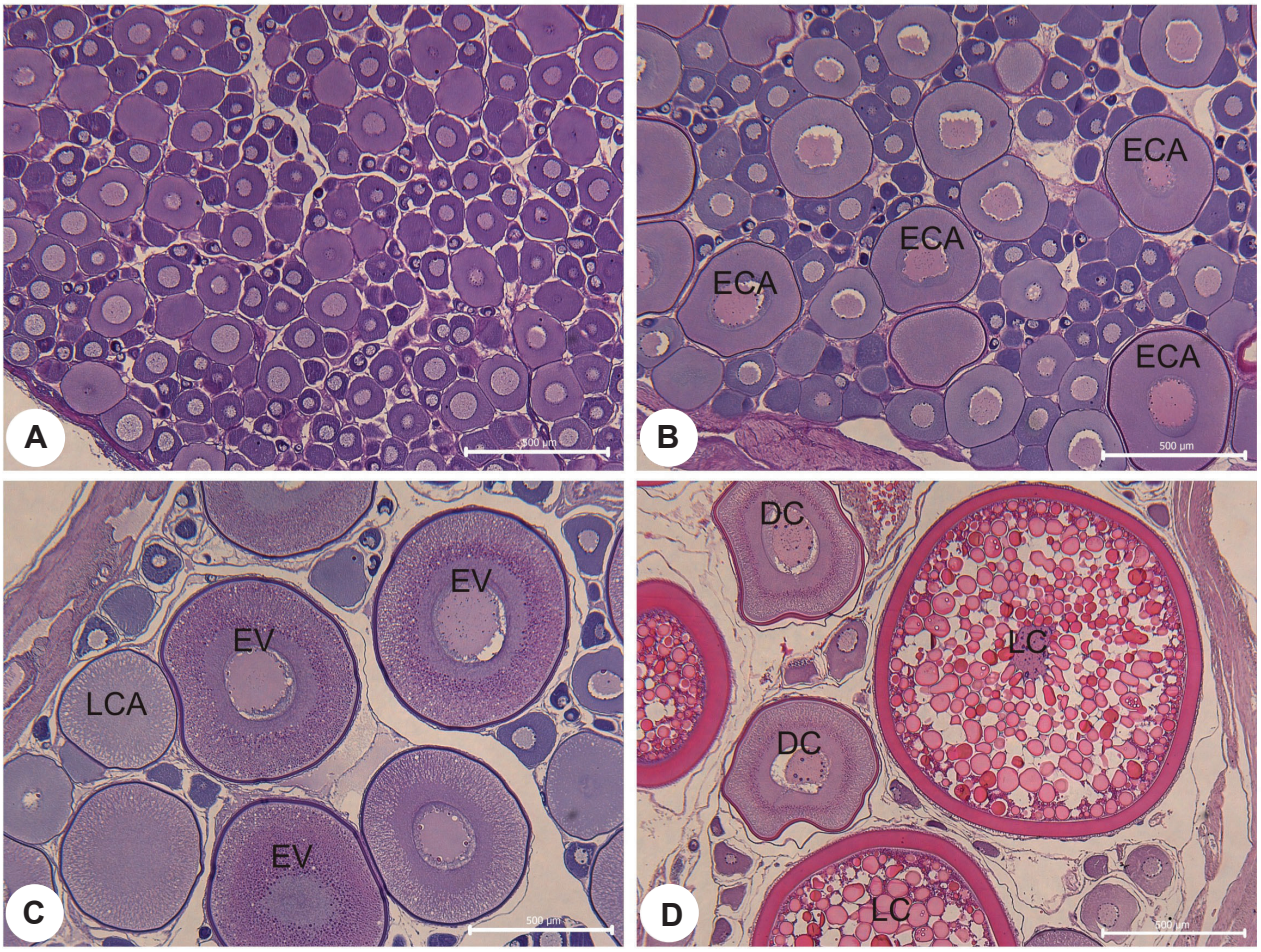

Fig. 2. Histological sections of Greenland halibut ovaries. (**A**) Immature ovaries contain primary stage oocytes. (**B**) Development begins with the formation of early cortical alveoli stage oocytes (ECA) followed by (**C**) the appearance of late stage cortical alveoli oocytes (LCA) and early vitellogenic oocytes (EV). (**D**) later in development two cohorts of vitellogenic oocytes are present, the leading cohort (LC) and the developing cohort (DC). Standard HandE stain. Scale bar = 500 µm.

extremely low and showed no trend with oocyte size. As oocyte size increased there was an associated increase in plasma vitellogenin concentration, with a maximum value of ~25 mg/ml for one individual. Despite the increasing trend there was a high degree of variability and there was no clear distinction in plasma vitellogenin level between fish with and without LC oocytes. In terms of histological maturity stage, plasma vitellogenin production peaked at maturity stage 6 (*i.e.* late vitellogenesis) with a mean value of 13.3 mg/ml. However, no spawning (stage 7) fish were collected in the current study so it was not possible to determine if vitellogenin concentration truly peaked prior to or during spawning.

Experimental fish

There was no consistent seasonal pattern with respect to vitellogenin production in Greenland halibut (Fig. 4 and 5). However, all of the fish that spawned did demonstrate a peak in plasma vitellogenin concentration during or just prior to spawning (Fig. 4). The maximum peak value observed for any individual fish was ~35 mg/ml. Patterns were less clear among fish that did not spawn. In a couple of fish vitellogenin peaked in a similar fashion to those fish that successfully spawned. In other cases vitellogenin demonstrated no real peak or peaked early in development and then declined gradually throughout the remainder of the study (Fig. 5).

Discussion

Histological data presented here support Kennedy *et al.*'s (2011) notion of an unusual reproductive strategy for Greenland halibut, wherein oocytes for two spawning seasons develop simultaneously. This conclusion is supported by the fact that there was no indication that the second group of oocytes remained dormant, were resorbed, or developed quicker than the leading group in order to be

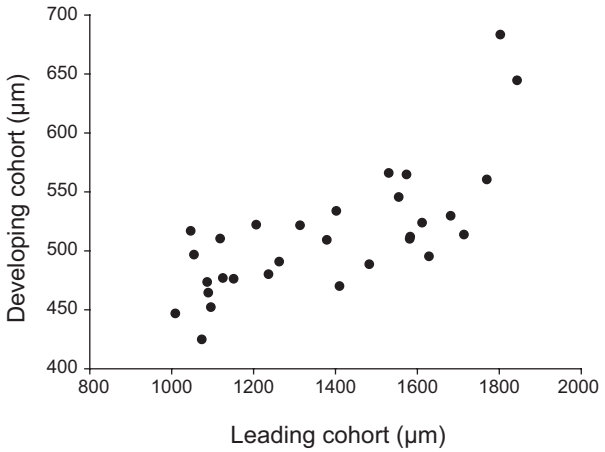

Fig. 3. Size of the most advanced group of developing Greenland halibut oocytes (*i.e.* leading cohort) in relation to the less advanced group of developing oocytes (*i.e.* developing cohort).

spawned at the same time, refuting previous suggestions (Fedorov, 1968; Junquera and Saborido-Rey, MS 1995; Rideout *et al.*, 1999). A comparison of mean oocyte size in the LC versus the DC within the same fish (Fig. 3) suggests that oocytes in the DC are increasing in diameter 4–6 times slower than those in the LC. Hence the more rapid period of oocyte growth does not begin until after the LC separates from the DC (*i.e.* after a hiatus forms). Based on the time interval between the first appearance of LC oocytes and the time when maximum oocyte size was observed, Kennedy *et al.* (2011) estimated that this stage alone (*i.e.* the period of more rapid growth) requires close to a year to complete. Females with only small vitellogenic oocytes (*i.e.* DC), therefore, could not possibly spawn within the next 12 months but rather must be developing for the subsequent year. The simultaneous development of two cohorts of oocytes enables Greenland halibut to spawn annually despite each cohort requiring greater than one year to complete vitellogenesis. While such a strategy appears to be highly unusual among North Atlantic fishes, it would not appear to be unique. Numerous species of Antarctic fishes appear to utilize this strategy in order to spawn annually despite a greater than annual period required to complete vitellogenesis (*e.g.* Sil'yanova, 1981; Butskaya and Faleeva, 1987; Shandikov and Faleeva, 1992 and numerous Russian references cited therein; Everson, 1994). Comparing these fishes to Greenland halibut would appear to support the notion that this oocyte development pattern evolved in response to conditions that made completing vitellogenesis in a single year impossible (*i.e.* uncommonly large oocytes and/or low environmental

Table 4. Growth and reproductive data for female Greenland halibut studied in captivity.

Tag	No. days monitored	Spawn	Initial length	Δ Length (cm)	Growth rate (cm per d)	Growth per 365 d
116946447A	362	Y	53.3	1.7	0.0047	1.7
132148217A	307	Y	54.0	1.4	0.0046	1.7
132279295A	365	Y	56.9	3.1	0.0085	3.1
132319564A	362	Y	52.0	2.0	0.0055	2.0
132165753A	365	Y	48.8	1.2	0.0033	1.2
132267380A	365	Y	57.0	0.2	0.0005	0.2
135814744A	362	Y	66.3	1.5	0.0041	1.5
132321517A	362	Y	48.5	4.0	0.0110	4.0
132326647A	300	N	52.2	4.7	0.0157	5.7
132356531A	362	N	51.9	3.4	0.0094	3.4
132221662A	362	N	43.5	6.0	0.0166	6.0
135533647A	362	N	51.3	5.3	0.0146	5.3
135609667A	365	N	63.0	2.8	0.0077	2.8
135639650A	365	N	52.5	5.8	0.0159	5.8
132936125A	365	N	55.6	2.1	0.0058	2.1
133962316A	365	N	54.5	3.0	0.0082	3.0
132213470A	365	N	56.3	2.7	0.0074	2.7
132162092A	362	N	57.5	1.9	0.0052	1.9

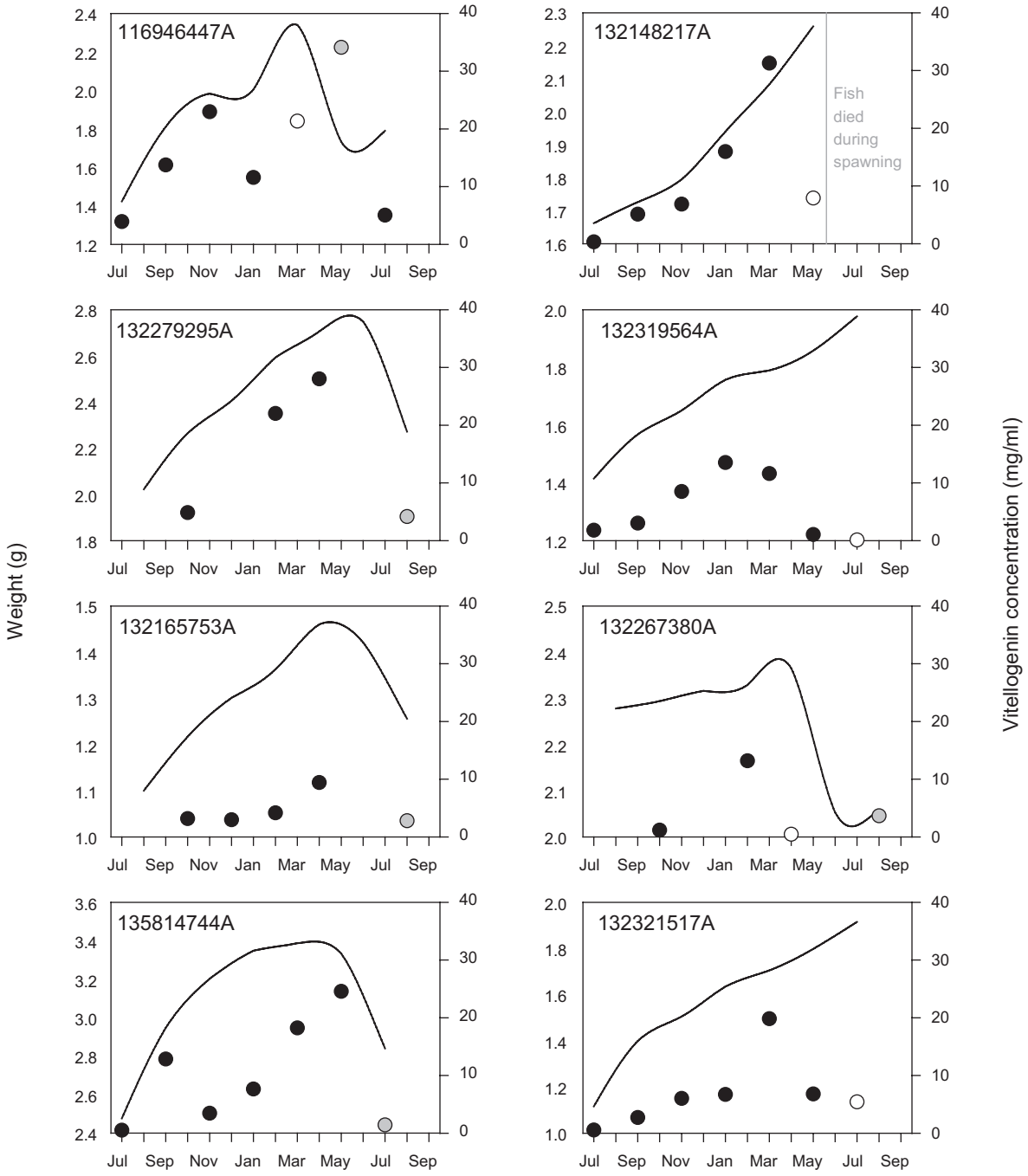

Fig. 4. Changes in whole body weight (solid line) and blood plasma vitellogenin concentration (circles) for individual experimental Greenland halibut that spawned successfully in captivity. Circle color indicates estimated maturity status based on external observations and ultrasound: solid symbol represents 'developing', white symbol represents 'spawning', and grey symbol represents 'spent'. Tag numbers are presented in the top left corner of each panel and correspond to those in Table 4. Note that the scale for weight is not uniform across panels.

temperatures; Kennedy *et al.* (2011)). The oocytes of these Antarctic fishes are as large as those produced by Greenland halibut and the environmental conditions are perhaps more extreme. Common wolfish *Anarhichas lupus* are also faced with the challenges associated with producing very large oocytes. They cope in a similar manner by always maintaining a reserve of oocytes at the cortical alveoli stage of development (Gunnarsson *et al.*, 2006). This provides a head start to each year's egg development but unlike Greenland halibut and Antarctic fishes, there does not appear to be any evidence that these reserve oocytes in wolfish start vitellogenesis prior to the spawning of the advanced mode of oocytes.

The unusual nature of reproductive development in Greenland halibut is an important consideration when it comes to assessing maturities in this species. Maturity scales that assume all fish with vitellogenic oocytes will spawn within the current year (*e.g.* the Templeman *et al.* (1978) scale initially developed for haddock and subsequently applied to other demersal fishes including Greenland halibut (*e.g.* Walsh and Bowering, 1981)) will categorize fish with only DC oocytes (*i.e.* without LC oocytes) as mature. Considering the reproductive strategy of this species (*i.e.* the continuous presence of vitellogenic oocytes once sexually mature), such fish would likely be developing oocytes for the first time (*i.e.* primiparous) and would be small in size relative to previously mature individuals. Such a maturity scale would therefore result in both an underestimation of the length at 50% maturity (L_{50}) and an overestimation of spawning stock biomass (SSB) and should be rejected in favour of those that distinguish between fish with and without LC oocytes (Riget and Boje, 1989; Gundersen, 2003). Fish containing only DC oocytes might be considered biologically mature (*i.e.* reproductive hormones, plasma vitellogenin, etc.) but are 'functionally immature' from a management perspective since they would not have contributed to the current SSB.

It is important to point out that Greenland halibut populations are often not characterized by a well defined spawning period but rather can have multiple peaks in spawning activity or even some degree of spawning activity throughout the entire year (Fedorov, 1968; Junquera *et al.*, 2003). Given the asynchrony in reproductive timing it is clear that an individual with LC oocytes and one with only DC oocytes need not spawn a full year apart (especially if oocyte sizes are not largely different, *e.g.* 200 µm). It would be more accurate to say that females with LC oocytes will spawn within the next twelve months whereas those with only DC oocytes would not be capable of spawning until sometime in the subsequent 12 months. This does not appear to be the case for species of Antarctic fishes, where conditions suitable for spawning likely occur over a restricted time period and result in a large degree of synchrony with respect to spawning time. For example, *Notothenia coriiceps* at Signy Island spawn in May each year (Everson, 1994). In such instances there is a greater degree of certainty that the two groups of vitellogenic oocytes within the ovary will be spawned a year apart.

The unusual pattern of oocyte development in Greenland halibut raises questions regarding the control mechanisms of vitellogenin production in this species. In more traditional scenarios (*i.e.* fish that produce only one mode of developing oocytes), a seasonal surge in reproductive hormones causes the liver to produce vitellogenin which reaches maximum levels in the blood plasma at or near spawning. After spawning, plasma vitellogenin levels fall again to almost negligible levels (*e.g.* Methven *et al.*, 1992; Mosconi *et al.*, 1998; Mandich *et al.*, 2004). Unlike these more typical species, however, Greenland halibut contain a mode of vitellogenic oocytes even after the completion of spawning, suggesting the potential for differences in the annual vitellogenin production cycle. Interestingly, the production of vitellogenin in Greenland halibut appears to follow a very similar cycle to that described for other species. The data for wild fish showed a slightly increasing trend throughout early development (histological stages 1–3), followed by a more rapid increase in vitellogenin in prespawning fish. A general lack of spent fish in the wild samples, however, combined with a high degree of variability in plasma vitellogenin levels for captive spent fish made it difficult to resolve the overall pattern in the vitellogenin cycle following spawning.

There was also no evidence that the two coexisting cohorts of vitellogenic oocytes in Greenland halibut ovaries were dependent on unusually high levels of plasma vitellogenin. The mean plasma vitellogenin concentration at the most advanced observed stage of maturity for wild fish was less than 15 mg/ml, with individuals having values as high as 25 mg/ml. These values are very comparable with those obtained from the captive fish, although a few of the captive fish reached values as high as 35 mg/ml. It should be pointed out that no wild spawning individuals were collected during the present study so it is possible that vitellogenin levels may get higher then the maximum observed value of 25 mg/ml in wild fish as well. The maximum levels of plasma vitellogenin recorded here for Greenland halibut are much higher than levels reported in several other species (reported mean peak values: gilthead seabream *Sparus aurata* 1.5 mg/ml Mosconi *et al.*, 1998; amberjack *Seriola dumerilii* 5 mg/ml Mandich *et al.*, 2004; Senegalese sole *Solea senegalensis* 4 mg/ml Guzmán *et al.*, 2008) but less than the maximum reported value for

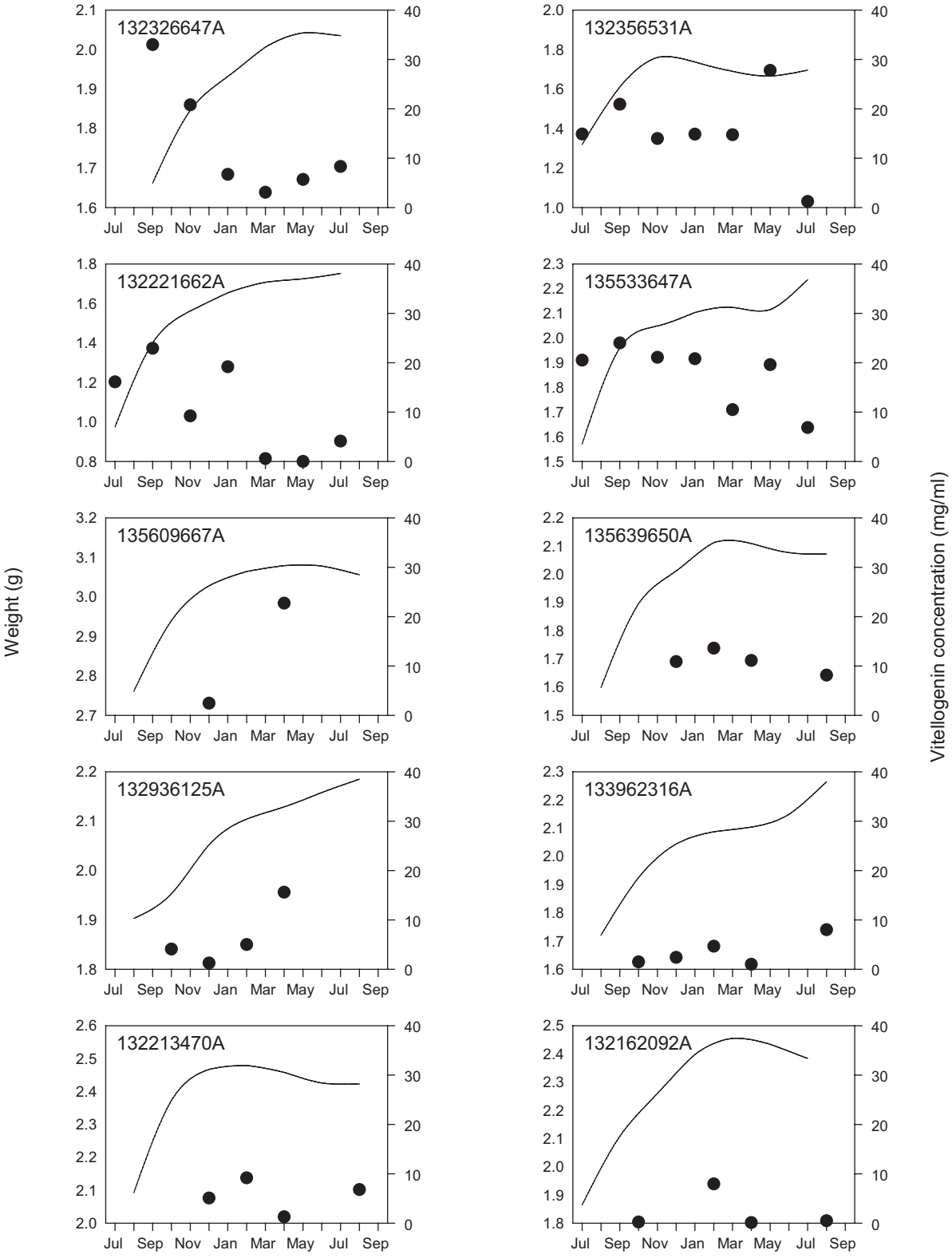

Fig. 5. Changes in whole body weight (solid line) and blood plasma vitellogenin concentration (circles) for individual experimental Greenland halibut that appeared healthy but did not successfully spawn in captivity. Tag numbers are presented in the top left corner of each panel and correspond to those in Table 4. See Fig. 4 caption for details of circle colors. Note that the scale for weight is not uniform across panels.

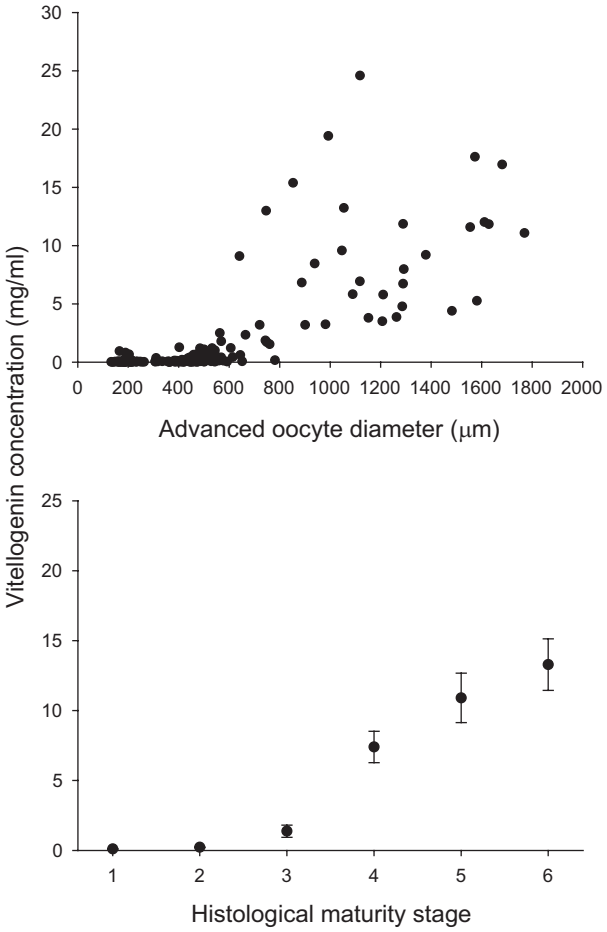

Fig. 6. Blood plasma vitellogenin concentration for Northwest Atlantic Greenland halibut in relation to (upper panel) mean oocyte diameter of the most advanced group of oocytes and (lower panel) histologically determined maturity stages. Error bars are 1 standard deviation.

Atlantic halibut *Hippoglossus hippoglossus* (mean peak value: 56 mg/ml Methven *et al.*, 1992). It should be noted that most of the vitellogenin levels obtained until the last decade were based on both mono and polyclonal immuno assays. Therefore, any comparison between different analytical platforms should be considered provisional until complete validation. For Greenland halibut vitellogenin, no commercial antibodies were available at the time of our studies. Nevertheless, mass spectrometry assays in this field have already been successfully validated with existing immuno assays (Simon *et al.*, 2010; Lau *et al.*, 2011).

It is possible that some aspects of the true pattern of vitellogenin production in Greenland halibut were masked by the fact that captive fish were only sampled every two months. For example, based on observations of the captive fish it is uncertain if vitellogenin levels peak prior to or during spawning. Vitellogenin peaked in one individual when the ovary was in a spent condition while in others it appeared to drop off while the fish was still spawning. Plasma vitellogenin concentration has been shown to peak during vitellogenesis (*i.e.* before spawning) in several other species, including Chinese loach *Misgurnus anguillicaudatus* (Lv *et al.*, 2009), Senegalese sole (Guzmán *et al.*, 2008), amberjack (Mandich *et al.*, 2004) and gilthead seabream (Mosconi *et al.*, 1998). On the other hand, vitellogenin in the more closely related Atlantic halibut peaked during spawning (Methven *et al.*, 1992). The approach of sampling fish only every two months was taken to minimize the impacts of handling stress on the fish. The frequency of this sampling, however, was such that peaks and subsequent declines in plasma vitellogenin could easily have been missed. Our results clearly indicate that spawning activity could easily be overlooked with such a sampling routine since some fish for which spawning was not observed during the study were found to have residual oocytes at the final lethal sampling. It is suggested that future research that does not involve repeated collection of blood samples should monitor individuals more closely (*i.e.* at a higher frequency). Fish with largely swollen abdomens should be gently rubbed to test for the readiness of the individual to release eggs in the same manner used to monitor Atlantic halibut (Norberg *et al.*, 1991).

In conjunction with studying the vitellogenin production cycle, the monitoring of Greenland halibut in captivity provided other typically hard to obtain data. For example, tag and recapture data have recently suggested that the growth rate of Greenland halibut may be less than half of what was previously reported (Treble *et al.*, 2008), with current estimates for adult fish ranging from less than 1 cm per year (Albert *et al.*, 2009) to 3 cm per year (Treble *et al.*, 2008). Here we monitored fish over a complete year and therefore were able to provide the first data on growth in captivity. These data appear to corroborate the published tag-recapture data with growth over the year averaging 3.87 ± 1.64 cm for females that did not spawn but only 1.92 ± 1.16 cm for those females that spawned successfully, likely due to a trade-off between growth and reproduction (Roff, 1983; Lambert and Dutil, 2000; Jørgensen and Fiksen, 2006).

Failure of fish to spawn in captivity is not a novel finding, and is perhaps not unexpected for a species that has never been maintained in captivity before and for which husbandry practices have not been refined. For example, Ndjaula *et al.* (2009) reported that horse mackerel *Trachurus trachurus* held in captivity underwent vitellogenesis but did not complete oocyte maturation and did not spawn. Failure of Greenland halibut to spawn in captivity, however, is not necessarily linked to unsuitable

conditions, especially since some fish did spawn successfully. It is possible that at least some of the fish that did not spawn may have been developing for the first time but were still within their first year of development and hence did not spawn during the one year observation period. It has been suggested that this so-called adolescent period may be even longer than one year in Greenland halibut (Junquera *et al.*, 2003; Simonsen and Gundersen, 2005). For example, Junquera *et al.* (2003) reported that there was a time lag of four years between when cortical alveoli first appeared in Greenland halibut oocytes and when they first spawned. Wolffish *Anarhichas lupus* are an even more extreme case with a reported adolescent phase of 8–10 years in Icelandic waters (Gunnarsson *et al.*, 2006). It is also possible that fish started to ripen but subsequently stopped and resorbed any oocytes that had started to develop. The continuous atresia of oocytes with cortical alveoli or just beginning vitellogenesis appears to be very common for wild Greenland halibut (Fedorov, 1968; Walsh and Bowering, 1981; Junquera *et al.*, 1999; Tuene *et al.*, MS 2001) and thus would not necessarily be an artifact of captive conditions. The fact that plasma vitellogenin levels sometimes were relatively high at the start of the experiment and subsequently declined would appear to support the notion of vitellogenesis beginning and then being interrupted.

Many questions remain pertaining to Greenland halibut reproduction. The unusual oocyte development pattern has clear implications for estimating SSB and the potential for correcting previously collected data is unknown. Further work is needed to explore effective methods for estimating maturity status, the quantitative relationship between LC and DC oocytes, linkages between reproductive strategy, reproductive potential, fish energetic status and environmental conditions, and how the unusual oocyte development pattern influences the reproductive potential of Greenland halibut stocks. Continued refinements in husbandry and experimental protocols for the study of Greenland halibut in captivity should provide a means to answer some of these questions.

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References

ALBERT, O. T., M. KVALSUND, T. VOLLEN and A. SALBERG. 2009. Towards accurate age determination of Greenland halibut. *J. Northw. Atl. Fish. Sci.,* **40:** 81–95. http://dx.doi.org/10.2960/J.v40.m659

BOJE, J. 2002. Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. *Fish. Bull.,* **100:** 414–422.

BOWERING, W. R. 1984. Migrations of Greenland halibut, *Reinhardtius hippoglossoides*, in the Northwest Atlantic from tagging in the Labrador–Newfoundland region. *J. Northw. Atl. Fish. Sci.,* **5:** 85–91. http://dx.doi.org/10.2960/J.v5.a11

BOWERING, W. R. and G. R. LILLY. 1992. Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland (Northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). *Neth. J. Sea Res.,* **29:** 211–222. http://dx.doi.org/10.1016/0077-7579(92)90021-6

BUTSKAYA, N. A. and T. I. FALEEVA. 1987. Seasonal changes in the gonads and fecundity of Antarctic Fishes *Trematomus bernacchii*, *Trematomus hansoni* and *Pagothenia borchgrevinki* (Nototheniidae). *J. Ichthyol.,* **27:** 27–36.

COHEN, A. M., F. JAHOUH, S. SIOUD, R. M. RIDEOUT, M. J. MORGAN and J. H. BANOUB. 2009. Quantification of Greenland halibut serum vitellogenin: a trip from the deep sea to the mass spectrometer. *Rapid Commun. Mass Spectrom.,* **23:** 1049–1060. http://dx.doi.org/10.1002/rcm.3966

DE GROOT, S. J. 1970. Some notes on an ambivalent behaviour of Greenland halibut *Reinhardtius hippoglossoides* (Walb.). Pisces: Pleuronectiformes. *J. Fish Biol.,* **2:** 275–279. http://dx.doi.org/10.1111/j.1095-8649.1970.tb03285.x

DENNARD, S. T., B. C. MCMEANS and A. T. FISK. 2009. Preliminary assessment of Greenland halibut diet in Cumberland Sound using stable isotopes. *Polar Biol.,* **32:** 941–945. http://dx.doi.org/10.1007/s00300-009-0624-3

EVERSON, I. 1994. Timescale of ovarian maturation in *Notothenia coriiceps*; evidence for a prolonged adolescent phase. *J. Fish Biol.,* **44:** 997–1004. http://dx.doi.org/10.1111/j.1095-8649.1994.tb01271.x

FEDOROV, K. Y. 1968. Ovogenez i polovoi tsikli chernogo paltusa. *Trudy PINRO* **23**: 425–450. [Oogenesis and sexual maturity of the Greenland halibut. *Canadian Fisheries and Aquatic Sciences Translation No.* **4559***,* 1979.]

GUNDERSEN, A. C. 2003. Sexual maturity, fecundity and nursery grounds of Northeast Arctic Greenland halibut

(*Reinhardtius hippoglossoides* (Walbaum)). Ph.D. Thesis. Department of Fisheries and Marine Biology, University of Bergen, Norway.

GUNDERSEN, A. C., C. STENBERG, I. FOSSEN, B. LYBERTH, J. BOJE and O. A. JØRGENSEN. 2010. Sexual maturity cycle and spawning of Greenland halibut *Reinhardtius hippoglossoides* in the Davis Strait. *J. Fish Biol.,* **77:** 211–226. http://dx.doi.org/10.1111/j.1095-8649.2010.02671.x

GUNNARSSON, Á., E. HJÖRLEIFSSON, K. THÓRARINSSON and G. MARTEINSDOTTIR. 2006. Growth, maturity and fecundity of wolffish *Anarhichas lupus* L. in Icelandic waters. *J. Fish Biol.,* **68:** 1158–1176. http://dx.doi.org/10.1111/j.0022-1112.2006.00990.x

GUZMÁN, J. M., B. NORBERG, J. RAMOS, C. C. MYLONAS and E. L. MAÑANÓS. 2008. Vitellogenin, steroid plasm levels and spawning performance of cultured female Senegalese sole (*Solea senegalensis*). *Gen. Comp. Endocrinol.,* **156:** 285–297. http://dx.doi.org/10.1016/j.ygcen.2008.02.002

JØRGENSEN, C. and Ø. FIKSEN. 2006. State–dependent energy allocation in cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.,* **63:** 186–199. http://dx.doi.org/10.1139/f05-209

JUNQUERA, S., E. ROMÁN, M. J. MORGAN, M. SAINZA and G. RAMILO. 2003. Time scale of ovarian maturation in Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum). *ICES J. Mar. Sci.,* **60:** 767–773. http://dx.doi.org/10.1016/S1054-3139(03)00073-0

JUNQUERA, S., E. ROMÁN, X. PAZ and G. RAMILO. 1999. Changes in Greenland halibut growth, condition and fecundity in the Northwest Atlantic (Flemish Pass, Flemish Cap and Southern Grand Bank). *J. Northw. Atl. Fish. Sci.*, **25:** 17–28. http://dx.doi.org/10.2960/J.v25.a2

JUNQUERA, S. and F. SABORIDO-REY. MS 1995. Histological assessment of sexual maturity in the Greenland halibut in Div. 3LM. *NAFO SCR Doc.*, No. 28, Serial No. N2537, 9 p.

JUNQUERA, S. and J. ZAMARRO. MS 1992. Sexual maturity and spawning of the Greenland halibut (*Reinhardtius hippoglossoides*) from Flemish Pass area. *NAFO SCR Doc.*, No. 41, Serial No. N2092, 10 p.

KENNEDY, J., A. C. GUNDERSEN, Å. HØINES and O. S. KJESBU. 2011. Greenland halibut (*Reinhardtius hippogolossoides*) spawn annually but successive cohorts of oocytes develop over two years, complicating correct assessment of maturity. *Can. J. Fish. Aquat. Sci.,* **68:** 201–209. http://dx.doi.org/10.1139/F10-149

LAMBERT, Y. and J. D. DUTIL. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Can. J. Fish. Aquat. Sci.,* **57:** 815–825. http://dx.doi.org/10.1139/f00-022

LAU, T. Y., B. C. COLLINS, P. STONE, N. TANG, W. M. GALLAGHER and S. R. PENNINGTON. 2011. Absolute quantification of toxicological biomarkers by multiple reaction monitoring. *Methods Mol. Biol.,* **691:** 417–427. http://dx.doi.org/10.1007/978-1-60761-849-2_25

LV, X., J. SHAO, Q. ZHOU, M. SONG and G. JIANG. 2009. Circannual vitellogenin levels in Chinese loach (*Misgurnus anguillicaudatus*). *Environ. Biol. Fishes,* **85:** 23–29. http://dx.doi.org/10.1007/s10641-007-9310-x

MANDICH, A., A. MASSARI, S. BOTTERO, P. PIZZICORI, H. GOOS and G. MARINO. 2004. Plasma sex steroid and vitellogenin profiles during gonad development in wild Mediterranean amberjack (*Seriola dumerilii*). *Mar. Biol.,* **144:** 127–138. http://dx.doi.org/10.1007/s00227-003-1185-6

MATTSON, N. S. and T. H. RIPLE. 1989. Metomidate, a better enesthetic for cod (*Gadus morhua*) in comparison with benzocaine, MS–222, chlorobutanol, and phenoxyethanol. *Aquaculture,* **83:** 89–94. http://dx.doi.org/10.1016/0044-8486(89)90063-X

METHVEN, D. A., L. W. CRIM, B. NORBERG, J. A. BROWN, G. P. GOFF and I. HUSE. 1992. Seasonal reproduction and plasma levels of sex steroids and vitellogenin in Atlantic halibut (*Hippoglossus hippoglossus*). *Can. J. Fish. Aquat. Sci.,* **49:** 754–759. http://dx.doi.org/10.1139/f92-084

MOSCONI, G., O. CARNEVALI, R. CARLETTA, M. NABISSI and A. M. POLZONETTI-MAGNI. 1998. Gilthead seabream (*Sparus aurata*) vitellogenin: Purification, partial characterization, and validation of an enzyme-linked immunosorbent assay. *Gen. Comp. Endocrinol.*, **110:** 252–261. http://dx.doi.org/10.1006/gcen.1998.7075

MURUA, H. and F. SABORIDO-REY. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *J. Northw. Atl. Fish. Sci.,* **33:** 23–31. http://dx.doi.org/10.2960/J.v33.a2

NAFO, 2011. Part B – Report of the June Meeting. *NAFO Scientific Council Reports,* 2010.

NDJAULA, H. O. N., T. HANSEN, M. KRÜGER-JOHNSEN and O. S. KJESBU. 2009. Oocyte development in captive Atlantic horse mackerel *Trachurus trachurus*. *ICES J. Mar. Sci.,* **66:** 623–630. http://dx.doi.org/10.1093/icesjms/fsp032

NORBERG, B., V. VALKNER, J. HUSE, I. KARLSEN and G. L. GRUNG. 1991. Ovulatory rhythms and egg viability in the Atlantic halibut (*Hippoglossus hippoglossus*). *Aquaculture,* **97:** 365–371. http://dx.doi.org/10.1016/0044-8486(91)90328-5

RIDEOUT, R. M., D. M. MADDOCK and M. P. M. BURTON. 1999. Oogenesis and the spawning pattern in Greenland halibut from the Northwest Atlantic. *J. Fish Biol.,* **54:** 196–207. http://dx.doi.org/10.1111/j.1095-8649.1999.tb00623.x

RIGET, F. and J. BOJE. 1989. Fishery and some biological aspects of Greenland halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. *NAFO Sci. Coun. Studies* **13:** 41–52.

ROFF, D. A. 1983. An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.,* **40:** 1395–1404. http://dx.doi.org/10.1139/f83-161

SHANDIKOV, G. A. and T. I. FALEEVA. 1992. Features of gametogenesis and sexual cycles of six notothenoid fishes from East Antarctica. *Polar Biol.,* **11:** 615–621. http://dx.doi.org/10.1007/BF00237956

SIL'YANOVA, Z. S. 1981. Oogenesis and stages of maturity of fishes of the familiy nototheniidae. *J. Ichthyol.,* **21:** 81–89.

SIMON, R., G. JUBEAUX, A. CHAUMOT, J. LEMOINE, O. GEFFARD and A. SALVADOR. 2010. Mass spectrometry as an alternative to the enzyme-linked immunosorbent assay test for biomarker quantitation in ecotoxicology: Application to vitellogenin in Crustacea (*Gammarus*

fossarum). *J. Chromatrogr. A,* **1217:** 5109–5115. http://dx.doi.org/10.1016/j.chroma.2010.06.015

SIMONSEN, C. S. and A. C. GUNDERSEN. 2005. Ovary development in Greenland halibut *Reinhardtius hippoglossoides* in west Greenland waters. *J. Fish Biol.,* **67:** 1299–1317. http://dx.doi.org/10.1111/j.1095-8649.2005.00825.x

SPECKER, J. L. and C. V. SULLIVAN, 1994. Vitellogenesis in fishes: status and perspectives. *In:* Perspective in Comparative Endocrinology. Davey, K. G., Peter, R. E. and Tobe, S. S., (eds). National Research Council Canada, Ottawa, Canada, p. 304–315.

SUN, B. and N. W. PANKHURST. 2003. Correlation between oocyte development and plasma concentrations of steroids and vitellogenin in greenback flounder *Rhombosolea tapirina*. *Fish Physiol. Biochem.,* **28:** 367–368. http://dx.doi.org/10.1023/B:FISH.0000030592.83257.59

TEMPLEMAN, W. 1973. Distribution and abundance of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Northwest Atlantic. *ICNAF Res. Bull.,* **10:** 83–98.

TEMPLEMAN, W., V. M. HODDER and R. WELLS. 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. *ICNAF Res. Bull.,* **13:** 53–65.

TREBLE, M. A., S. E. CAMPANA, R. J. WASTLE, C. M. JONES and J. BOJE. 2008. Growth analysis and age validation of a deepwater Arctic fish, the Greenland halibut (*Reinhardtius hippoglossoides*). *Can. J. Fish. Aquat. Sci.,* **65:** 1047–1059. http://dx.doi.org/10.1139/F08-030

TUENE, S., A. C. GUNDERSEN, W. EMBLEM, I. FOSSEN, J. BOJE, P. STEINGRUND and L. H. OFSTAD. MS 2001. Maturation and occurrence of atresia in oocytes of Greenland halibut (*Reinhardtius hipploglossoides*, Walbaum). *NAFO SCR Doc.*, No. 166, Serial No. N4561, 12 p.

TYLER, C. R., SANTOS, E. M. and PRAT, F. 2000. Unscrambling the egg-cellular, biochemical, molecular and endocrine advances in oogenesis. *In:* Proceedings of the 6th International Symposium on the Reproductive Physiology of Fish. Norberg, B., Kjesbu, O. S., Taranger, G. L., Andersson, E. and Stefansson, S. O., (eds). Bergen: Fish Symp 99, p. 273–280.

TYLER, C. R. and J. P. SUMPTER. 1996. Oocyte growth and development in teleosts. *Rev. Fish Biol. Fish.,* **6:** 287–318. http://dx.doi.org/10.1007/BF00122584

VOLLEN, T. and O. T. ALBERT. 2008. Pelagic behaviour of adult Greenland halibut (*Reinhardtius hippoglossoides*). *Fish. Bull.,* **106:** 457–470.

WALLACE, R. A. 1985. Vitellogenesis and oocyte growth in non-mammalian vertebrates. *In:* Developmental Biology: A Comprehensive Synthesis. **Vol. 1.** *Oogenesis*. Browder, L. W., (ed). New York: Plenum Press, p. 127–177.

WALLACE, R. A. and K. SELMAN. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *Amer. Zool.,* **21:** 325–343.

WALSH, S. J. and W. R. BOWERING. 1981. Histological and visual observations on oogenesis and sexual maturity in Greenland halibut off northern Labrador. *NAFO Sci. Coun. Studies,* **1:** 71–75.

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Demersal Fishes Caught with Bottom Gillnets and Baited Gears at 500–2 800 m on the Continental Slope off Nova Scotia, Canada

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Abstract

Fishing trials with bottom fixed gears (primarily gillnets but also shrimp and crab traps and longlines) were conducted on the continental slope off Nova Scotia in August 1991. Fishing was conducted at several depths between 500 and 2800 m in two areas, one on the open slope south of Emerald Bank and the other at the mouth of The Gully, a large canyon. Catches by gillnets accounted for about 90% of the total and were predominated by deepwater chimaera (*Hydrolagus affinis*), black dogfish (*Centroscyllium fabricii*) and Portuguese shark (*Centroscymnus coelolepis*). The most frequently caught species in traps were snubnose eel (*Simenchelys parasitica*) and abyssal grenadier (*Coryphaenoides armatus*). Variations in catches by depth and area are described, and comparisons are made with catches from otter trawl surveys at similar depths with regard to the most prominent species caught and their size compositions.

Keywords: Deep sea, fixed gears, exploratory fishing, The Gully, Emerald Bank.

Introduction

The use of non-trawl gears in deepwater fisheries conducted in various areas around the world was documented in a review of the commercial potential of deepwater resources off Atlantic Canada commissioned by the Canadian Department of Fisheries and Oceans (DFO) Maritimes Region. The review report (Pohle *et al*., 1992) suggested that inclusion of fixed gears in exploratory fishing programs in Canadian waters, for both fishes and invertebrates, was worthy of consideration. In response, DFO conducted fishing trials using a variety of fixed gears on the Scotian Shelf slope, south of Nova Scotia, in 500–2800 m in August 1991. The present paper reports on the fish catches made during these trials.

The primary purpose of the venture was developmental – to examine the practicalities of fishing fixed gears of various types and sizes in deep water and to determine their success in catching fish and crustaceans. However, the results are also of scientific interest as fishing was conducted, in large degree, according to a sampling design that was stratified by depth and area of fishing. This allows an account to be given of the composition of the fish fauna on the continental slope as portrayed by fixed gears, and for comparisons to be made with catches from otter trawl surveys conducted at similar depths.

Methods

Gear trials were conducted from the DFO research vessel Alfred Needler, a 50 m stern otter trawler, during 7–12 August 1991 (cruise designation - N156). Gears deployed were primarily bottom gillnets but included crab and shrimp traps and bottom longlines.

Gillnets were of nylon; the smallest used (6.0–8.9 cm mesh sizes, multifilament twine) were typical herring and mackerel fishing nets, the midsized nets (14.0–17.8 cm mesh sizes, monofilament twine) were those used for groundfish fishing and the largest (26.7 cm mesh size) was a lumpfish (*Cyclopterus lumpus*) net. Table 1 gives net specifications and the number of times each was fished. Mesh sizes were rounded to the nearest cm for data presentation and the 14.0 and 15.2 cm mesh data were amalgamated and presented as being for 15 cm mesh nets.

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Table 1. Number of nets set and gear specifications of gill nets used.

No. of nets set	Mesh sizes, stretched (cm)	Length of nets, stretched (m)	No. of vertical meshes
34	14.0 and 15.2	183	25
7	6.0–8.9	69	100–150
3	17.8	183	25
2	26.7	110	10

This amalgamation was justified by the observation that the numbers caught of each species were very similar for these mesh sizes and so too were the average lengths and weights of the most commonly caught species (Table 2). *Centroscymnus coelolepis* was an exception with larger sizes apparently being caught in 15.2 cm nets. However, this appeared attributable to an imbalance in the number of nets of each size fished at 1350 m in the Gully where particularly large specimens of this species were caught (see results).

Crab traps had a 100 kg conical steel frame (base diameter about 2 m) covered by 75 mm mesh polyethylene netting and equipped with four plastic entrance cones on top with minimum openings of about 35 cm. Shrimp traps were of steel mesh construction (1.27 cm bar length), rectangular in shape (about 75 cm long, 60 cm wide and 30 cm high) and equipped with entrances (of 2.5 or 5 cm minimum width) located either on top or on the side. Traps were baited with herring, squid or both, sometimes supplemented with other species. Twenty-three crab traps and 33 shrimp traps were set in total.

Longlines were deployed only once due to technical difficulties. The string consisted of Mustad circle hooks of sizes 10/0 (100 hooks), 12/0 (100 hooks) and 14/0 (200 hooks) baited with squid.

Table 2. Average lengths (L, cm) and weights (W, kg) of the six most abundant species caught by the two main gillnet mesh sizes fished and by area. (N – number of observations, NA – insufficient specimens from Emerald for comparison.)

Species		Gillnet mesh size (cm)		Area	
		14.0	15.2	Emerald	Gully
Hydrolagus affinis	L	107	106	105	107
	W	7.7	7.5	6.7	8.1
	(N)	(48)	(54)	(38)	(64)
Centroscymnus coelolepis	L	78	82	74	96
	W	3.3	4.5	2.5	7.6
	(N)	(53)	(114)	(114)	(53)
Centroscyllium fabricii	L	62	61	60	64
	W	1.2	1.3	1.1	1.4
	(N)	(253)	(237)	(306)	(184)
Macrourus berglax	L	60	59		
	W	1.4	1.4	NA	NA
	(N)	(37)	(53)		
Antimora rostrata	L	58	59	58	58
	W	1.5	1.8	1.6	1.7
	(N)	(30)	(53)	(23)	(60)
Reinhardtius hippoglossoides	L	60	61	59	61
	W	2.3	2.1	1.9	2.3
	(N)	(29)	(45)	(22)	(52)

Gears were usually set in arrays consisting of either four gillnets or of two crab traps along with up to five shrimp traps. When setting gillnets, the sequence was to attach an anchor, consisting of 45 kg of chain, to a 180 m rope, the other end of which was attached to one end of the net array. The other end of the array was attached, by a 180 m or 360 m rope to another chain anchor, weighing 45–90 kg. From this anchor, a vertical rope extended to a buoy at the surface. The nets were attached to a headline consisting of 16 mm diameter poly-rope and to a ground line of 10 mm diameter No. 33 lead rope. Traps were set about 30 m apart along the ground line. Because of their weight, no anchors were considered to be necessary. Indeed, for several tows, a mixed array of gillnets and traps was deployed, the traps being set at either end to serve as anchors.

The setting and hauling of gear did not follow a fixed schedule but setting occurred most commonly in the afternoon or evening. For both gillnets and traps, soak times ranged from 11 to 43 hours but were 22–25 hours in half the cases and the modal value was 24 hours. The effect of soak time on catches is unpredictable and may be negligible (Bérubé *et al*., 2000). Thus, variations in soak time are ignored in the present analysis.

Sampling occurred in two areas, one south of Emerald Bank and one in The Gully (Fig. 1). The 15 cm gillnets and the traps were set in both areas but the other sizes of gillnet were set only in The Gully and longlines only off Emerald Bank. In each area, gears were set at depths of approximately 500, 900, 1350, 1800 and 2800 m. In total, 21 gear arrays were set but in three cases the gear was lost.

Water temperature data were collected using expendable bathythermographs. Three casts were made at each of the sampling areas, over bottom depths of about 400, 700 and 1700 m (about the maximum range of the instruments used), to provide estimates of near bottom temperatures at the depths fished.

Results

Water temperature

Temperatures near bottom at 500 m, the shallowest depth fished, were about 4.9°C in The Gully and 5.3°C off Emerald Bank. Temperatures converged with increasing depth and at 1700 m, were about 3.5°C in both areas. Thus, at the same depths, temperatures in The Gully were slightly lower than south of Emerald Bank to a depth of 1700 m, but likely the same at deeper depths.

Catches by all gears

Catches were comprised of about 1400 specimens weighing 3.1 metric tons. Scientific and common names

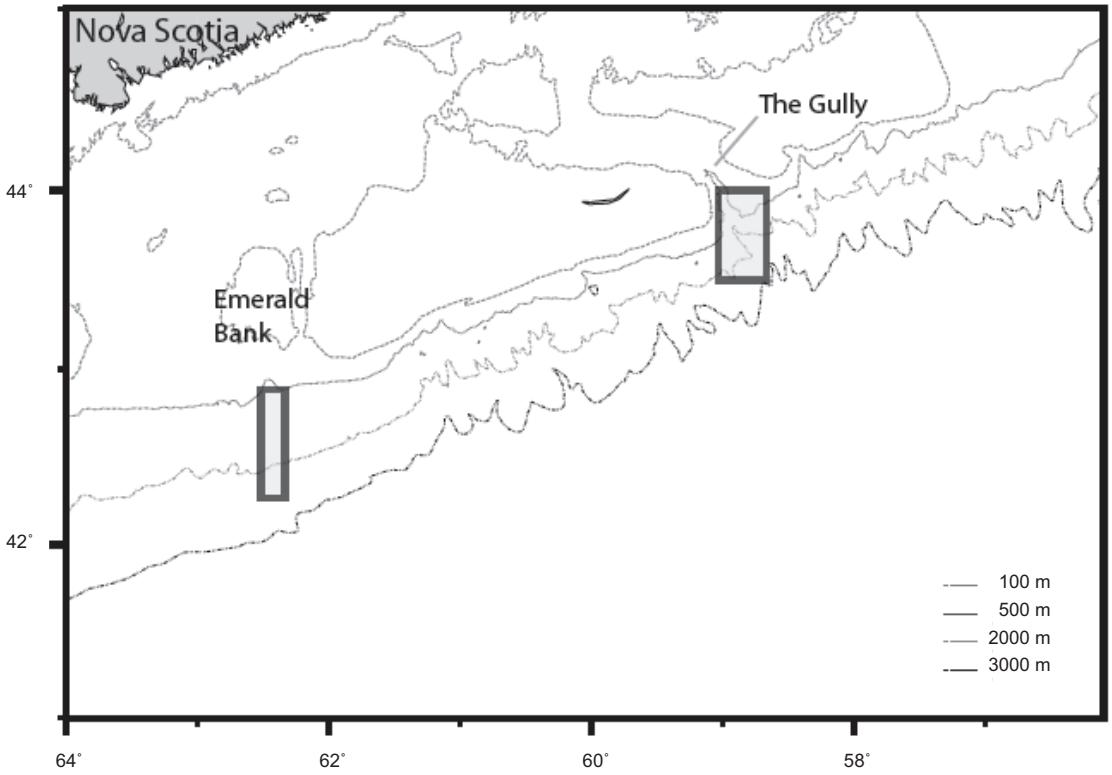

Fig. 1. Areas fished by the Alfred Needler in August 1991.

of the 21 taxa represented in these catches, the number and weight caught of each, and the depth range within which each was caught, are given in Table 3. None of the taxa represented new records for the area. *Centroscyllium fabricii* was dominant in catches numerically, comprising 43%. In terms of weight, however, *C. coelolepis* contributed about the same amount as *C. fabricii* and *Hydrolagus affinis* contributed more. Collectively, these three species accounted for 63% of catches by number and 73% by weight. The great majority of catches were taken in gillnets (87% by no. and 96% by wt.).

Catches by 15 cm mesh gillnets

The 15 cm mesh gillnets were the most extensively deployed. Four nets were fished at 900, 1350 and 1800 m in each sampling area, except that, at 1350 m in The Gully, seven nets were fished. Thus, for presentation, the data from The Gully/1350 m depth stratum were adjusted by x0.57 to standardize to a four-net unit. In addition, an array of 3 nets was fished at 2800 m in The Gully but only three fish were caught in those, one each of *H. affinis*, *Macrourus berglax* and *Antimora rostrata*, suggesting

Table 3. Fish taxa caught during fixed gear fishing by the Alfred Needler, August 1991, by number and weight, and their depth of capture. (D_{min} and D_{max} are the minimum and maximum depths fished during sets in which the taxon was caught.)

Order/Species	Common name	No.	Wt. (kg)	D_{min} (m)	D_{max} (m)
Petromyzontiformes					
Myxine glutinosa	Atlantic hagfish	5	1	967	967
Chimaeriformes					
Hydrolagus affinis	Deepwater chimaera	107	821	889	2 800
Harriotta raleighana	Longnose chimaera	6	11	993	1 500
Squaliformes					
Centroscyllium fabricii	Black dogfish	585	714	790	1 500
Centroscymnus coelolepis	Portuguese shark	170	711	914	1 843
Etmopterus princeps	Rough sagre	74[1]	150	950	1 306
Rajiformes					
Bathyraja spinicauda	Spinytail skate	1	28	1 843	1 843
Amblyraja jenseni	Shorttail skate	4	23	914	1 843
Albuliformes					
Notacanthus chemnitzii	Snubnosed spiny eel	2	1	790	914
Anguilliformes					
Simenchelys parasitica	Snubnose eel	68	17	485	1 500
Osmeriformes					
Alepocephalidae NS	Smoothheads	1	1	993	993
Gadiformes					
Coryphaenoides armatus	Abyssal grenadier	33	17	2 743	2 800
Macrourus berglax	Roughhead grenadier	110	144	889	2 800
Nezumia bairdi	Marlinspike	4	+	790	914
Antimora rostrata	Blue hake	97	158	790	2 800
Gaidropsarus ensis	Threebeard rockling	1	1	914	914
Urophycis tenuis	White hake	4	11	914	993
Scorpaeniformes					
Sebastes sp.	Redfish NS	1	1	790	790
Perciformes					
Anarhichas denticulatus	Northern wolfish	4	36	914	1 500
Pleuronectiformes					
Hippoglossus hippoglossus	Atlantic halibut	1	26	993	993
Reinhardtius hippoglossoides	Greenland halibut	103	225	889	1 843

[1]For one net, only catch weight was recorded - catch number for this net was estimated based on average weight of fish in the other three nets in array.

a gear malfunction and these results are not considered comparable to those at shallower depths.

The number of fish caught in 15 cm gillnets in The Gully was 25% fewer than off Emerald Bank for the same fishing effort (12 nets set per area), but the weight of fish caught was 10% greater (Table 4). *Centroscymnus coelolepis, C. fabricii* and *Etmopterus princeps* were all much less numerous in The Gully catches and increased abundance of *H.affinis* and several other species in The Gully did not fully compensate, numerically, for these reductions. However, average weights of the main species caught were greater in catches from The Gully than in catches from off Emerald Bank (Table 2). *Centroscymnus coelolepis* was particularly influential, being 30% longer and three times heavier in Gully catches.

Total numbers caught per unit of effort (*i.e.* per eight nets set) decreased with depth, at 1800 m being only 40% of that at 900 m, but weight caught increased with depth, at 1800 m being 40% higher than that at 900 m. Thus, the average weight of an individual fish caught increased with depth, from 1.5 kg at 900 m to 5 kg at 1800 m (Table 4). This difference by depth in the ratio of overall weight to numbers caught was attributable largely to replacement of the relatively small-bodied species *C. fabricii* and *E. princeps* that dominated the 900 m zone with lesser numbers of the much larger *H. affinis* at greater depths (Table 4). Also, in some species, mean weight increased with depth, *e.g. C. coelolepis* and *Reinhardtius hippoglossoides*, but did not in others, *e.g. M. berglax* and *A. rostrata*.

Length frequencies of the six most commonly caught species (Fig. 2) show that few fish smaller than 40 cm were caught. Specimens of the largest species in catches, *H. affinis*, were 80–142 cm long.

Catches by gillnets with other mesh sizes

Small numbers of nets with mesh sizes of 6–9, 18 and 27 cm were fished in 900–1350 m in The Gully and their catches are compared to those of the 15 cm mesh nets at 900 m at this location (Table 5). No attempt is made to standardize for the different sizes of nets but it can be concluded that the 18 cm mesh nets did not differ greatly from the 15 cm nets in species, or numbers, caught whereas the substantially larger 27 cm net caught very little. Catches in the small mesh nets differed by including a number of small-bodied species, *Notacanthus chemnitzi*, *Nezumia bairdi, Gaidropsarus ensis* and *Sebastes* sp., while failing to catch any of the larger-bodied *R. hippoglossoides*.

Table 4. Numbers of each species caught in 15 cm mesh gillnets by area and depth (m), average weight (kg) of each species by depth and total weight caught by area and depth (Statistics by area are per 12 nets and by depths are per eight nets.)

Species	Number by Area		Number by Depth			Average Weight by Depth		
	Emerald	Gully[1]	900	1 350[1]	1 800	900	1 350	1 800
Hydrolagus affinis	38	55	1	12	80	6.7	7.4	7.5
Harriotta raleighana	2	2	2	2	–	0.8	2.6	–
Centroscymnus coelolepis	114	41	–	105	50	–	3.5	4.3
Centroscyllium fabricii	306	163	342	127	–	1.2	1.2	–
Etmopterus princeps	55	1	53	3	–	2.5	1.2	–
Bathyraja spinicauda	–	1	–	–	1	–	–	27.7
Amblyraja jenseni	1	2	–	1	2	–	2.0	6.3
Simenchelys parasitica	1	–	–	1	–	–	0.3	–
Alepocephalidae NS	1	–	1	–	–	1.4	–	–
Macrourus berglax	7	62	30	33	6	1.4	1.5	0.9
Antimora rostrata	22	53	2	22	51	1.9	1.4	1.8
Urophycis tenuis	3	1	4	–	–	2.8	–	–
Hippoglossus hippoglossus	1	–	1	–	–	26.0	–	–
Reinhardtius hippoglossoides	22	40	35	23	4	1.6	2.4	5.5
Total numbers:	573	422	471	330	194	Overall Average Weight		
Total weights (kg):	1 145	1 288	694	761	978	1.5	2.3	5.0

[1]Numbers at 1350 m in The Gully are adjusted by 0.57 to standardize effort with other sampling units.

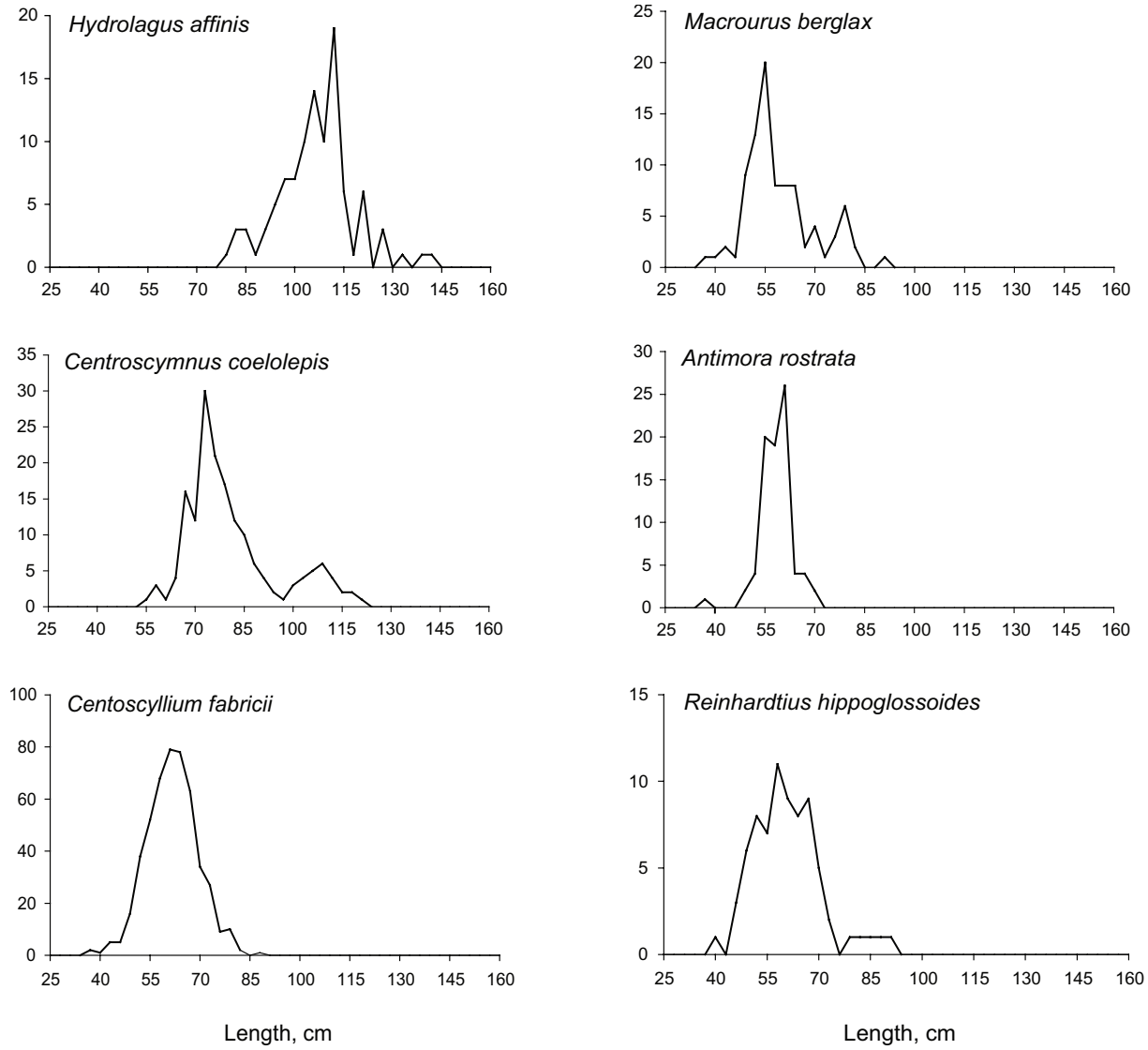

Fig. 2. Numbers caught at length for the six most frequently caught species in 15 cm gillnets. (Note that y-axis scale varies by species.)

Catches by longline

The single longline set at 950 m south of Emerald Bank caught primarily *C. fabricii* and *E. princeps* (Table 6), as did gillnets at this location. The smallest hooks (10/0) were the most successful in catching these species whereas the largest (14/0) hooks caught only *C. fabricii*, and in lesser numbers than the smaller hooks despite twice as many 14/0 hooks being set compared to the smaller sizes.

Catches by crab and shrimp traps

Crab and shrimp traps were fished at four or five depths in both locations, although in small numbers (Table 7). Trap catches were composed in large part of species not taken by gillnets and longlines. *Coryphaenoides armatus* and *Anarhichas denticulatus* were caught only in crab traps (except for one *C. armatus* in a shrimp trap). Shrimp traps provided the only records of *Myxine glutinosa* and accounted for the great majority of *Simenchelys parasitica* catches (61 of 68 fish, five more coming from crab traps and one each from gillnets and longlines).

Discussion

The primary objective of the present exploratory deep-water fishing operation was to test-fish a wide variety of fixed gear types and sizes, but the main gillnet gear tested (15 cm mesh), and crab and shrimp traps, were fished in general conformity with an area/depth stratified sampling design. This allows broad inferences to be made about the composition and spatial distribution of the demersal fish fauna on the slope off Nova Scotia that is available to fixed gears. The other fixed gear fishing experiments that have

Table 5. Numbers caught by species in gillnets of different mesh size fished at similar depths in The Gully.

Mesh Size (cm)	6–9	15	18	27
No. of Nets Fished	7	4	3	2
Depth Fished (m)	900	900	900–1 350	900
Hydrolagus affinis	–	1	–	–
Harriotta raleighana	–	–	1	–
Centroscymnus coelolepis	–	–	2	–
Centroscyllium fabricii	11	137	48	1
Etmopterus princeps	1	–	4	–
Amblyraja jenseni	1	–	–	–
Notacanthus chemnitzii	1	–	–	–
Macrourus berglax	13	30	6	1
Nezumia bairdi	4	–	–	–
Antimora rostrata	6	2	2	–
Gaidropsarus ensis	1	–	–	–
Urophycis tenuis	–	1	–	–
Sebastes sp.	1	–	–	–
Reinhardtius hippoglossoides	–	21	24	1
Totals:	39	192	87	3

Table 6. Numbers caught by species on longlines with different hook sizes at 950m south of Emerald Bank.

Hook size (circle)	10/0	12/0	14/0
Number of hooks	100	100	200
Centroscyllium fabricii	16	12	8
Etmopterus princeps	17	–	–
Simenchelys parasitica	1	–	–
Reinhardtius hippoglossoides	3	–	–

been conducted in deep water in the Northwest Atlantic were in more northern areas, Davis Strait (Jørgensen, 1995) and Flemish Pass (Murua and de Cárdenas, 2005), and these used longlines only (a gear not deployed successfully during the present trials).

Variations in the catches of 15 cm gillnets were observed between areas and among depths sampled. There were differences between areas in the relative abundance of species, in species catch rates and in the average sizes of species. These areas are separated by only 4° of longitude and the amount of sampling was minimal, so the differences noted could be largely a reflection of sampling variation. Nonetheless, the areas are topographically different, the eastern sampling area being at the mouth of The Gully, the largest canyon on the east coast of North America (designated by the Canadian Government as a protected area in 2004), whereas south of Emerald Bank sampling was in an area of open slope (and the few near bottom temperature observations made suggest that the water was slightly warmer at fishing depths in the latter area). It is possible therefore that present results do indeed reflect local differences in faunal characteristics. With depth, total numbers caught declined but total weight caught increased. This reflected changes in species composition, the small-bodied species that occurred in abundance at the shallowest stations being replaced at deeper stations by less abundant but larger-bodied species.

Gillnets of sizes other than 15 cm were not fished frequently enough to allow for more than the following speculations

Table 7. Numbers caught by species, area and depth in crab and shrimp traps. (Number of traps set is in parentheses.)

Crab traps – South of Emerald Bank					
Depth in metres (no. of traps)	500 (2)	900 (2)	1 350 (2)	1 800 (2)	2 800 (2)
Coryphaenoides armatus	–	–	–	–	26
Antimora rostrata	–	–	–	2	–
Crab traps – The Gully					
Depth in metres (no. of traps)	–	900 (4)	1 350 (2)	1 800 (1)	2 800 (1)
Simenchelys parasitica		–	5	–	–
Coryphaenoides armatus		–	–	–	6
Antimora rostrata		–	1	4	–
Anarhichas denticulatus		3	1	–	–
Reinhardtius hippoglossoides		–	1	–	–
Shrimp traps – South of Emerald Bank					
Depth in metres (no. of traps)	500 (5)	900 (5)	1 350 (3)	1 800 (3)	2 800 (5)
Centroscymnus coelolepis	–	–	–	1	–
Simenchelys parasitica	8	19	4	–	–
Coryphaenoides armatus	–	–	–	–	1
Shrimp traps – The Gully					
Depth in metres (no. of traps)	–	900 (4)	1 350 (2)	1 800 (1)	2 800 (1)
Myxine glutinosa		5	–	–	–
Notacanthus chemnitzii		1	–	–	–
Simenchelys parasitica		18	12	–	–

about how catches in these might differ. Indications were that gillnets smaller than 15 cm would catch a greater diversity of small-bodied species, whereas nets with meshes larger than 15–18 cm would catch progressively fewer of the same species caught in these nets.

The crab and shrimp traps were fished to determine the abundance of various crustacean species that had been identified by Pohle *et al*. (1992) as potential candidates for commercial exploitation, but almost no invertebrate species were caught in these other than the deep-sea red crab (*Chaceon quinquedens*) (Halliday and Cooper, 1991), for which there was already an established fishery. However, the data on fish bycatches in these traps provide additional information on the abundance of some species. The species caught in traps were benthic scavengers. While these included specimens of several species that were caught frequently also in 15 cm gillnets, *e.g. A. rostrata*, traps (shrimp traps in particular) accounted for virtually all catches of the slender-bodied species *M. glutinosa* and *S. parasitica*. Although *C. armatus* also was caught only in traps, all catches were from those set at 2800 m. This species has a minimum depth limit of about 2000 m (King *et al*., 2006). Thus, its absence from gillnet catches could be due to the failure to fish gillnets successfully below about 1800 m. *Anarhichas denticulatus* was the only large-bodied species (four fish, 67–104 cm) caught only in traps when traps and gillnets were fished on the same gear string.

All of the species caught during the fixed gear fishing trials described here have been caught previously in otter trawl surveys on the Scotian Shelf slope (Markle *et al*., 1988; Halliday *et al*., 2012). However, there were substantial differences between fixed and mobile gears in the relative importance of species in catches, and in species size compositions.

The relative contributions, by weight, of the top five species caught in gillnets are compared in Fig. 3 to those of the top five species in the otter trawl catches made by Halliday *et al.* (2012). The percentages contributed

to the total catch by *C. fabricii* and *R. hippoglossoides* were similar between gears. However, *H. affinis* and *C. coelolepis*, dominant species in gillnet catches, were of much lesser relative importance in trawl catches. Conversely, *Coryphaenoides rupestris*, a co-dominant with *C. fabricii* in trawl catches, and *Alepocephalus agassizii*, were completely absent from gillnet catches (except that the one unidentified alepocephalid could have been an *A. agassizii*).

Mean, minimum and maximum lengths of the six species caught in most abundance in 15 cm gillnets are compared with the same statistics for catches of these species in otter trawls (Table 8). Mean lengths were greater in gillnet catches than in small mesh otter trawl catches in four cases. Minimum sizes of these four species in gillnet catches were substantially higher than in otter trawl catches, as would be expected, but maximum sizes were also higher. However, mean sizes of *M. berglax* and *R. hippoglossoides* were similar between gears, likely indicating a scarcity of small fish of these species on the Scotian Shelf slope (Halliday *et al*., 2012).

Despite these differences in species importance, and in species size compositions, between gillnet and otter trawl surveys, both demonstrate the importance of Chimaeriformes and sharks in the Scotian Slope fauna. These groups comprised about one third of the numbers and almost half the weight in the otter trawl catches of Halliday *et al*. (2012), and 70% by number and 80% by weight in present gillnet catches. The large mesh size of most gillnets fished in the present study likely causes the relative importance in the fauna of these large-bodied species to be over-emphasized. Conversely, the paucity of records of these species in otter trawl surveys of the slope fauna in adjacent areas (Markle and Musick, 1974; Haedrich *et al*., 1975; Sulak, 1982; Snelgrove and Haedrich, 1985) is likely attributable to a low vulnerability to the small trawls used.

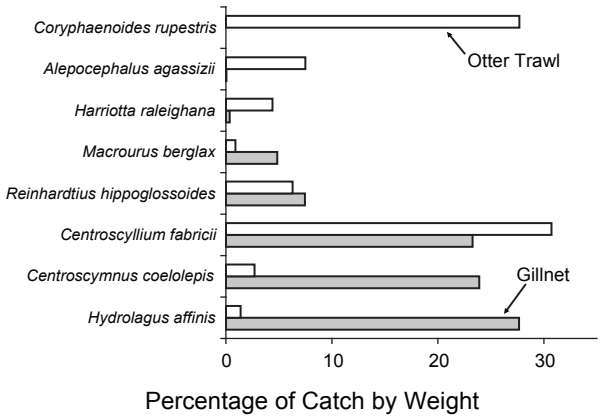

Fig. 3. The relative contributions, by weight, of the top five species caught in all gillnets compared to the relative contributions of the top five species to otter trawl catches made on the Scotian Shelf Slope at similar depths (Halliday *et al*., 2012)

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Table 8. Mean, minimum and maximum lengths (cm) of the six most abundant species caught in 15 cm gillnets compared to those of catches by small mesh otter trawl (Halliday *et al.*, 2012).

Species	15 cm Gillnet			Otter Trawl (with small mesh liner)		
	Mean	Min	Max	Mean	Min	Max
Hydrolagus affinis	106	80	142	78	23	132
Centroscymnus coelolepis	81	56	120	70	49	100
Centroscyllium fabricii	62	36	88	51	14	84
Macrourus berglax	59	40	91	61	26	98
Antimora rostrata	58	37	69	41	7	65
Reinhardtius hippoglossoides	61	40	90	64	29	88

References

BÉRUBÉ, M., H. BOURDAGES and A. FRÉCHET. MS 2000. Effects of soak time on catch per unit effort using longline and gillnets for the Northern Gulf of St. Lawrence cod stock. Canadian Science Advisory Secretariat (CSAS) Research Document, 2000/150: 28 p.

HAEDRICH, R. L., G. T. ROWE and P. T. POLLONI. 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *J. Mar. Res.*, **33**: 191–212.

HALLIDAY, R. G. and C. COOPER. 1991. Exploration of deepwater resources off the Scotian Shelf. DFO Scotia-Fundy Region, Halifax, N.S., Project Summary, No. 32, Dec. 1991: 4 p.

HALLIDAY, R.G., L. VAN GUELPEN and D. E. THEMELIS. 2012. Demersal fish fauna of the continental slope off Nova Scotia, Canada, based on exploratory bottom trawl surveys in 1994–95. *J. Northw. Atl. Fish. Sci.,* **44**, 41–60. doi:10.2970/J.v44.m681

JØRGENSEN, O. A. 1995. A comparison of deep water trawl and long-line research fishing in the Davis Strait. *In*: Deep-water fisheries of the North Atlantic oceanic slope, A. G. Hopper (ed.) Kluwer Academic Publishers, p. 235–250.

KING, N. J., P. M. BAGLEY and I. G. PRIEDE. 2006. Depth zonation and latitudinal distribution of deep-sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42° to 53°N. *Mar Ecol Prog Ser*, **319**: 263–274. http://dx.doi.org/10.3354/meps319263

MARKLE, D. F., M. J. DADSWELL and R. G. HALLIDAY. 1988. Demersal fish and decapod crustacean fauna of the upper continental slope off Nova Scotia from LaHave to St. Pierre Banks. *Can. J. Zool.*, **66**: 1952–1960. http://dx.doi.org/10.1139/z88-286

MARKLE, D. F. and J. A. MUSICK. 1974. Benthic-slope fishes found at 900 m depth along a transect in the western N. Atlantic Ocean. *Mar. Biol.*, **26**: 225–233. http://dx.doi.org/10.1007/BF00389253

MURUA, H. and E. DE CÁRDENAS. 2005. Depth-distribution of deepwater species in Flemish Pass. *J. Northw. Atl. Fish. Sci.*, **37**: 1–12. http://dx.doi.org/10.2960/J.v37.m563

POHLE, G., T. J. KENCHINGTON and R. G. HALLIDAY. 1992. Potentially exploitable deepwater resources off Atlantic Canada. *Can. Tech. Rep. Fish. Aquat. Sci.*, **1843**: 85 p.

SNELGROVE, P. V. R. and R. L. HAEDRICH. 1985. Structure of the deep demersal fish fauna off Newfoundland. *Mar Ecol. Prog. Ser.*, **27**: 99–107. http://dx.doi.org/10.3354/meps027099

SULAK, K. J. 1982. A comparative taxonomic and ecological analysis of temperate and tropical demersal deep-sea fish faunas in the western North Atlantic. Ph.D. dissertation, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA, 211 p.

J. Northw. Atl. Fish. Sci., Vol. 44: 41–60 Publication (Upload) date: 26 Oct 2012

Demersal Fish Fauna of the Continental Slope off Nova Scotia, Canada, Based on Exploratory Bottom Trawl Surveys in 1994–95

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Abstract

The demersal fish fauna at 900–1800 m depths off Nova Scotia, Canada, is described using data from exploratory bottom trawl surveys conducted in November 1994 and March 1995 by a commercial fishing trawler. Approximately 25 metric tons (39 000 specimens) of demersal fish belonging to at least 82 species were caught, 30% of which had not previously been recorded from the area. However, more than half the catch consisted of the two species *Centroscyllium fabricii* (black dogfish) and *Coryphaenoides rupestris* (roundnose grenadier). Catches were higher in the shallower depth strata fished and cluster analysis showed that depth was the primary factor determining species composition of catches. It is suspected, however, that the vessel fished less effectively at depths greater than about 1500 m, contributing to the reduction in catch quantities at these depths. The importance in catches of large bodied species, particularly Chimaeriformes and sharks, contrasts with results from surveys in adjacent areas. This likely reflects the greater fishing power of the vessel/gear used in present surveys rather than real differences in faunal composition. Catches of mesopelagic species during these surveys, and during an earlier deepwater trawling survey in this area, are also described.

Keywords: *Centroscyllium fabricii; Coryphaenoides rupestris;* distribution; deepsea fish; Scotian Shelf slope

Introduction

In the early 1990s, interest by the Canadian fishing industry in developing fisheries for new species in deep water provided an opportunity for a joint Industry - Government venture to explore the commercial potential of fish resources on the Scotian Shelf slope, south of Nova Scotia. The only previous survey of the demersal fish fauna in this area had been conducted by a research vessel, and sampling was restricted to depths shallower than 1200 m (Markle *et al.*, 1988). The presently reported surveys were conducted by a commercial fishing trawler in November 1994 and in March 1995, at bottom depths of 910–1830 m. This paper reports on the fish catches made during these surveys, examines patterns in species distributions, and compares results with those of Markle *et al.* (1988), and with those from other studies in adjacent geographical areas.

An account of catches of pelagic fish species made during these 1994–95 surveys is provided also. Markle *et al.* (1988) did not include pelagic fish catches in their report, but their records were available to the authors of the present study and are provided here for comparison with 1994–95 catches.

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Methods

The surveys were conducted by the commercial fishing trawler Cape Chidley (length – 43 m; tonnage – 792; horsepower – 2400) on 6–16 November 1994 and 7–16 March 1995 (labelled C19 and C20 respectively). A commercial Engel high-lift bottom trawl was used with 1500 kg polyvalent trawl doors and a 51.8 m footrope equipped with 53 and 61 cm disc rock-hopper foot gear. Netting was of regulation 145 mm mesh but a 30 mm small mesh liner was inserted in the belly extension and codend to retain small specimens and a 20 mm diameter tickler chain was attached ahead of the footrope to enhance capture of bottom dwelling fauna. A headline transducer was deployed on all tows to measure vertical opening of the net. Headline height was typically about 6 m and no marked differences were observed between surveys or among depth zones. No instrumentation was available to measure horizontal net opening but, according to the vessel owners, previous performance data for this net (in shallower waters) indicated that the normal spread from wingtip to wingtip was 24 m and between the trawl doors was 69 m.

Sampling was stratified by area and depth, and fishing locations within strata were chosen randomly. On the first survey (C19), four discrete areas were fished. These were located south of Browns, LaHave, Western and Banquereau banks (Fig. 1, top panel). During the second survey (C20), four larger, contiguous, areas located south of Browns, LaHave, Emerald and Western - Sable Island banks were fished (Fig.1, bottom panel). Each fishing area was divided into five depth strata at 100 fm (183 m) intervals, but for presentation of data, stratum boundaries are defined in metres (rounded to the nearest 10 m). Fishing was conducted on a 24-hour basis, and stations were occupied in the order that minimized transit time.

The vessel's standard fishing procedure was to tow the net at 3.0 knots for one hour, measured from completion of shooting to start of haul back. However, there was insufficient trawl warp to maintain the same scope for deeper as for shallower tows and towing speed had to be reduced to 2.5 knots for the two deepest strata to get the net on bottom. Also, the actual start of trawling was taken as the time that resistance was felt due to bottom contact and it was found that actual time on bottom varied from 51 minutes in the shallowest, to 46 minutes in the deepest, stratum. Thus, distance towed was about 2.5 nautical miles for tows in the three shallowest strata, but the lower towing speed and reduced time on bottom for tows in the deeper strata resulted in the distance towed in the 1460–1650 m stratum being about 0.80, and in the 1650–1830 m stratum being about 0.75, of that in the shallower strata. Thus, abundance estimates for these deep strata were adjusted by x1.25 and x1.33 respectively.

The at-sea scientific protocol was to obtain the weight, number and length frequency (total length to the nearest cm) of each taxon in every catch. Particularly large catches of a taxon were sub-sampled by weight, numbers and length compositions subsequently being adjusted by the ratio of total to sample weight. Species that occurred in high volume were either retained by the vessel for commercial purposes or discarded, with scientific personnel retaining voucher specimens. In addition, a miscellany of taxa that occurred rarely, or that were recognized as presenting identification difficulties, was retained. All kept specimens were identified subsequently by the authors and the at-sea records were edited based on these laboratory results. In the majority of cases, voucher specimens confirmed at-sea species identifications but, in some, the taxonomic situation proved more complex than initially recognized at sea. In the latter circumstance, the authors reassigned taxonomic designations at the species level when the evidence was convincing but to higher taxonomic levels in the other cases. All retained specimens were deposited at the Atlantic Reference Centre (ARC), Huntsman Marine Science Centre (HMSC), St. Andrews, New Brunswick, Canada. Taxonomy follows Eschmeyer and Fricke (2012).

Comparisons of catches between areas, depths and surveys were restricted to those tows that were considered 'problem free'. Problematic tows were defined as those during which severe damage to the net occurred, when tow time was substantially reduced due to hang-ups on bottom obstacles, or when catches contained atypically low numbers of demersal species, indicating that the net was fishing off bottom. Species compositions were compared among stations using Bray-Curtis similarity coefficients following fourth root transformation of abundance data. Samples were partitioned using the CLUSTER routine in PRIMER version six (Clarke and Gorley, 2006). Length frequencies (by 3 cm groups) and mean lengths were calculated for the five species that contributed most to catches (by weight) by combining numbers per tow at length within each depth zone for two areas, Northwest Atlantic Fisheries Organization (NAFO) Divisions 4X (Browns -LaHave sampling areas) and 4W (Emerald-Western-Sable banks sampling areas). Estimates of the area of bottom within each depth/NAFO Division category (DFO: unpublished) were then used to obtain the following depth strata/Division weightings for amalgamation of the data from each survey:

Stratum (m)	4X	4W
910–1 100	0.05	0.09
1 100–1 280	0.06	0.10
1 280–1 460	0.08	0.12
1 460–1 650	0.09	0.14
1 650–1 830	0.12	0.15
	0.40	0.60

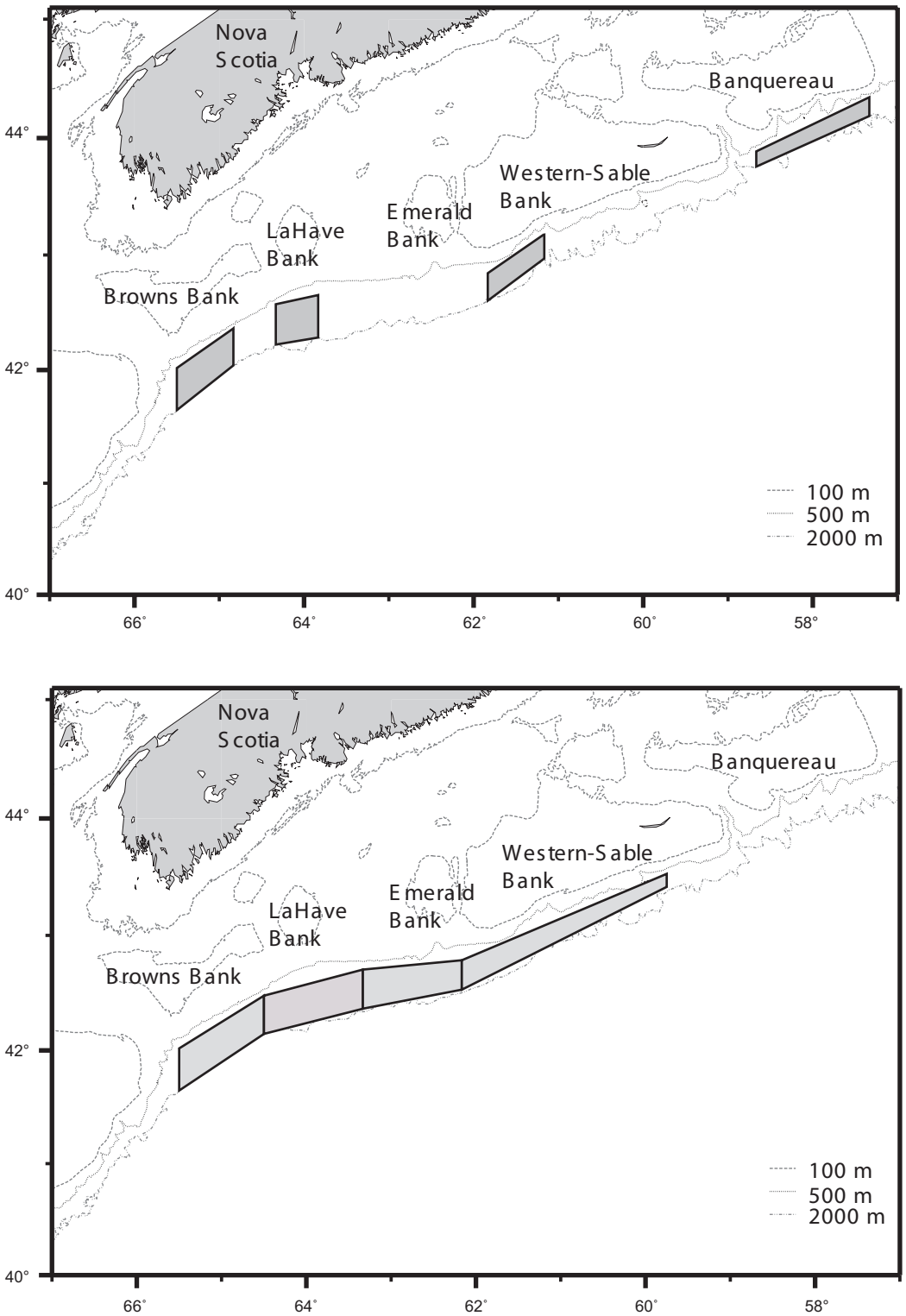

Fig. 1. Areas fished by the Cape Chidley: top panel – C19, November 1994, bottom panel – C20, March 1995.

Distributional records in the primary literature were used to determine which species in the present collections had not previously been reported from the study area. Online sources based on shared, disparate data collections were utilized only when records of interest could be verified through personal communication. The assignment of taxa to demersal or pelagic categories was based on their designations by Moore *et al.* (2003), species listed by them as benthic or benthopelagic in habit being classed here as demersal, and others as pelagic species. Common names, in Tables 1 and 2, follow usage by presently cited authors, particularly Moore *et al.* (2003), but cannot be provided for all species as some do not have accepted common names. Depth categorizations, upper slope (200–750 m), mid slope (750–1500 m) and lower slope (1500–2250 m), follow Haedrich and Merrett (1988). The Northwest Atlantic is equated to the NAFO Statistical Area.

Results

The surveys were largely successful in implementing a stratified-random sampling design with at least two sampling locations being fished in each depth stratum in each fishing area. Fishing areas differed between surveys, however (Fig. 1). On C19, the rate of successful completion of tows in the Banquereau area was low, only six of the 11 tows made there being classifiable as problem free, and thus this area was excluded from the sampling plan for C20. The sampling areas on C20 were contiguous and encompassed the other, discrete, areas used on C19. In these areas, 29 (of 31) tows on C19, and 44 (of 47) tows on C20, were considered problem free. It is the data from these tows that were used in analyses of geographic and bathymetric distributions, and size compositions. However, catches made in the Banquereau area on C19 are described separately and included in the listing of catches overall.

Demersal Species

Taxonomic composition

Approximately 25 metric tons (39 000 specimens) of demersal fish, belonging to at least 82 species, were caught (Tables 1 and 2). Among these, 10 taxa accounted for 90% of the catch by weight and these 10 accounted also for 80% by number. More than half the catch (by weight and number) consisted of *Centroscyllium fabricii* and *Coryphaenoides rupestris*.

For instances in Table 1 where catches are reported at a taxonomic level higher than species, the predominant species can be inferred quite reliably when voucher specimens were available (Table 2), *e.g.* it is likely that most of the fish listed as Rajidae NS in Table 1 were *Amblyraja jenseni*. Inferences about the abundance of the secondary species in a category relative to the primary species would be inappropriate, however. This is because relatively few voucher specimens were kept for abundant species, but most or all specimens of taxa recognized as 'different' were retained. Records reported in Table 1 at the family level that were not supported by voucher specimens (Alepocephalidae, Ipnopidae, Ophidiformes, Gadiformes and Zoarcidae) are mostly of little numerical importance and consist of inadequately documented records. There are, in addition, two special cases:

- *Apristurus* spp.: Markle *et al.* (1988) recognized two forms in their catches but (Moore *et al.*, 2003) listed four species as possibly occurring off New England, all of which might occur also in the present study area. See also Hartel *et al.* (2008).
- *Bathyraja* spp.: while species-level identifications were recorded at sea, there was an association between identifications and surveys (two *B. richardsoni* on C19, two *B. spinicauda* on C20) that raises doubt about their reliability. Thus, the species level identifications were not accepted.

Almost 30% (23) of the species listed in Tables 1 and 2 had not been recorded previously from off Nova Scotia. Thirteen of these new records were of species documented as having ranges that include adjacent areas, primarily to the southwest off New England (Moore *et al.*, 2003), and thus they represent only minor range extensions. The remaining 10 species are ones that previously have not been recorded, or have been recorded only rarely, from the NAFO Statistical Area, *i.e.* north of Cape Hatteras (35°N). Capture information, ARC catalogue numbers, and distributional notes are provided for these in Table 3.

Among the minor range extensions, it is noteworthy that the records of *Rajella bathyphila* are not in conformance with the convention accepted by Moore *et al.* (2003) that this species does not occur southwest of the Grand Banks (and thus that all records to the southwest must be of the closely-related *Rajella bigelowi*). More recently, Sulak *et al.* (2009) ignored this convention by recording *R. bathyphila* from the Mid-Atlantic-Bight. The latter authors are followed here, as the two specimens from off Western Bank had total lengths of 92 and 96 cm, greatly exceeding the maximum length of 50 cm that has been recorded for *R. bigelowi* (Sulak *et al.*, 2009).

Geographic and bathymetric distributions

Variation with depth of the catch rate (no. and wt. per tow) of all demersal species combined showed a similar pattern in both surveys (Fig. 2), with highest values occurring in one of the two shallowest strata and lowest values in one of the two deepest strata. The average time

Table 1. Demersal taxa: total number (No.) and weight (Wt.) caught and depth range of captures (D_{min} and D_{max} - minimum and maximum depths fished during tows in which the taxon was caught). (* - range extension, ** - not or seldom recorded previously from the NW Atlantic (see Table 3), (1) - see Table 2 for supplementary information on species composition, (2) - published by Caruso (2002).)

Order/Family	**Species** (or lowest taxon)	**Common Name**	No.	Wt. (kg)	D_{min} (m)	D_{max} (m)
Chimaeriformes						
Chimaeridae	*Hydrolagus affinis*	Deepwater chimaera	107	354	971	1 820
Rhinochimaeridae	*Harriotta raleighana*	Longnose chimaera	904	1 118	909	1 820
	Rhinochimaera atlantica	Knifenose chimaera	129	354	909	1 750
Carcharhiniformes						
Scyliorhinidae	*Apristurus* spp.	Catsharks	707	1 037	913	1 820
Squaliformes						
Somniosidae	*Centroscymnus coelolepis*	Portuguese shark	262	688	940	1 778
Etmopteridae	*Centroscyllium fabricii*	Black dogfish	10 572	7 816	909	1 809
	Etmopterus princeps	Rough sagre	545	548	918	1 776
Squalidae	*Squalus acanthias*	Spiny dogfish	1	3	1 280	1 428
Rajiformes						
Arhynchobatidae	*Bathyraja* spp.	–	4	62	940	1 820
Rajidae	*Rajella bathyphila**	Deepwater ray	2	16	1 094	1 256
	Rajella bigelowi	Bigelow's ray	37	12	940	1 820
	Rajidae NS (1)		75	74	909	1 803
Notacanthiformes						
Halosauridae	*Aldrovandia* spp. (1)	–	424	18	909	1 803
	*Halosaurus guentheri**	–	1	1	940	1 074
	Halosauropsis macrochir	–	311	110	918	1 820
Notacanthidae	*Lipogenys gillii*	Backfin tapirfish	3	1	1 333	1 748
	Notacanthus chemnitzii	Snubnosed spiny eel	48	32	909	1 809
	Polyacanthonotus rissoanus	Shortspine tapirfish	10	1	940	1 717
Anguillformes						
Synaphobranchidae	*Ilyophis brunneus*	–	15	1	958	1 695
	Simenchelys parasitica	Snubnose eel	350	61	909	1 820
	Synaphobranchus kaupii	Northern cutthroat eel	3 189	497	909	1 820
Nettastomatidae	*Venefica procera*	–	20	4	1 280	1 820
Osmeriformes						
Alepocephalidae	*Alepocephalus agassizii*	Agassiz' smoothhead	4 330	1 908	913	1 820
	Alepocephalus australis	–	2	1	1240	1 655
	Alepocephalus bairdii	Baird's smoothhead	93	241	953	1 794
	Bajacalifornia megalops	Bigeye smoothhead	20	6	940	1 803
	*Bathytroctes microlepis**	Smallscale smoothhead	1	0	1 747	1 794
	Narcetes stomias	Blackhead salmon	28	35	1 531	1 820
	Rouleina attrita	Softskin smoothhead	564	259	953	1 820
	Alepocephalidae NS	–	82	36	909	1 611
Aulopiformes						
Bathysauridae	*Bathysaurus ferox*	–	90	38	913	1 820
Ipnopidae	*Bathypterois dubius***	Spiderfish	5	1	1 483	1 629
	*Bathypterois grallator**	Tripodfish	1	0	1 710	1 803
	*Bathypterois phenax**	Blackfin spiderfish	3	0	940	1 776
	Bathypterois quadrifilis	–	19	0	940	1 664
	*Bathypterois viridensis**	–	3	0	1 313	1 565
	*Bathytyphlops marionae**	–	2	1	1 377	1 459
	Ipnopidae NS	–	6	0	940	1 556
Notosudidae	*Scopelosaurus lepidus*	–	4	1	940	1 547
Ophidiiformes						
Ophidiidae	*Barathrites parri***	–	2	0	1 384	1 533

(Continued)

Table 1. (Continued).

Order/Family	**Species** (or lowest taxon)	**Common Name**	No.	Wt. (kg)	D_{min} (m)	D_{max} (m)
	*Barathrodemus manatinus**	–	1	0	1 313	1 428
	Bassogigas gillii	–	12	16	913	1 820
	Dicrolene introniger	–	295	37	913	1 776
	*Monomitopus agassizii**	–	2	0	971	1 015
Bythitidae	*Cataetyx laticeps***	–	1	1	1 384	1 423
	Ophidiformes NS	–	4	0	634	901
Gadiformes						
Macrouridae	*Cetonurus globiceps***	–	1	0	1 672	1 748
	*Coelorinchus occa?**	Swordsnout grenadier	1	1	1 500	1 618
	Coryphaenoides rupestris	Roundnose grenadier	9 605	7 046	909	1 820
	Coryphaenoides spp. (1)	Grenadiers	738	28	918	1 803
	*Gadomus arcuatus***	–	2	1	913	1 068
	Macrourus berglax	Roughhead grenadier	140	228	909	1 794
	Nezumia bairdii	Marlinspike	3 203	270	909	1 809
	Macrouridae NS (1)	–	77	17	1 130	1 820
Moridae	*Antimora rostrata*	Blue hake	633	383	909	1 820
	*Guttigadus latifrons***	–	1	0	1 682	1 820
	Halargyreus johnsonii	Dainty mora	22	10	1 130	1 820
	Laemonema barbatulum	Smallscale mora	4	0	940	1 522
Lotidae	*Gaidropsarus argentatus*	Silver rockling	1	0	1 362	1 469
	Gaidropsarus ensis	Threebeard rockling	258	119	1 033	1 820
Phycidae	*Phycis chesteri*	Longfin hake	115	29	909	1 778
	Urophycis tenuis	White hake	11	23	913	1 613
	Gadiformes NS	–	32	0	1 077	1 533
Lophiformes						
Chaunacidae	*Chaunacops roseus** (2)	–	1	0	1 653	1 743
Ogcocephalidae	*Dibranchus atlanticus*	Atlantic batfish	1	0	1 324	1 346
Zeiformes						
Oreosomatidae	*Neocyttus helgae**	–	15	9	971	1 820
Scorpaeniformes						
Psychrolutidae	*Cottunculus thomsonii*	Pallid sculpin	194	208	909	1 646
Liparidae	*Paraliparis* spp. (1)	Snailfishes	50	1	909	1 717
Perciformes						
Anarhichadidae	*Anarhichas denticulatus*	Northern wolffish	1	23	1 357	1 428
	Anarhichas minor	Spotted wolffish	2	2	953	1 646
Zoarcidae	*Lycodonus mirabilis*	–	9	0	1 287	1 695
	Lycodes terraenovae	Atlantic eelpout	39	6	918	1 772
	*Pachycara crassiceps***	–	2	1	1 646	1 693
	Zoarcidae NS	–	1	0	1 280	1 428
Pleuronectiformes						
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch flounder	30	6	909	1 629
	Hippoglossus hippoglossus	Atlantic halibut	4	50	918	1 256
	Reinhardtius hippoglossoides	Greenland halibut	575	1 601	909	1 820

of day that fishing occurred did not vary systematically with depth. Thus, time of sampling in relation to diurnal vertical migration patterns does not explain the observed progressive decline in catch rates in the three deepest strata in both surveys. The number of demersal taxa caught per tow did not vary with depth but was about 19 on C19 and 22 on C20. There was a broad similarity in catch rates among areas and between surveys except that, on C20, catch rates in 1100–1280 m and 1280–1460 m strata in the LaHave area were more than double those in other areas. These high catches were composed primarily of *C. rupestris*.

Table 2. Supplementary information on the demersal species contributing to cases where taxa are grouped at genus or family level in Table 1, from laboratory identifications of retained specimens. (No. - number of specimens identified. * - range extension, ** - not or seldom recorded previously from the NW Atlantic (see Table 3).)

Taxon	Species	Common Name	No.
Rajidae NS	*Amblyraja jenseni*	shorttail skate	8
	Rajella fyllae	round skate	1
Aldrovandia spp.	*Aldrovandia affinis*	–	10
	*Aldrovandia gracilis***	–	10
	Aldrovandia oleosa	–	4
	Aldrovandia phalacra	–	83
Coryphaenoides spp.[1] and Macrouridae NS[2]	*Coryphaenoides alateralis***	–	1
	Coryphaenoides armatus	abyssal grenadier	1
	Coryphaenoides carapinus	–	44
	Coryphaenoides guentheri	Günther's grenadier	5
	*Coryphaenoides mediterraneus***	–	4
	*Nezumia longebarbata**	–	1
Liparidae	*Paraliparis copei*	Blacksnout snailfish	19
	Paraliparis garmani	Pouty snailfish	3

[1]Predominantly *C. carapinus*
[2]Predominantly *C. guentheri*

Cluster analyses based on catch numbers (Fig. 3) resulted in dendrograms showing that the depth strata were more important in ordering the stations than sampling area. For C19, three station groups formed, one containing the two tows in the shallowest stratum off Browns Bank, a second composed of the remaining tows in the three shallowest strata plus one at 1460–1650m off Browns Bank, and a third group composed of the remaining tows in the two deepest strata. The two shallow Browns Bank sets differed from the larger 'shallow' group (average dissimilarity = 43%) due primarily to the presence of *Glyptocephalus cynoglossus* and the absence of *Alepocephalus agassizi* and *Etmopterus princeps*. The average dissimilarity between the two large station groups (48%) was due particularly to higher abundance of *C. fabricii* and *C. rupestris* in the 'shallow' strata and *Halosauropsis macrochir* and *A. agassizi* in the deeper strata. For C20, sampling was more intensive and seven groups formed but, nonetheless, there were two main groups, one containing most of the tows in the three shallow strata and another with most of the tows in the two deep strata, analogous to the two main groups in C19. The average dissimilarity between these two groups (49%) was also comparable to that observed in C19, and was due to the same species except that, in C20, *Coryphaenoides* spp. replaced *A. agassizi* in importance in the deep strata. In C20, a secondary deep group formed containing two stations that differed from the main deep group (average dissimilarity = 46%) due to low catches of *Synaphobranchus kaupii* and the absence of *Aldrovandia* spp. and *Simenchelys parasitica*. The three smaller clusters on the left of the dendrogram are composed largely of tows in the shallowest stratum, and differ variously from the main 'shallow' group by the presence of the upper slope species, *G. cynoglossus* and *Phycis chesteri*, and lesser abundance of mid-slope species. Thus, the patterns of species distributions described by the two surveys were in general agreement.

A combined list for the two surveys of the taxa that were among the top 10 numerically within at least one depth stratum (Table 4) illustrates how the predominant species varied with depth. *Centroscyllium fabricii, C. rupestris* and *Nezumia bairdii* dominated catches in the three shallowest strata. *Alepocephalus agassizii* and *S. kaupi* were moderately abundant in all depths but rose to prominence in rankings in the two deepest strata due primarily to the much reduced abundance, at these depths, of the three species that dominated at shallower depths. The species that actually had their highest abundance in the two deepest strata were *H. macrochir, Gaidropsarus ensis*, *Hydrolagus affinis* and *Rouleina attrita*.

Ranking the top 10 taxa by weight rather than by number replaced four small-bodied taxa (*S. parasitica, Coryphaenoides* spp., *Dicrolene intronigerand Aldrovandia* spp.) by larger-bodied ones (*Centroscymnus coelolepis*, *Rhinochimaera atlantica*, *Cottunculus thompsonii* and *Macrourus berglax*) (Table 4). This resulted in differences in rankings, particularly in a substantially higher ranking of *Reinhardtius hippoglossoides*, but did not materially change the perceptions based on numbers on how the fauna changed with depth.

Table 3. Demersal species not or seldom recorded previously from the NW Atlantic: number caught (*n*), capture latitude and longitude, depth (min–max tow depth, m), Atlantic Reference Centre (ARC) catalogue number, and notes. (KU – University of Kansas Natural History Museum, MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA., USA.)

Aldrovandia gracilis: *n* = 10: 41°55'N, 65°19'W – 42°48'N, 61°26'W, 1313–1776 m. ARC 26788 (*n* = 1), ARC 9713153 (*n* = 1), ARC 9713155 (*n* = 3), ARC 9713157 (*n* = 1), ARC 9813168 (*n* = 1), 9813171 (*n* = 2), ARC 9813173 (*n* = 1). Northern limit previously accepted as Virginia (Sulak, 1990), an unverifiable record from 42°31'N, 63°40'W (Roule and Angel, 1933) being regarded as doubtful. Present records lend credence to that of Roule and Angel (1933).
Bathypterois dubius: *n* = 5: four at 42°08'N 65°08'W, 1483–1629 m, ARC 25403; one at 42°33'N 64°12'W, 1183–1203 m, ARC 9914871. Recorded previously from Grand Bank (ARC 9111413) by Templeman (1966) and from Bear Seamount by Moore *et al.* (2003). Other verified specimens from the vicinity of Bear Seamount are KU 8450, MCZ 165866 (one specimen), and MCZ 167902 (three spec.) (K. Hartel, MCZ, pers. comm.).
Barathrites parri: *n* = 2: one at 42°33'N 63°25'W, 1494–1533 m, ARC 9914912; 1 at 42°39'N 62°25'W, 1384–1423 m, ARC 9914914. Moore *et al.* (2003) report two specimens from off southern New England.
Cataetyx laticeps: *n* = 1: 42°39'N 62°25'W, 1384–1423 m, ARC 27729. Previously reported from off Grand Bank at 42°54'N, 51°18'W (Bänón, 2001) (one specimen), and from the Gulf of Mexico (McEachran and Fechhelm, 1998).
Cetonurus globiceps: *n* = 1: 42°07' 64°57'W, 1672–1748 m, ARC 27641. Previously reported from the Caribbean – Gulf of Mexico (Geistdoerfer, 1986; Geistdoerfer, 1990; McEachran and Fechhelm, 1998).
Gadomus arcuatus: *n* = 2: one at 42°21'N 64°51'W, 913–1053 m, ARC 27758; one at 42°45' 62°40'W, 918–1068 m, ARC 27759. Previously reported from the Caribbean, Gulf of Mexico and northeastern coast of South America (Cohen *et al.*, 1990; Geistdoerfer, 1986; Geistdoerfer, 1990; Goode and Bean, 1896; Iwamoto, 2002; McEachran and Fechhelm, 1998).
Coryphaenoides alateralis: *n* = 1: 42°45'N 62°40'W, 918–1068 m, ARC 27678. Only four specimens have been recorded previously (Moore *et al.,* 2003), from the Gulf of Mexico, Hudson Canyon and Bear Seamount (39°55'N 67°30'W, two specimens).
Coryphaenoides mediterraneus: *n* = 4: one at 42°08'N 64°56'W, 1670–1772 m, ARC 27752; two at 42°51'N 61°24'W, 1653–1743 m, ARC27640; 1 at 42°58'N 61°18'W, 1653–1750 m, ARC27744. Previously recorded from the Gulf of Mexico (Geistdoerfer, 1986; Geistdoerfer, 1990; Iwamoto, 2002; McEachran and Fechhelm, 1998).
Guttigadus latifrons: *n* = 1: 43°50'N 58°20'W, 1682–1820 m, ARC 25404. This is the first record from the NW Atlantic.
Pachycara crassiceps: *n* = 2: one at 42°27'N 63°33'W, 1646–1664 m. ARC 9914939; one at 42°33'N 63°07'W, 1659–1693 m, ARC 9914940. These are the first records from the NW Atlantic.

Some of the taxa in these comparisons consisted of more than one species, distorting the results to some extent. Nothing can be added to clarify the species composition of *Apristurus* spp., but it is clear that the *Aldrovandia* spp. group was largely comprised of *Aldrovandia phalacra* (Table 2). The bi-modal depth distribution of *Coryphaenoides* spp. presents a more complex situation. The abundance of specimens taken in the three deepest strata increased with depth, as did their mean length (12, 14 and 19 cm), and these fish were likely to have been in large part *Coryphaenoides carapinus*. However, of the 123 specimens caught in the shallowest stratum (mean length 25 cm), only one was kept for subsequent laboratory identification and it proved to be *Coryphaenoides alateralis*, a species not previously reported from the area (see Table 3). This is too weak a basis on which to make an inference about the identity of the remaining specimens in this stratum. It is clear, however, that at least two species of *Coryphaenoides*, with different depth distributions, were making important contributions to the present collection.

The six tows made off Banquereau Bank that were classed as problem-free were combined into two depth groups, 1100–1460 m and 1460–1830 m, for data presentation (Table 5). *Alepocephalus bairdii* and *R. attrita* were prominent components of these catches, and *C. rupestris* and *C. fabricii* were less dominant than elsewhere. However, such differences from the more western sampling areas are as likely to be due to the vagaries of sampling in this area as to differences in faunal composition.

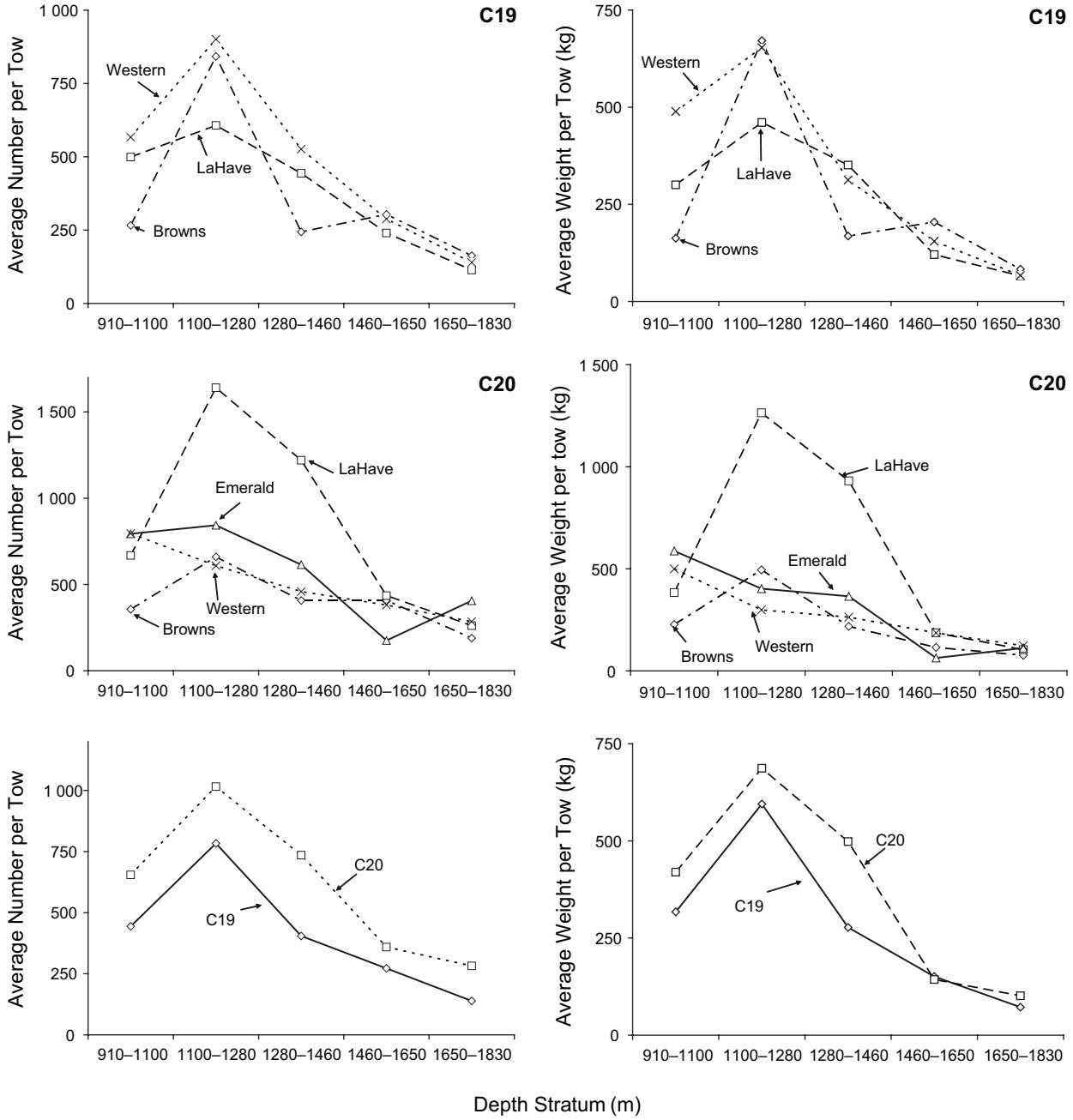

Fig. 2. Average catch rates of demersal species by number and weight for each sampling area by depth stratum for C19 (top panels) and C20 (mid-panels) and by survey overall (bottom panels). (Banquereau Bank data excluded; averages for 1460–1650 m and 1650–1830 m strata adjusted by x1.25 and x1.33 respectively - see text; scales for Y-axes vary.)

Size compositions

Total length, the measurement used for all species on the Cape Chidley surveys, is not the preferred metric for those species with fragile tails that are easily damaged during capture, *e.g.* Macrouridae and Chimaeriformes, *e.g.* ICES (2008). However, the conclusions made here from comparisons of size compositions between surveys and depth strata are relative, and conclusions are not likely to be affected by whatever bias the use of total length may have introduced.

Area-weighted length frequencies, indicative of the length compositions of the populations available to

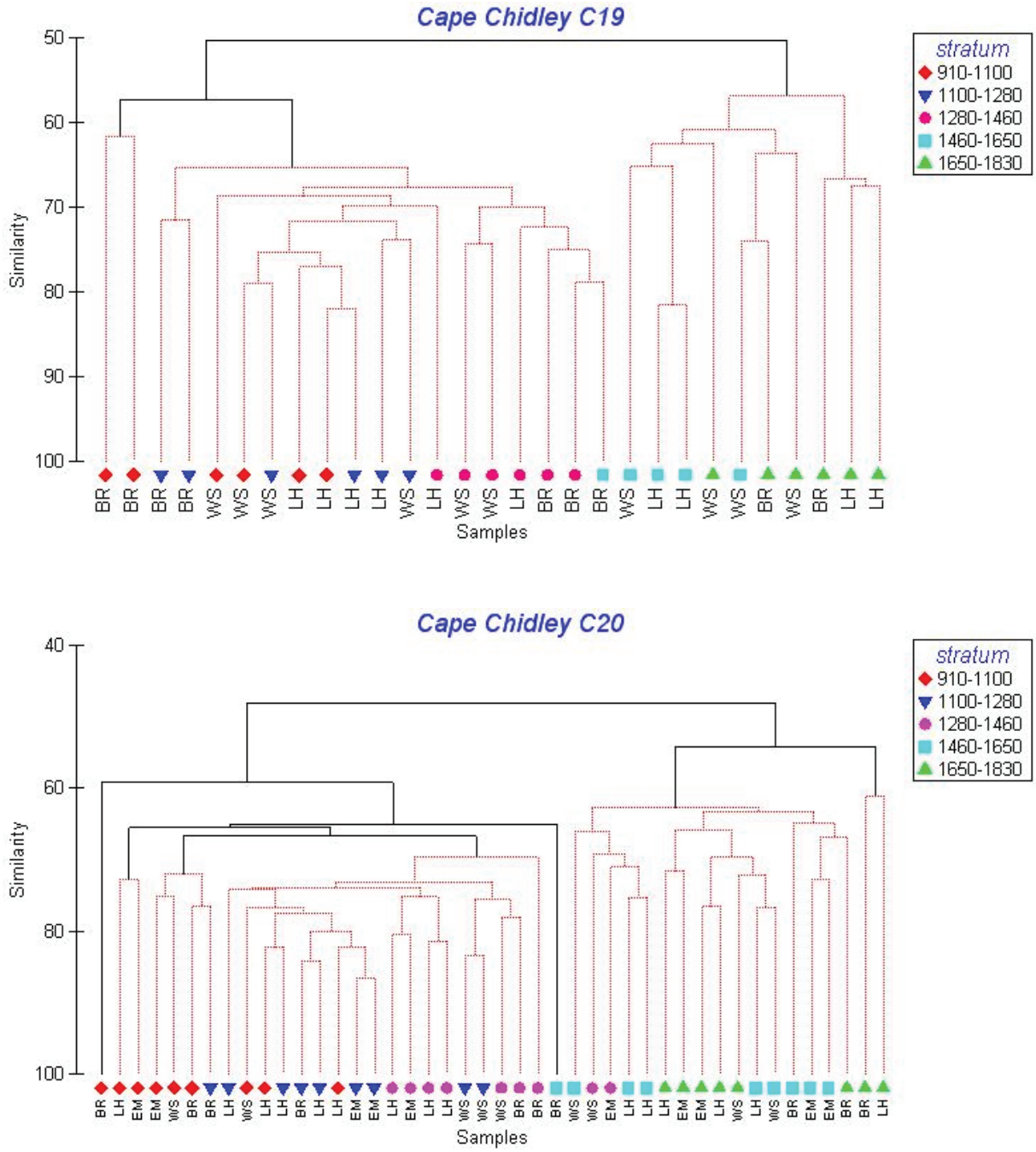

Fig. 3. Hierarchical clustering using fourth-root transformation of catch numbers for all species and stations from Cape Chidley cruises C19 (top panel) and C20 (bottom panel). (Letters indicate banks: BR- Browns; LH-LaHave; EM-Emerald; WS – Western). Symbols indicate depth strata in metres (see key on right).

the gear, were generally similar between surveys for the five species that contributed most, by weight, to catches (Fig. 4). For *R. hippoglossoides* and *Harriotta raleighana*, the relative numbers by length group were almost identical between surveys. In the other three cases, *C. rupestris, C. fabricii* and *A. agassizii*, population estimates from C19 contained fewer small fish than did those from C20. The C19 estimates of large specimens of *C. rupestris* were lower also, and total population number was 60% of that for C20. In the cases of *C. fabricii* and *A. agassizii,* population number estimates from C19 were 85% and 70% respectively, of those from C20.

For these five species, the size of fish caught varied with depth in most cases (Fig. 5). Typically, average lengths were smallest in the shallowest tows, increasing with depth to the 1280–1460 m stratum or to the 1460–1650 m stratum. Catches in the deepest stratum suggested a levelling off in average size but catch numbers in this stratum were so few that any conclusion is speculative. The clearest example of increasing size with depth is provided by *R. hippoglossoides*, average lengths in 910–1100 m being about 60 cm, increasing to about 65 cm in 1100–1280 m and 65–70 cm in 1280–1650 m, and trends for *C. rupestris* and *A. agassizii* were roughly similar in scale. In contrast, the size of *C. fabricii* showed only a slight tendency to increase with depth and *H. raleighana* showed none, average length being lowest at the middle of the depth range sampled.

Pelagic Species

The Cape Chidley bottom trawl surveys caught at least 40 taxa of pelagic fishes, consisting of approximately 1500 specimens weighing almost 60 kg (Table 6). There were cases of catches reported at a taxonomic level higher than species for pelagic taxa also and, for a number of these, voucher specimens were available that give an indication of their species composition (Table 7). However, the data from these voucher specimens are too scant to allow inferences to be made about the relative abundance of these species in catches.

The survey reported on by Markle *et al*. (1988), conducted in 1984 by the government-chartered vessel, Lady Hammond, using a Western IIA bottom otter trawl, similarly caught about 40 taxa of pelagic fishes, consisting of almost 1000 specimens (Table 8). Included in Table 8 are three species of liparid, and the trichiurid *Benthodesmus tenuis*, species that would be considered demersal under present criteria, but presumably were considered pelagic by Markle *et al.* (1988).

There was a strong similarity in the pelagic taxa caught by bottom trawl on the two surveys, about 70% being in common, despite differences in gear design and depths fished, and most of these taxa occurred also in midwater trawl samples from the same area (Themelis and Halliday, 2012), or in waters to the immediate southwest of the sampling area (Moore *et al.*, 2003). Of note, however, is the record of *Platytroctes apus* (Cape Chidley, 42°45'N 61°41'W, 1498–1522 m, ARC 9914821), only two specimens of which have been reported previously from the NW Atlantic, one at about 40°N (Hartel *et al.*, 2008), the other off Greenland ((Møller *et al.*, 2010), and the record of *Benthodesmus tenuis* (Lady Hammond, 42°57'N 61°41'W, 558–585 m, ARC 8600838), which is only the second record north of Cape Hatteras, the first being off Browns Bank (Scott and Scott, 1988).

Discussion

The reason why the number of benthic taxa caught per tow differed between surveys, being about 15% higher on C20 than on C19, is not clear. The surveys were quasi-commercial in character, and close cooperation between ship's crew and scientific personnel was required to meet the needs of both. It is possible that this cooperation improved between surveys, explaining the higher number of taxa per tow observed on C20. It is also possible, however, that minor differences in the trawl nets, the net used on C19 being lost at sea and replaced on C20 with another built to the same specifications, contributed to this, and other, differences in results between surveys.

The much higher catches of *C. rupestris* in the LaHave area than in other areas on C20 occurred, in large part, in a series of tows added at the end of the sampling program. It is possible that these tows did not conform to the randomized sampling design, biasing results. Nonetheless, when these added tows are disregarded, abundance estimates for this species in the LaHave area, although reduced, remain higher than in other areas. In contrast, C19 estimates of *C. rupestris* in the LaHave area were not higher than elsewhere. However, sampling on C19 was restricted to non-contiguous blocks, which could have introduced bias to abundance estimates from this survey if, for example, areas of high density of *C. rupestris* were excluded from the sampling blocks. An association of *C. rupestris* with canyons, as has been noted by Snelgrove and Haedrich (1985) in data from southeastern Grand Bank and off New England, could underlie such a bias. While there is no evidence for such an association in data from the present study, differences in sampling design nonetheless may have been an important factor causing variability in quantities caught between surveys.

While areas fished differed to some extent between surveys, cluster analysis did not find area to be a factor of importance in determining species composition; rather it was depth that had an over-riding influence. Catch rates were high in the three shallowest strata (910–1460 m) but declined to much lower levels in 1460–1650 m and to minima in 1650–1830 m on both surveys. In the present

Table 4. Demersal species abundance (by number, and weight, per tow) and dominance (ranking) within depth strata. (Banquereau Bank data excluded. **A**: 910–1100 m, **B**: 1100–1280 m, **C**: 1280–1460 m, **D**: 1460–1650 m, **E**: 1650–1830 m. **D** and **E** adjusted by x1.25 and x1.33, respectively. + denotes <0.5/tow.)

	Average/tow					Ranking				
Depth stratum	**A**	**B**	**C**	**D**	**E**	**A**	**B**	**C**	**D**	**E**
Number of tows	15	15	15	14	14	15	15	15	14	14
A. By number										
Centroscyllium fabricii	327	281	98	20	4	1	2	2	5	–
Coryphaenoides rupestris	74	330	201	28	8	2	1	1	3	6
Nezumia bairdii	53	71	68	18	4	3	3	4	6	–
Synaphobranchus kaupii	36	46	68	49	31	4	5	5	2	3
Harriotta raleighana	17	17	15	9	5	5	8	6	–	9
Alepocephalus agassizii	15	55	89	98	56	6	4	3	1	1
Reinhardtius hippoglossoides	13	14	9	1	1	7	9	8	–	–
Apristurus spp.	12	24	7	3	3	8	7	10	–	–
Simenchelys parasitica	9	4	4	5	3	9	–	–	–	–
Coryphaenoides spp.	9	0	2	21	33	10	–	–	4	2
Etmopterus princeps	5	27	4	1	1	–	6	–	–	–
Dicrolene introniger	2	9	5	4	+	–	10	–	–	–
Antimora rostrata	7	6	13	11	7	–	–	7	9	8
Aldrovandia spp.	1	6	8	14	4	–	–	9	7	–
Rouleina attrita	+	+	2	13	8	–	–	–	8	7
Halosauropsis macrochir	+	+	+	9	17	–	–	–	10	4
Gaidropsarus ensis	+	+	1	9	13	–	–	–	–	5
Hydrolagus affinis	+	+	1	1	4	–	–	–	–	10
B. By weight (kg)										
Centroscyllium fabricii	242	206	74	14	3	1	2	2	3	–
Reinhardtius hippoglossoides	30	38	30	6	3	2	3	4	8	–
Coryphaenoides rupestris	25	237	177	26	6	3	1	1	2	6
Harriotta raleighana	22	20	17	10	7	4	7	5	4	3
Apristurus spp.	18	38	9	4	1	5	4	7	10	–
Centroscymnus coelolepis	15	22	7	3	1	6	6	9	–	–
Rhinochimaera atlantica	14	9	1	1	1	7	9	–	–	–
Cottunculus thompsonii	7	4	3	+	0	8	–	–	–	–
Synaphobranchus kaupii	5	7	12	7	4	9	10	6	5	8
Etmopterus princeps	4	28	4	1	+	10	5	–	–	–
Alepocephalus agassizii	3	14	46	38	18	–	8	3	1	1
Antimora rostrata	4	3	7	7	5	–	–	8	6	7
Nezumia bairdii	3	6	7	1	1	–	–	10	–	–
Rouleina attrita	+	+	+	6	3	–	–	–	7	10
Hydrolagus affinis	1	2	6	5	11	–	–	–	9	2
Halosauropsis macrochir	+	+	+	4	6	–	–	–	–	4
Gaidropsarus ensis	+	+	1	4	6	–	–	–	–	5
Macrourus berglax	3	4	2	4	3	–	–	–	–	9

Table 5. Demersal species abundance (by number, and weight, per tow) and dominance (ranking) within depth strata in the Banquereau Bank area. (Deep strata adjusted as in Table 4. + denotes <0.5/tow.)

	Average/tow		Ranking	
Depth Strata	1 100–1 460 m	1 460–1 830 m	1 100–1 460 m	1 460–1 830 m
Number of tows	3	3	3	3
A. By number				
Nezumia bairdii	32	12	1	5
Coryphaenoides rupestris	32	22	2	4
Alepocephalus bairdii	20	+	3	–
Rouleina attrita	16	115	4	1
Synaphobranchus kaupii	15	24	5	3
Centroscyllium fabricii	10	0	6	–
Alepocephalus agassizii	8	98	7	2
Harriotta raleighana	6	5	8	10
Antimora rostrata	5	11	9	6
Reinhardtius hippoglossoides	5	2	10	–
Halosauropsis macrochir	+	9	–	7
Bathysaurus ferox	0	9	–	8
Macrouridae	1	7	–	9
B. By weight (kg)				
Alepocephalus bairdii	64	2	1	–
Coryphaenoides rupestris	18	6	2	8
Reinhardtius hippoglossoides	14	7	3	6
Harriotta raleighana	11	12	4	3
Centroscyllium fabricii	9	0	5	–
Hydrolagus affinis	8	6	6	9
Alepocephalus agassizii	5	141	7	1
Nezumia bairdii	4	2	8	–
Rouleina attrita	4	62	9	2
Antimora rostrata	4	8	10	5
Bathyraja sp.	3	10	–	4
Bathysaurus ferox	0	6	–	7
Narcetes stomias	0	5	–	10

study, it was necessary to apply correction factors to catches to account for a reduction in towing speed, and hence distance towed, when fishing in the two deepest strata, but their adequacy is not known. An inference about the affects of this difference in sampling procedure with depth can be made based on catches of several large-bodied species that are perhaps the most capable of avoiding slow-moving nets. According to Moore *et al.* (2003), the depth distribution of *H. raleighana* extends to 2452 m, that of *C.coelolepis* to 3675 m, and of *E. princep*s to 2213 m, but these species were caught by the Cape Chidley primarily in 910–1460 m. This suggests that, relative to catches in these strata, catches in the two deepest strata may have underestimated abundance of these, and perhaps other, species. Nonetheless, these particular species were not among the most important in determining the dissimilarity between the two main groups and, despite the confounding effect of changes in fishing procedure with depth, present results are consistent with those of other studies which have found a distinction between mid slope and lower slope assemblages. In particular, cluster analysis of fish occurrence data from a video survey at 53°–56°W (Baker

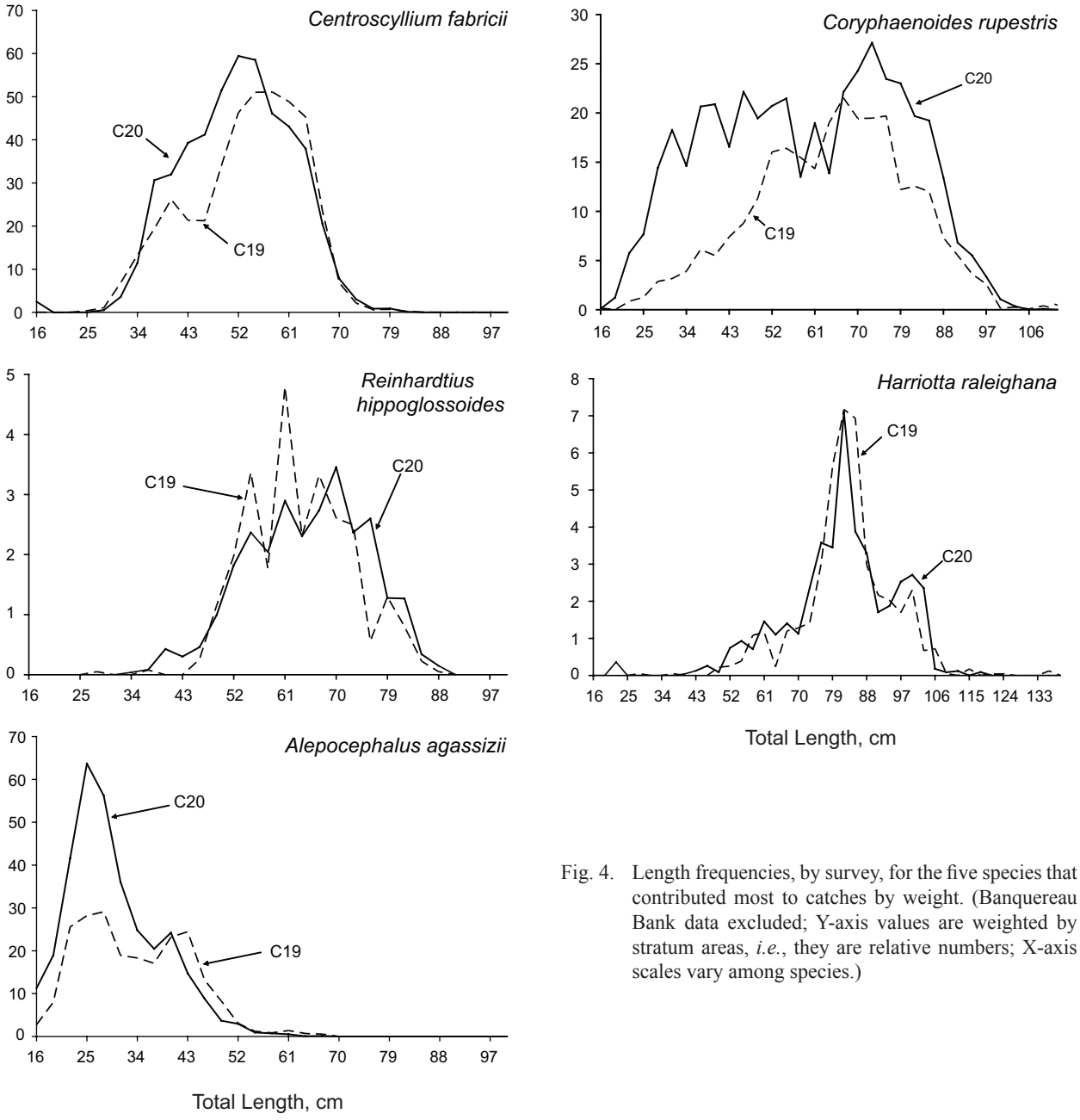

Fig. 4. Length frequencies, by survey, for the five species that contributed most to catches by weight. (Banquereau Bank data excluded; Y-axis values are weighted by stratum areas, *i.e.*, they are relative numbers; X-axis scales vary among species.)

et al., 2012), immediately to the east of the present surveys, defined a boundary between species assemblages at about 1300m, and these authors cite other such cases.

The bottom trawl survey off Nova Scotia by the Lady Hammond (Markle *et al.*, 1988) extended from LaHave Bank to St. Pierre Bank (56°W) and thus overlapped strongly, geographically, with the Cape Chidley surveys. Depths surveyed by the Lady Hammond extended from 400 m to 1200 m and thus catches contained many upper slope species that were not available to Cape Chidley surveys. However, in those depth strata that overlapped (strata 3+4: 800–1200 m of Markle *et al.* (1988), their Table 5, versus 910–1280 m, present data), the species predominating in catches were similar. However, in these overlapping strata, the Cape Chidley caught more than five times the number, and ten times the weight, per tow of the Lady Hammond (all taxa combined), and caught almost twice as many species per tow. The Western IIa net used by Markle *et al.* (1988) was smaller than the Engel trawl used by the Cape Chidley (headline height 4.6 m, wingspread 10.7 m (Carrothers, 1988) versus 6.0 m and

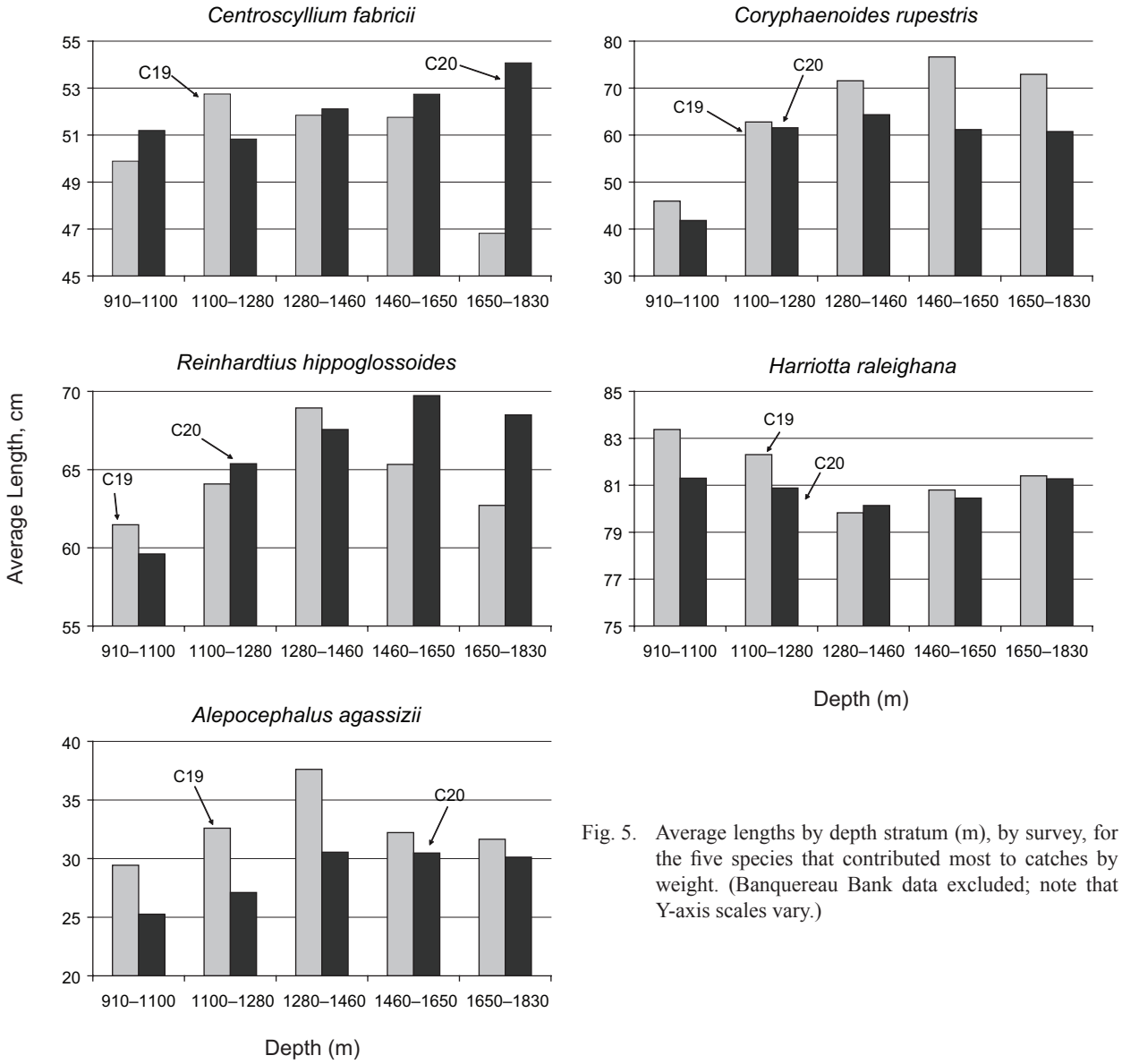

Fig. 5. Average lengths by depth stratum (m), by survey, for the five species that contributed most to catches by weight. (Banquereau Bank data excluded; note that Y-axis scales vary.)

24 m, respectively) and nominal tow time was half as long. These factors likely account for much of the difference in catches. Also, however, the Lady Hammond was fishing at the limit of its capability at these depths, a factor that likely reduced further its fishing power relative to the Cape Chidley.

The video survey of Baker *et al.* (2012) of the fish fauna in canyons off SW Newfoundland in 350–2250 m provided a list of species observed that was very similar to the lists of species caught by the Lady Hammond and Cape Chidley at comparable sampling depths. There were differences in the relative importance of these species between trawl and video surveys which could reflect differences in gear selection or sampling design, *e.g.* restriction of video sampling to canyons.

Markle *et al.* (1988) found the slope fauna off Nova Scotia to have many similarities with the temperate fauna of the Mid-Atlantic Bight, *i.e.* the area from south of Georges Bank to Cape Hatteras, as characterized by Sulak (1982). Other descriptions of that fauna are given by Markle and Musick (1974) and Haedrich *et al.* (1975). Markle *et al.* (1988) did, however, note substantial differences between the Scotian Slope fauna and that off southeastern Grand Bank (Snelgrove and Haedrich, 1985) in terms of dominant species, diversity and depth distributions. Pinhorn and Halliday (1997) subsequently proposed, based on research vessel trawl surveys conducted in 1949–91, that The Tail of Grand Bank (about 51°W) was a boundary of importance to the distribution of slope fish species, 'northern' species occurring at reduced densities (and/or at greater depth) to the west and 'southern' species

Table 6. Pelagic taxa, Cape Chidley exploratory fishing 1994–95: number caught (No.) and number of occurrences (Occur.) by taxon. ((1) – see Table 7 for supplementary information on species composition.)

Order/Family	**Species** (or lowest taxon)	No.	Occur.
Anguilliformes			
Derichthyidae	*Derichthys serpentinus*	1	1
Nemichthyidae	*Nemichthys scolopaceus*	117	50
Serrivomeridae	*Serrivomer beanii*	294	77
Saccopharyngiformes			
Eurypharyngidae	*Eurypharynx pelecanoides*	17	12
Osmeriformes			
Bathylagidae	*Bathylagus euryops*	65	29
Platytroctidae	*Holtbyrnia anomala*	1	1
	Maulisia microlepis	4	4
	Platytroctes apus	1	1
Stomiiformes			
Gonostomatidae	*Sigmops bathyphilus*	9	8
	Sigmops elongatum	15	14
Sternoptychidae	*Argyropelecus aculeatus*	10	9
	Argyropelecus gigas	2	2
Stomiidae	*Borostomias antarcticus*	6	5
	Chauliodus sloani	101	48
	Stomias boa ferox	67	38
	Melanostomias bartonbeani	3	3
	Malacosteus niger	8	7
	Stomiiformes NS	6	4
Aulopiformes			
Paralepididae	Paralepididae NS (1)	13	13
Anotopteridae	*Anotopterus pharao*	3	3
Alepisauridae	*Alepisaurus ferox*	6	6
	Alepisaurus brevirostris	3	3
Myctophiformes			
Myctophidae	Myctophidae NS (1)	546	68
Lophiiformes			
Melanocetidae	*Melanocetus* spp. (1)	5	5
Himantolophidae	*Himantolophus albinares*	2	2
Ceratiidae	*Cryptopsaras couesii*	4	3
Gigantactinidae	*Gigantactis vanhoeffeni*	3	3
Beloniformes			
Scomberesocidae	*Scomberesox saurus*	1	1
Stephanoberyciformes			
Melamphaidae	Melamphaidae NS (1)	91	43
Cetomimiformes			
Rondeletiidae	*Rondeletia loricata*	3	4
Cetomimidae	*Cetostoma regani*	1	1

(Continued)

Table 6. (Continued).

Order/Family	**Species** (or lowest taxon)	No.	Occur.
Beryciformes			
Anoplogastridae	*Anoplogaster cornuta*	18	16
Perciformes			
Howellidae	*Howella brodiei*	28	14
Caristiidae	*Caristius* sp.	1	1
Chiasmodontidae	*Chiasmodon* sp.	25	21
	Pseudoscopelus sp.	3	3
Zoarcidae	*Melanostigma atlanticum*	2	1

occurring in lesser abundance to the east. This was attributed to the influence of the cold Labrador Current, which bathes northeastern slopes with water less than 4°C to depths of at least 1000 m but turns offshore at about this location. However, their data for southern Grand Bank and west was restricted very largely to upper slope depths.

Direct comparisons of faunal composition and species abundances obtained from present data with those from previous surveys at similar depths are confounded by differences in survey design and by the large differences in gear size and vessel fishing power. The differences in vessels and gears used are particularly pertinent to comparisons with those surveys in the Mid Atlantic Bight that used shrimp trawls (Markle and Musick, 1974; Haedrich *et al.*, 1975; Haedrich *et al.*, 1980; Sulak, 1982). These trawls were substantially smaller (headline height of about 2.0 m) than that used in present surveys and they were towed at half the speed (1.5 knots). Testimony to a difference in fishing capability is provided by the Cape Chidley captures of large mobile species, which would have the greatest capability for avoidance of small slow-moving nets. While Chimaeriformes and sharks comprise a third of numbers and almost half the weight caught on Cape Chidley surveys, these taxa were of minor to no importance in Mid-Atlantic Bight survey catches, and this must surely be an effect of sampling.

In areas to the north and east of the present study area (NAFO Subareas 2–3), the existence of substantial populations of *C. rupestris* (Atkinson, 1995), *R. hippoglossoides* (Bowering and Brodie, 1995) and *M. berglax* (Murua *et al.*, 2005) has been well established. Present data show that a substantial population of *C. rupestris* occurs also on the Scotian Slope and that it is a dominant member of the upper – mid slope fauna in that area. Pinhorn (1976) cites an observation of spawning and post-spawning fish "off Nova Scotia", and sexually maturing fish have been observed in the area by one of the present authors (DET). The size at sexual maturation of this species in more northern areas is 40–50 cm (Atkinson, 1995). Thus, the occurrence in present catches of substantial numbers of *C. rupestris* in the length range 15–40 cm supports a view that the species resides within the surveyed area throughout its life cycle. *Reinhardtius hippoglossoides* was of moderate abundance in Scotian Shelf slope catches, but nonetheless ranked fourth by weight as all catches were of large fish (>40 cm). This suggests that they were progeny of a more northern spawning population, perhaps that in the Gulf of St. Lawrence (Bowering, 1983). The contribution of *M. berglax* to present catches was minor. Thus, the data for *M. berglax* and *R. hippoglossoides* are consistent with The Tail of Grand Bank being of some biogeographic importance, but there is no clear support for this in the case

Table 7. Pelagic taxa, Cape Chidley exploratory fishing 1994–1995: supplementary information on the species contributing to cases where taxa are grouped at genus or family level, from laboratory identifications of retained specimens (except Myctophidae includes at-sea identifications also). (No. – the number of specimens identified.)

Taxon	**Species**	No.
Paralepididae NS	*Magnisudis atlantica*	1
Myctophidae NS	*Benthosema glaciale*	140
	Ceratoscopelus maderensis	3
	Lampadena speculigera	3
	Lampanyctus macdonaldi	24
Melanocetus spp.	*Melanocetus johnsonii*	1
	Melanocetus murrayi	2
Melamphaidae NS	*Poromitra crassiceps*	4
	Scopelogadus beanii	6
	Scopelogadus mizolepis	1

Table 8. Pelagic taxa, Lady Hammond bottom trawling 1984: number caught (No.) and number of occurrences (Occur.) by taxon.

Order/Family	**Species** (or lowest taxon)	No.	Occur.
Anguilliformes			
Derichthyidae	*Nessorhamphus ingolfianus*	5	5
Nemichthyidae	*Nemichthys scolopaceus*	90	27
Serrivomeridae	*Serrivomer beanii*	89	22
Saccopharyngiformes			
Eurypharyngidae	*Eurypharynx pelecanoides*	3	3
Osmeriformes			
Bathylagidae	*Bathylagus euryops*	17	4
	Bathylagus sp.	59	15
	Melanolagus bericoides	1	1
Stomiiformes			
Gonostomatidae	*Cyclothone* sp.	3	2
	Gonostoma elongatum	47	16
Sternoptychidae	*Argyropelecus aculeatus*	7	6
	Polyipnus clarus	9	3
	Sternoptyx diaphana	4	4
Stomiidae	*Chauliodus sloani*	143	27
	Stomias boa ferox	123	25
	Melanostomias bartonbeani	1	1
	Malacosteus niger	9	7
	Photostomias guernei	2	2
	Stomiiformes NS	2	2
Aulopiformes			
Paralepididae	Paralepididae NS	26	12
Myctophiformes			
Myctophidae	*Benthosema glaciale*	89	16
	Ceratoscopelus maderensis	59	10
	Lampanyctus sp.	15	7
	Lampadena sp.	3	3
	Myctophum punctatum	23	4
	Notoscopelus sp.	14	3
	Myctophidae NS	8	2
Gadiformes			
Moridae	Moridae NS	1	1
Melanonidae	*Melanonus zugmayeri*	3	3
Lophiformes			
Gigantactinidae	*Gigantactis vanhoeffeni*	1	1
Beloniformes			
Scomberesocidae	*Scomberesox saurus*	1	1
Stephanoberyciformes			
Melamphaidae	*Melamphaes suborbitalis*	1	1
	Poromitra sp.	6	5
	Scopelogadus sp.	104	8
Cetomimiformes			
Rondeletiidae	*Rondeletia loricata*	1	1
Beryciformes			
Anoplogasteridae	*Anoplogaster cornuta*	2	2
Scorpaeniformes			
Liparidae	*Paraliparis calidus*	1	1

(Continued)

Table 8. (Continued).

Order/Family	**Species** (or lowest taxon)	No.	Occur.
	Paraliparis copei	2	2
	Paraliparis garmani	3	2
Perciformes			
Howellidae	*Howella brodiei*	5	5
Caristiidae	*Caristius* sp.	1	1
Chiasmodontidae	*Chiasmodon* sp.	4	3
Zoarcidae	*Melanostigma atlanticum*	8	3
Trichiuridae	*Benthodesmus tenuis*	1	1

of *C. rupestris*. Kulka (2006) identified the Laurentian Channel, immediately adjacent to the Scotian Shelf slope, as the pupping area for *C. fabricii*, and the high catches in present surveys are consistent with the survey area being the centre of the species distribution.

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References

ATKINSON, D. B. 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the Northwest Atlantic. *In*: Deep-water fisheries of the North Atlantic oceanic slope. A. G. Hopper, (ed.). Kluwer Academic Publishers, p. 51–111.

BAKER, K. D., R. L. HAEDRICH, P. V. R. SNELGROVE, V. E. WAREHAM, E. N. EDINGER and K. D GILKINSON. 2012. Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. *Deep-Sea Research I*, **65**: 171–188. http://dx.doi.org/10.1016/j.dsr.2012.03.012

BOWERING, W. R. 1983. Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian Northwest Atlantic. *Fish. Bull*., **81**: 599–611.

BOWERING, W. R. and W. B. BRODIE. 1995. Greenland halibut (*Reinhardtius hippoglossoides*). A review of the dynamics of its distribution and fisheries off eastern Canada and Greenland. *In*: Deep-water fisheries of the North Atlantic oceanic slope. A. G. Hopper, (ed.). Kluwer Academic Publishers, p. 113–160.

BÄNÓN, R. 2001. New record of *Cataetyx laticeps* (Bythitidae) in Northwestern Atlantic. *Cybium*, **25**: 93–94.

CARROTHERS, P. J. G. 1988. Scotia-Fundy groundfish survey trawls. *Can. Tech. Rep. Fish. Aquat. Sci.*, **1609:** iv+27 p.

CARUSO, J. H. 2002. Order Lophiiformes: Chaunacidae. *In*: The Living Marine Resources of the Western Central Atlantic. K. E. Carpenter, FAO. Rome, **2**: 1052–1053.

CLARKE, K. R. and R. N. GORLEY. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK. 190 p.

COHEN, D. M., T. INADA, T. IWAMOTO and N. SCIALABBA. 1990. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. *FAO species catalogue* **Vol. 10**, *FAO Fisheries Synopsis,* No. 125.

ESCHMEYER, W. N. and R. FRICKE. 2012. Catalog of Fishes electronic version (12 Jan 2012). http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp.

GEISTDOERFER, P. 1986. Macrouridae. *In:* Fishes of the North-eastern Atlantic and the Mediterranean. P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.). FAO, Paris, **2**: 644–676.

GEISTDOERFER, P. 1990. Macrouridae. *In:* Check-list of the fishes of the tropical Atlantic, Clofeta. J. C. Quéro, J. C. Hureau, C. Karrer, A. Post, and L. Saldanha. UNESCO, Junta Nacional de Investigação Cientifica e Tecnológica, Lisbon, **2**: 541–563.

GOODE, G. B. and T. H. BEAN. 1896. Oceanic Ichthyology. Deep-sea and pelagic fishes of the world. Spec. Bull. *U.S. Nat. Mus.*, **2**: 553 p.

HAEDRICH, R. L. and N. R. MERRETT. 1988. Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *J. Nat. Hist.*, **22**: 1325–1362. http://dx.doi.org/10.1080/00222938800770811

HAEDRICH, R. L., G. T. ROWE and P. T. POLLONI. 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *J. Mar. Res.*, **33**: 191–212.

HAEDRICH, R. L., G. T. ROWE and P. T. POLLONI. 1980. The

megabenthic fauna in the deep sea south of New England, USA. *Mar. Biol.*, **57**: 165–179. http://dx.doi.org/10.1007/BF00390735

HARTEL, K. E., C. P. KENALEY, J. K. GALBRAITH and T. T. SUTTON. 2008. Additional records of deep-sea fishes from off Greater New England. *Northeastern Naturalist*, **15**: 317–334. http://dx.doi.org/10.1656/1092-6194-15.3.317

ICES. 2008. Report of the Planning Group on the North-east Atlantic Continental Slope Survey (PGNEACS). ICES CM 2008/LRC:02, 38 p.

IWAMOTO, T. 2002. Macrouridae. *In*: The living marine resources of the Western Central Atlantic. K. E. Carpenter, FAO, Rome. **Vol. 2**: 977–987.

KULKA, D. W. MS 2006. Abundance and distribution of demersal sharks on the Grand Banks with particular reference to the NAFO Regulatory Area. *NAFO SCR Doc.,* 06/20 Serial No. N5237, 36 p.

MARKLE, D. F., M. J. DADSWELL and R. G. HALLIDAY. 1988. Demersal fish and decapod crustacean fauna of the upper continental slope off Nova Scotia from LaHave to St. Pierre Banks. *Can. J. Zool.*, **66**: 1952–1960. http://dx.doi.org/10.1139/z88-286

MARKLE, D. F. and J. A. MUSICK. 1974. Benthic-slope fishes found at 900 m depth along a transect in the western N. Atlantic Ocean. *Mar. Biol.,* **26**: 225–233.

McEACHRAN, J. D. and J. D. FECHHELM. 1998. Fishes of the Gulf of Mexico. University of Texas Press, Austin, 1112 p.

MOORE, J., K. E. HARTEL, J. E. CRADDOCK and J. K. GALBRAITH. 2003. An annotated list of deepwater fishes from off the New England region, with new area records. *Northeastern Naturalist*, **10**: 159–248.

MURUA, H., F. GONZÁLEZ and D. POWER. 2005. A review of the fishery and the investigations of roughhead grenadier (*Macrourus berglax*) in Flemish Cap and Flemish Pass. *J. Northw. Atl. Fish. Sci.*, **37**: 13–27. http://dx.doi.org/10.2960/J.v37.m567

MØLLER, P. R., J. G. NIELSEN, S. W. KNUDSEN, J. Y. POULSEN, K. SÜNKSEN and O. A. JØRGENSEN. 2010. A checklist of the fish fauna of Greenland waters. *Zootaxa*, **No. 2378**: 1–845.

PINHORN, A. T. and R. G. HALLIDAY. 1997. The Tail of the Grand Bank, southeast of Newfoundland, as a geographical boundary for continental slope fishes. *Can. J. Zool.*, **75**: 1753–1772. http://dx.doi.org/10.1139/z97-805

PINHORN, A. T. (ed.) 1976. Living marine resources of Newfoundland - Labrador: status and potential. *Bull. Fish. Res. Bd. Can.*, **194**: 64 p.

ROULE, L. and F. ANGEL. 1933. Poissons provenant des campagnes du Prince Albert I de Monaco. *Résult. Camp. Scient. Prince Albert I*, **86**: 1–115, 4 pl.

SCOTT, W. B. and M. G. SCOTT. 1988. Atlantic Fishes of Canada. *Can. Bull. Fish. Aquat. Sci.*, **219**: 731 p.

SNELGROVE, P. V. R. and R. L. HAEDRICH. 1985. Structure of the deep demersal fish fauna off Newfoundland. *Mar Ecol. Prog. Ser.*, **27**: 99–107. http://dx.doi.org/10.3354/meps027099

SULAK, K. J. 1982. A comparative taxonomic and ecological analysis of temperate and tropical demersal deep-sea fish faunas in the western North Atlantic. Ph.D. dissertation, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA, 211 p.

SULAK, K. J. 1990. Halosauridae. *In*: Checklist of the fishes of the tropical Atlantic, Clofeta. J. C. Quéro, J. C. Hureau, C. Karrer, A. Post and L. Saldanha. UNESCO, Junta Nacional de Investigação Cientifica e Tecnológica, Lisbon, **1**: 126–132.

SULAK, K. J., P. D. MACWHIRTER, K. E. LUKE, A. D. NOREM, J. M. MILLER, J. A. COOPER and L. E. HARRIS. 2009. Identification guide to skates (Family Rajidae) of the Canadian Atlantic and adjacent regions. *Can. Tech. Rep. Fish. Aquat. Sci.*, **2850**: viii+34 p.

TEMPLEMAN, W. 1966. A record of *Bathypterois dubius* Vaillant from the western North Atlantic, and review of status of the species. *J. Fish. Res. Bd. Canada*, **23**: 715–722. http://dx.doi.org/10.1139/f66-061

THEMELIS, D. E. and R. G. HALLIDAY. 2012. Species composition and relative abundance of the mesopelagic fish fauna in the Slope Sea off Nova Scotia, Canada. *Northeastern Naturalist*, **19**: 177–200. http://dx.doi.org/10.1656/045.019.0204

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Ocean Acidification Decreases Growth and Development in American Lobster (*Homarus americanus*) Larvae

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Abstract

Ocean acidification resulting from the global increase in atmospheric CO_2 concentration is emerging as a threat to marine species, including crustaceans. Fisheries involving the American lobster (*Homarus americanus*) are economically important in eastern Canada and United States. Based on ocean pH levels predicted for 2100, this study examined the effects of reduced seawater pH on the growth (carapace length) and development (time to molt) of American lobster larvae throughout stages I–III until reaching stage IV (postlarvae). Each stage is reached after a corresponding molt. Larvae were reared from stage I in either acidified (pH = 7.7) or control (pH = 8.1) seawater. Organisms in acidified seawater exhibited a significantly shorter carapace length than those in control seawater after every molt. Larvae in acidified seawater also took significantly more time to reach each molt than control larvae. In nature, slowed progress through larval molts could result in greater time in the water column, where larvae are vulnerable to pelagic predators, potentially leading to reduced benthic recruitment. Evidence was also found of reduced survival when reaching the last stage under acidified conditions. Thus, from the perspective of larval ecology, it is possible that future ocean acidification may harm this important marine resource.

Keywords: Crustacea, Decapoda, *Homarus*, lobster, ocean acidification

Introduction

The increasing concentration of atmospheric carbon dioxide (CO_2) because of anthropogenic sources is driving an increase in ocean CO_2 concentration. This is causing a decrease in seawater pH (ocean acidification), potentially putting additional stress on marine organisms already threatened by rising ocean temperatures (Pörtner *et al.*, 2004; 2005; Raven *et al.*, 2005; Widdicombe and Spicer, 2008). Ocean acidification has been acknowledged by the Intergovernmental Panel on Climate Change to have decreased seawater pH by 0.1 units since the industrial revolution (Meehl *et al.*, 2007) and is predicted to result in a further decrease of 0.3-0.4 units by the end of this century (Caldeira and Wickett, 2005; Raven *et al.*, 2005).

With the increase in ocean CO_2 concentration, there is a concomitant decrease in carbonate saturation state (Feely *et al.*, 2004; Orr *et al.*, 2005). The outcome is lower concentration of carbonate ions available for the biosynthesis of calcium carbonate ($CaCO_3$) for building calcified body structures (*e.g.*, shells), as well as higher rates of dissolution of $CaCO_3$ from existing structures. Additionally, increased energetic costs for building and maintaining $CaCO_3$ structures may pull resources from other important biological processes such as growth and reproduction. Therefore, calcifying organisms including mollusks (Michaelidis *et al.*, 2005; Gazeau *et al.*, 2007), echinoderms (Kurihara and Shirayam, 2004), and reef-building corals (Langdon and Atkinson, 2005; Doney *et al.*, 2009) have been a strong focus of study in ocean acidification research, looking at a variety of effects on growth and reproduction (Doney *et al.*, 2009; Hendriks *et al.*, 2010; Kroeker *et al.*, 2010). One of the dominant messages coming from this research is that there is a great deal of variability in responses to decreasing pH between, and even within, taxonomic groups (Ridgwell *et al.*, 2009; Pistevos *et al.*, 2011).

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American lobster (*Homarus americanus*) is a commercially important crustacean on the Atlantic coast of Canada and the United States. This species supports valuable fisheries, with annual landings of $ 562 million in Canada (Fisheries and Oceans Canada, 2012) and $ 228 million in the United States (Singer *et al.*, 2012). Thus, anticipating potential effects of ocean acidification on lobster is relevant to predicting the sustainability of this resource. Crustaceans in general have received little attention on how they may respond to acidification, and research to date has reported variable results (Whiteley, 2011). In a recent study, larvae and postlarvae of the European lobster (*Homarus gammarus*) growing in seawater at pH levels predicted for 2100 exhibited less mineralization of the carapace (Arnold *et al.*, 2009). Softer shells could put the lobster at greater risk for predation soon after molting (Factor, 1995) and may also reduce feeding ability through decreased strength of claws, which are more heavily calcified than the carapace to provide crushing strength for consuming prey (Bosselmann *et al.*, 2007). Conversely, American lobster juveniles exhibited no change in calcification rates at pH levels predicted for 2100 (Ries *et al.*, 2009). Other invertebrates, such as brittle stars (Echinodermata), have been shown to increase calcification rates with decreasing pH, but have done so at the cost of reduced energy available for other processes. In *Amphiura filiformis*, this was seen as muscle wastage (Wood *et al.*, 2008) and, in *Ophiura ophiura*, as reduced arm regeneration (Wood *et al.*, 2010). This was not tested for American lobster, but maintenance of shell mineralization may reduce energy available for important processes such as growth and molting. Some life stages may be more sensitive to lower pH than others, and the most susceptible stage is species-specific (Kurihara, 2008). In particular, lobster larvae may be most sensitive to decreases in pH due to the frequent molting required during their development. Research on the effects of ocean acidification on the various life-history stages of American lobster is necessary to understand how they may respond to future conditions. Here, we present the results of an examination of the effects of CO_2-induced acidification on American lobster larval growth and development at pH levels predicted for 2100. We hypothesized that larvae would exhibit reduced growth and development with reduced pH.

Materials and Methods

We obtained stage-I larvae from the Pictou Lobster Hatchery and Museum (Pictou, Nova Scotia, Canada), where ovigerous females were supplied by local fishermen. Our experiment was carried out in June 2011, corresponding to the natural occurrence of lobster larvae in the Northumberland Strait, in the southern Gulf of St. Lawrence, Canada. Larvae were transferred from the hatchery to the Marine Ecology Lab at Saint Francis Xavier University (Antigonish, Nova Scotia) within 3 h of hatching, and randomly distributed amongst experimental containers (15 larvae per container, 6 containers per each of 2 pH treatments, 180 larvae in total) within minutes upon arrival to the lab. We placed 15 larvae per container to be able to have at least one organism to measure in each container at successive sampling dates, as we anticipated that mortality would occur during the experiment. Each container was supplied with 1 L of constantly aerated, filtered seawater from the Northumberland Strait (temperature ~20 °C, salinity ~31 psu). Seawater in each container was partially changed every two to three days. Molted exoskeletons and dead organisms (due to natural mortality or cannibalism) were removed as they occurred. Larvae were fed live brine shrimp (*Artemia* spp., ~5 individuals ml^{-1}) daily.

For the experiment, we considered two levels of seawater pH (control and acidified), which were produced by bubbling either ambient air or CO_2-enriched air into each replicate container through diffusing stones during the entire experiment. CO_2 concentrations of 400 ppm and 1200 ppm were chosen to represent current conditions and year-2100 conditions (Meehl *et al.*, 2007), respectively. This approach resulted in pH values of 8.1 for the control treatment and 7.7 for the acidified treatment. The CO_2-enriched air was produced by mixing ambient air with CO_2, controlling flow rates with Sierra Instruments Smart Trak mass flow controllers (Provan Control Associates, Quebec, Canada). CO_2 concentration was verified daily using a Qubit S151 CO_2 analyzer (Qubit Systems, Ontario, Canada). Measurements of pH were recorded to the nearest 0.01 units with a pHep5 pH Tester (Hanna Instruments, Quebec, Canada) every second day for the duration of the experiment. With this setup, the two desired levels of pH remained stable during the experiment at the precision level needed for the study (0.1 units of pH).

We evaluated the effects of seawater acidification on the growth and development of American lobster larvae throughout stages I-III until reaching stage IV (postlarvae). To assess effects on growth, we measured carapace length once larvae molted to each stage (day one of the experiment for stage I). To test for effects on development, we recorded the number of days to reach each successive molt. After all larvae reached each stage in a container (n = 6 containers per pH treatment), one individual was randomly selected from each container and its carapace length was measured out of the water using a dissecting microscope to the nearest 0.1 mm. Number of days to reach the molt to each stage was

also recorded, using one average value per container for data analyses whenever the larvae in that container molted at different days. We identified stages using morphological characteristics previously described for this species (Factor, 1995). After carapace measurements, the measured individuals were permanently removed from the experiment. We measured carapace length for one individual per container for each molt to prevent any handling effects (due to manipulation out of the water) from occurring on the individuals that were to be measured for growth and development at later dates. The experiment was terminated after all larvae molted to stage IV (day 13), as three containers in the acidified treatment then had no organisms left because of mortality between stages III and IV. We tested for acidification effects on growth and development using Student's *t*-tests done with SYSTAT 13.0 (SYSTAT, 2009), wherever applicable depending on the occurrence of data variation within molts (see Results). The *t*-test is a statistically robust procedure, especially when sample sizes for both treatments are equal (Mead, 1991); we used the separate-variances procedure (instead of the pooled-variance procedure) to calculate *t* values to ensure reliable results.

Results

Carapace length

Carapace length (Fig. 1) was statistically similar in both pH treatments for stage-I larvae at the beginning of the experiment ($t = 0.75$, $p = 0.472$), indicating an adequate random assignment of larvae to both treatments. Carapace length was, however, significantly lower in acidified seawater than in control seawater for each successive life-history stage: stage II ($t = 8.95$, $p < 0.001$), stage III ($t = 4.05$, $p = 0.002$), and stage IV ($t = 2.88$, $p = 0.024$). All analyses were done using data for six individuals per treatment (one random individual per container), except for stage IV (postlarvae), since six individuals reached stage IV in the control treatment (one in each of the six containers) but only three individuals reached stage IV in the acidified treatment (one in each of three containers) because of mortality between stages III and IV.

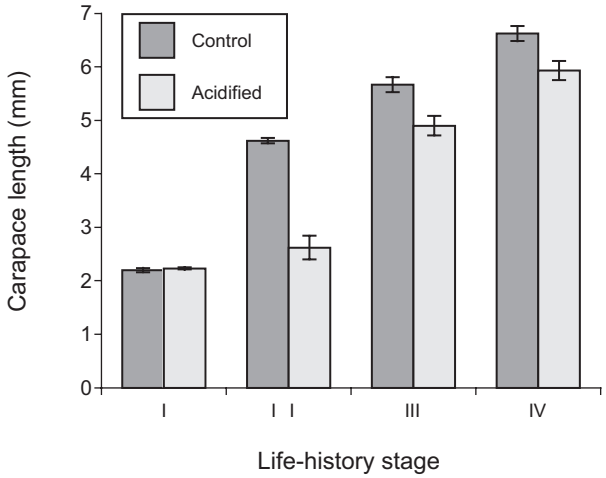

Fig. 1. Carapace length (mean ± SE) for the successive early life-history stages of American lobster grown in control and acidified seawater. Stages I-III correspond to larvae, while stage IV represents postlarvae.

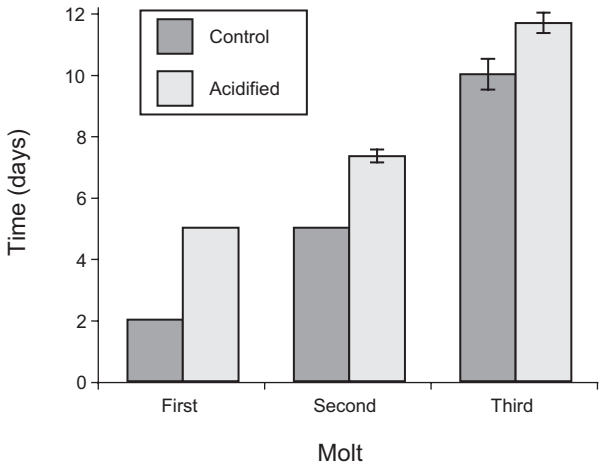

Fig. 2. Cumulative number of days (mean ± SE where it corresponds; see Results) to reach successive molts for American lobster larvae grown in control and acidified seawater. The first molt occurs between larval stages I-II, the second molt between larval stages II-III, and the third molt between larval stage III and stage IV (postlarvae).

Development

Cumulative number of days to molt to successive life-history stages was used to track development rates. Number of days to molt to stages II, III, and IV (Fig. 2) was always higher in acidified seawater. All stage-I larvae in control seawater molted to stage II at day two, while all stage-I larvae in acidified seawater molted to stage II at day five. The lack of within-treatment variation in both treatments prevented statistical tests from being done, but differences were evident, as molting in acidified conditions took more than twice the control time. All stage-II larvae in control seawater molted to stage III at day five, while stage-II larvae in acidified seawater molted to stage III at an average of 7.3 days, which was a significant difference ($t = 11.07$, $p < 0.001$). Stage-III larvae in control seawater molted to stage IV (postlarvae) at an average of 10 days,

while stage-III larvae in acidified seawater molted to stage IV at an average of 12 days, which was a significant difference (t = 2.42, p = 0.046). As noted above, only three stage-III larvae (one per container) survived and molted to stage IV in acidified seawater, while the last six stage-III larvae in control water (one per container) molted to stage IV.

Discussion

Negative species responses to ocean acidification have been commonly found in marine invertebrates. Here, it is shown that American lobster larvae exhibit reduced rates of growth and development under the lower levels of seawater pH predicted for 2100, compared with current levels. Similar responses have been observed for other marine invertebrates, such as sea stars, mussels, and corals (Fabry *et al.*, 2008). Crustacean examples include the shrimp *Pandalus borealis*, which displayed increased development time under acidified conditions (Bechmann *et al.*, 2011), and the spider crab *Hyas araneus*, which displayed both decreased growth and development rates (Walther *et al.*, 2010), although pH levels were not always exactly the same across studies.

American lobster larvae may respond to decreased pH with reduced growth and development rates as a result of reallocation of energy to other processes. Such a response has been seen in brittlestars, which displayed muscle wastage (*Amphiura filiformis,* Wood *et al.*, 2008) or a reduced ability to regenerate lost limbs (*Ophiura ophiura,* Wood *et al.*, 2010) while maintaining growth of calcified structures in acidified seawater. This suggests that maintenance of calcified structures may occur at the cost of somatic tissue loss or alterations to other biological processes, possibly implying indirect effects on fitness and survival. In lobster larvae, additional energy may be allocated to powering proton pumps for maintenance of internal acid-base balance or mineralization of the calcified exoskeleton (Pörtner *et al.*, 2004), reducing investment in growth and delaying the energy-expensive molting process. Effects of decreased pH on calcification of the exoskeleton in American lobster larvae remain to be tested, although it was recently reported that juveniles exhibit no change in calcification rates at pH levels predicted for 2100 (Ries *et al.*, 2009). While different life-history stages of some species may respond differently to acidification (Kurihara, 2008), our results on lobster larvae fit well with results for juveniles, with reductions in larval growth possibly resulting from maintenance of calcification rates in an acidified environment. Research is required on the effects of ocean acidification on calcification in lobster larvae and on growth in juveniles to test this possibility.

The slower growth and development of American lobster larvae under acidified conditions results in delays to reaching each molt, including the key metamorphosis from stage III (last larval stage) to stage IV (postlarvae), which marks the transition from a pelagic to benthic life. A delay in this transition extends the time spent in the water column, where there is little protection from predation (Factor, 1995), which might lead to an increase in predation-related mortality. This, as well as an increase in mortality unrelated to predation between stages III and IV, as found towards the end of our experiment, might lead to reduced lobster recruitment to the seafloor and subsequent reductions in populations.

Our results differ from those for European lobster (*H. gammarus*) larvae, as their growth rate remained unaffected by acidification between stages I-IV (Arnold *et al.*, 2009). That study also found a decrease in carapace mineral content (magnesium) for stage-III larvae in acidified seawater. These results suggest an emerging pattern of differing responses to ocean acidification within taxonomic groups (Ridgwell *et al.*, 2009; Pistevos *et al.*, 2011). Larvae of *H. gammarus* might maintain growth rates at the cost of reduced carapace mineralization. Similarly, adult velvet swimming crab (*Necora puber*) was also found to decrease exoskeletal mineralization in acidified seawater due to partial dissolution of its shell to compensate for extracellular acidosis (Spicer *et al.*, 2007; Small *et al.*, 2010). Decreased calcification has also been seen in other taxonomic groups in response to acidification (*e.g.*, corals, Kleypas and Yates, 2009, and coccolithophores, Beaufort *et al.*, 2011), although tested conditions were not always identical among studies. Response differences between closely related species emphasize the need for research on a range of organisms from various geographic ranges. In doing so, it will be important to test for the same range of abiotic values to facilitate comparisons.

Overall, our results suggest that American lobster larvae may exhibit reduced performance in response to ocean acidification at pH levels predicted for 2100. It remains to be tested whether reduced growth and development would also occur in juveniles and adults. Effects on fertility and hatching also require investigation. Since some crustaceans (*e.g.*, crabs) decrease thermal tolerance at lower pH (Metzger *et al.*, 2007; Walther *et al.*, 2009), the interactive effects of acidification and rising temperature should be investigated as well. It is also unknown whether lobsters have the potential for adaptation to predicted ocean conditions to some extent. These key questions need investigation in order to best inform industry, policy-

makers, and conservation programs on possible future scenarios. From the perspective of larval ecology, our study suggests that future ocean acidification may harm this important marine resource.

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References

ARNOLD, K. E., H. S. FINDLAY, J. I. SPICER, C. L. DANIELS and D. BOOTHROYD. 2009. Effect of CO_2-related acidification on aspects of the larval development of the European lobster, *Homarus gammarus* (L.). *Biogeosciences*, **6**: 1747–1754. http://dx.doi.org/10.5194/bg-6-1747-2009

BEAUFORT, L., I. PROBERT, T. de GARIDEL-THORON, E. M. BENDIF, D. RUIZ-PINO, N. METZL, C. GOYET, N. BUCHET, P. COUPEL, M. GRELAUD, B. ROST, R. E. M. RICKABY and C. DE VARGAS. 2011. Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. *Nature*, **476**: 80–83. http://dx.doi.org/10.1038/nature10295 PMid:21814280

BECHMANN, R. K., I. C. TABAN, S. WESTERLUND, B. F. GODAL, M. ARNBERG, S. VINGEN, A. INGVARSDOTTIR and T. BAUSSANT. 2011. Effects of ocean acidification on early life stages of shrimp (*Pandalus borealis*) and mussel (*Mytilus edulis*). *J. Toxicol. Envir. Health*, **7**: 424–438. http://dx.doi.org/10.1080/1528739.2011.550460 PMid:21391089

BOSSELMANN, F., P. ROMANO, H. FABRITIUS, D. RAABE and M. EPPLE. 2007. The composition of the exoskeleton of two Crustacea: the American lobster *Homarus americanus* and the edible crab *Cancer pagurus*. *Thermochimica Acta*, **463**: 65–68. http://dx.doi.org/10.1016/j.tca.2007.07.018

CALDEIRA, K. and M. E. WICKETT. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *J. Geophys. Res.*, **110**: C09S04. http://dx.doi.org/10.1029/2004JC002671

DONEY, S. C., V. J. FABRY, R. A. FEELY and J. A. KLEYPAS. 2009. Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci.*, **1**: 169–192. http://dx.doi.org/10.1146/annurev.marine.010908.163834

FABRY, V. J., B. A. SEIBEL, R. A. FEELY and J. C. ORR. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.*, **65**: 414–432. http://dx.doi.org/10.1093/icesjms/fsn048

FACTOR, J. R., 1995. Biology of the lobster *Homarus americanus*. Academic Press, San Diego, 528 p.

FEELY, R. A., C. L. SABINE, K. LEE, W. BERELSON, J. KLEYPAS, V. J. FABRY and F. J. MILLERO. 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science*, **305**: 362–366.

FISHERIES AND OCEANS CANADA, 2012. Commercial fisheries. Available from http://www.dfo-mpo.gc.ca/stats/commercial-eng.htm (last accessed on 25 June).

GAZEAU, F., C. QUIBLIER, J. M. JANSEN, J. P. GATTUSO, J. J. MIDDELBURG and C. H. R. HEIP. 2007. Impact of elevated CO_2 on shellfish calcification. *Geophys. Res. Lett.*, **34**: L07603. http://dx.doi.org/10.1029/2006GL028554

HENDRIKS, I. E., C. M. DUARTE and M. ÁLVAREZ. 2010. Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuar., Coast. Shelf Sci.*, **86**: 157–164. http://dx.doi.org/10.1016/j.ecss.2009.11.022

KLEYPAS, J. A. and K. K. YATES. 2009. Coral reefs and ocean acidification. *Oceanography*, **22**: 108–117. http://dx.doi.org/10.5670/oceanog.2009.101

KROEKER, K. J., R. L. KORDAS, R. N. CRIM and G. G. SINGH. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.*, **13**: 1419–1434. http://dx.doi.org/10.1111/j.1461-0248.2010.01518.x PMid:20958904

KURIHARA, H. 2008. Effects of CO_2-driven ocean acidification on the early developmental stages of invertebrates. *Mar. Ecol. Prog. Ser.*, **373**: 275–284. http://dx.doi.org/10.3354/meps07802

KURIHARA, H. and Y. SHIRAYAM. 2004. Effects of increased atmospheric CO_2 on sea urchin early development. *Mar. Ecol. Prog. Ser.*, **274**: 161–169. http://dx.doi.org/10.3354/meps274161

LANGDON, C. and M. J. ATKINSON. 2005. Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *J. Geophys. Res.*, **110**: C09S07. http://dx.doi.org/10.1029/2004JC002576

MEAD, R. 1991. The design of experiments. Statistical principles for practical applications. Cambridge University Press, Cambridge, 620 p.

MEEHL, G. A., T. F. STOCKER, W. D. COLLINS, P. FRIEDLINGSTEIN and A. T. GAYE. 2007. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

METZGER, R., F. J. SARTORIS, M. LANGENBUCH and H. O. PÖRTNER. 2007. Influence of elevated CO_2 concentrations on thermal tolerance of the edible crab *Cancer pagurus*. *J. Thermal Biol.*, **32**: 144–151. http://dx.doi.org/10.1016/j.jtherbio.2007.01.010

MICHAELIDIS, B., C. OUZOUNIS, A. PALERAS and H. O. PÖRTNER. 2005. Effects of long-term moderate

hypercapnia on acid-base balance and growth rate in marine mussels (*Mytilus galloprovincialis*) *Mar. Ecol. Prog. Ser.*, **93**: 109–118. http://dx.doi.org/10.3354/meps293109

ORR, J. C., V. J. FABRY, O. AUMONT and L. BOPP. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**: 681–686. http://dx.doi.org/10.1038/nature04095 PMid:16193043

PISTEVOS, J. C. A., P. CALOSI, S. WIDDICOMBE and J. D. D. BISHOP. 2011. Will variation among genetic individuals influence species responses to global climate change? *Oikos*, **120**: 675–689. http://dx.doi.org/10.1111/j.1600-0706.2010.19470.x

PÖRTNER, H. O., M. LANGENBUCH and B. MICHAELIDIS. 2005. Synergistic effects of temperature extremes, hypoxia and increases in CO_2 on marine animals: from Earth history to global change. *J. Geophys. Res.*, **110**: C09S10. http://dx.doi.org/10.1029/2004JC002561

PÖRTNER, H. O., M. LANGENBUCH and A. REIPSCHLÄGER, 2004. Biological impact of elevated ocean CO_2 concentrations: lessons from animal physiology and earth history. *J. Oceanogr.*, **60**: 705–718. http://dx.doi.org/10.1007/s10872-004-5763-0

RAVEN, J., K. CALDEIRA, H. ELDERFIELD, O. HOEGH-GULDBERG, P. LISS, U. RIEBESELL, J. SHEPHERD, C. TURLEY and A. WATSON. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. Policy document 12/05. The Royal Society, London, 57 p.

RIDGWELL, A., D. N. SCHMIDT, C. TURLEY, C. BROWNLEE, M. T. MALDONADO, P. TORTELL and J. R. YOUNG. 2009. From laboratory manipulations to Earth system models: scaling calcification impacts of ocean acidification. *Biogeosciences*, **6**: 2611–1623. http://dx.doi. org/10.5194/bg-6-2611-2009

RIES, J. B., A. L. COHEN and D. C. McCORKLE. 2009. Marine calcifiers exhibit mixed responses to CO_2-induced ocean acidification. *Geology*, **37**: 1131–1134. http://dx.doi.org/10.1130/G30210A.1

SINGER, L. T. 2012. Maine Department of Marine Resources, Coastal Fishery Research Priorities, Lobster (*Homarus americanus*). Available from http://www.maine.gov/dmr/research/priorities10 (last accessed on 25 June).

SMALL, D., P. CALOSI, D. WHITE, J. I. SPICER and S. WIDDICOMBE. 2010. Impact of medium-term exposure to CO_2-enriched seawater on the physiological functions of the velvet swimming crab *Necora puber*. *Aq. Biol.*, **10**: 11–21.

SPICER, J. I., A. RAFFO and S. WIDDICOMBE. 2007. Influence of CO_2-related seawater acidification on extracellular acid–base balance in the velvet swimming crab *Necora puber*. *Mar. Biol.*, **151**: 1117–1125. http://dx.doi.org/10.1007/s00227-006-0551-6

SYSTAT. 2009. SYSTAT for Windows, Version 13.0. SYSTAT Software Inc., Richmond, California.

WALTHER, K., K. ANGER and H. O. PÖRTNER. 2010. Effects of ocean acidification and warming on the larval development of the spider crab *Hyas araneus* from different latitudes (54° vs. 79° N). *Mar. Ecol. Prog. Ser.*, **417**: 159–170. http://dx.doi.org/10.3354/meps08807

WALTHER, K., F. J. SARTORIS, C. BOCK and H. O. PÖRTNER. 2009. Impact of anthropogenic ocean acidification on thermal tolerance of the spider crab *Hyas araneus*. *Biogeosciences*, **6**: 2207–2215. http://dx.doi.org/10.5194/bg-6-2207-2009

WHITELEY, N. M. 2011. Physiological and ecological responses of crustaceans to ocean acidification. *Mar. Ecol. Prog. Ser.*, **430**: 257–271. http://dx.doi.org/10.3354/meps09185

WIDDICOMBE, S. and J. I. SPICER. 2008. Predicting the impact of ocean acidification on benthic biodiversity: what can animal physiology tell us? *J. Exp. Mar. Biol. Ecol.*, **366**: 187–197. http://dx.doi.org/10.1016/j.jembe.2008.07.024

WOOD, H. L., J. I. SPICER, D. M. LOWE and S. WIDDICOMBE. 2010. Interaction of ocean acidification and temperature: the high cost of survival in the brittlestar *Ophiura ophiura*. *Mar. Biol.*, **157**: 2001–2013. http://dx.doi.org/10.1007/s00227-010-1469-6

WOOD, H. L., J. I. SPICER and S. WIDDICOMBE. 2008. Ocean acidification may increase calcification rates, but at a cost. *Proc. Royal Soc. B*, **275**: 1767–1773. http://dx.doi.org/10.1098/rspb.2008.0343 PMid:18460426 PMCid:2587798

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Atlantic Bluefin Tuna (*Thunnus thynnus*) Diet in the Gulf of St. Lawrence and on the Eastern Scotian Shelf

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Abstract

The stomach contents of 68 Atlantic bluefin tuna (*Thunnus thynnus*) landed in Port Hood and Canso, Nova Scotia, in 2010, were analyzed to characterize the diet of bluefin tuna at the two locations. Of the sampled fish, 54 stomachs had contents. Pelagic schooling fish such as herring (C*lupea harengus*) and mackerel (*Scomber scombrus*) dominated the diets in both regions. However, a number of rare species, including demersal species, were also observed. Despite the difference in location and the significantly larger size of the Atlantic bluefin tuna landed in Port Hood, the diets of the Atlantic bluefin tuna landed at both sites were similar.

Keywords: Atlantic bluefin tuna, diet, Nova Scotia, stomach content analysis.

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) are a top predator in neretic and pelagic ecosystems of the North Atlantic as well as a valuable catch for commercial and recreational fisheries. The species is widespread and in recent years it has been found in the Western Atlantic from Newfoundland and Labrador in the north to Gulf of Mexico in the south (ICCAT, 2011). Archival and satellite tag data indicate that Atlantic bluefin tuna from both western and eastern Atlantic populations migrate to Canadian waters (Block *et al.*, 2005; Galuardi *et al.*, 2010; Lawson *et al.*, 2010; Wilson *et al.*, 2011) in order to take advantage of rich summer foraging grounds (Walli *et al.*, 2009). Of the fish that travel to Canada, the majority are large, mature individuals weighing over 150 kg (Neilson *et al.*, 2009). The Atlantic bluefin tuna's capacity to warm muscle, viscera, and brain tissues, along with cardiac specializations (Landeira-Fernandez *et al.*, 2011), increases its performance as a predator in cool temperatures (Carey and Teal, 1969; Graham and Dickson, 2004) and may have evolved to facilitate niche expansion into cooler northern waters (Block *et al.*, 1993).

Diet studies provide insight into the food preferences of the Atlantic bluefin tuna. Stomach content analyses (SCA) performed on catches in the Mid Atlantic Bight (Eggleston and Bochenek, 1990; Butler *et al.*, 2010; Logan *et al.*, 2011), the Gulf of Maine (Chase, 2002), and Newfoundland (Butler, 1971) indicate that Atlantic bluefin tuna feed preferentially on pelagic schooling fish and opportunistically on other species. Similar diet content data are not yet available for waters off Nova Scotia and Prince Edward Island. In this study, the stomach contents of Atlantic bluefin tuna caught by the Canadian commercial fishery in the Gulf of St. Lawrence (GSL) and landed in Port Hood and caught on the Scotian Shelf and landed in Canso were analysed in order to quantify diet composition in these key foraging regions.

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Methods

Atlantic bluefin tuna stomachs were collected from the 2010 commercial rod and reel fishery. The samples from the GSL were collected in Port Hood (Fig. 1), Nova Scotia, between 27 September, 2010 and 5 October, 2010. The samples from the eastern Scotian Shelf were collected in Canso (Fig. 1), Nova Scotia, between 15 September, 2010 and 20 November, 2010. Port staff recorded the date and time of capture, geographic coordinates of the capture location, type of bait, curved fork length (CFL), weight of the entire fish (*RW*), weight after gutting the fish (*DW*), and sex. A least squares linear regression was created using the 24 pairs of *DW* and *RW* data collected in this study ($RW = (1.2374*DW) + 7.0754$; $r^2 = 0.98$) and used to calculate the *RW* of sampled fish for which *DW* was available but *RW* was not. Weight and CFL were compared using the one-tailed Mann-Whitney test. Stomachs were removed from the fish at sea in Canso and once they reached the ice house in Port Hood. The samples were frozen and analyzed at a later date.

Stomach contents were thawed and rinsed with fresh water. Prey items were identified to the lowest possible taxon and were weighed together and separately to the nearest 0.1g. A prey that could not be identified was recorded as unidentified. Bait items were identified by their cut marks and these were not included in the quantitative analysis. For each sampling port, stomach contents were described by prey-specific percent weight (%W), which was calculated as the total weight of each taxon divided by the total weight of all stomach contents. Stomach contents were also described as prey-specific frequency of occurrence (%O) for each port, which was calculated as the number of stomachs in which a taxon occurred divided by the total number of stomachs with contents. Only stomachs containing prey were included in the analyses. The diets at both locations were compared using principal components analysis (PCA) on the normalized %O data as proposed by De Crespin de Billy *et al*. (2000) using R (version 2.11.1, The R Foundation for Statistical Computing). Prey %O was plotted against prey-specific %W (P_i) to examine prey dominance, individual and population-wide niche widths, and feeding strategies at both locations, as described by Amundsen *et al*. (1996).

Prey species were grouped by family and cumulative prey curves (CPCs) were created *a posteriori* to determine whether the sample sizes were sufficiently large to be used to describe prey abundance in both port locations. The CPCs were built by randomly resampling the stomachs 1000 times (Bizzarro *et al*., 2007) and plotting the mean cumulative number of identified taxa against the number of stomachs sampled (Ferry and Cailliet, 1996). CPCs

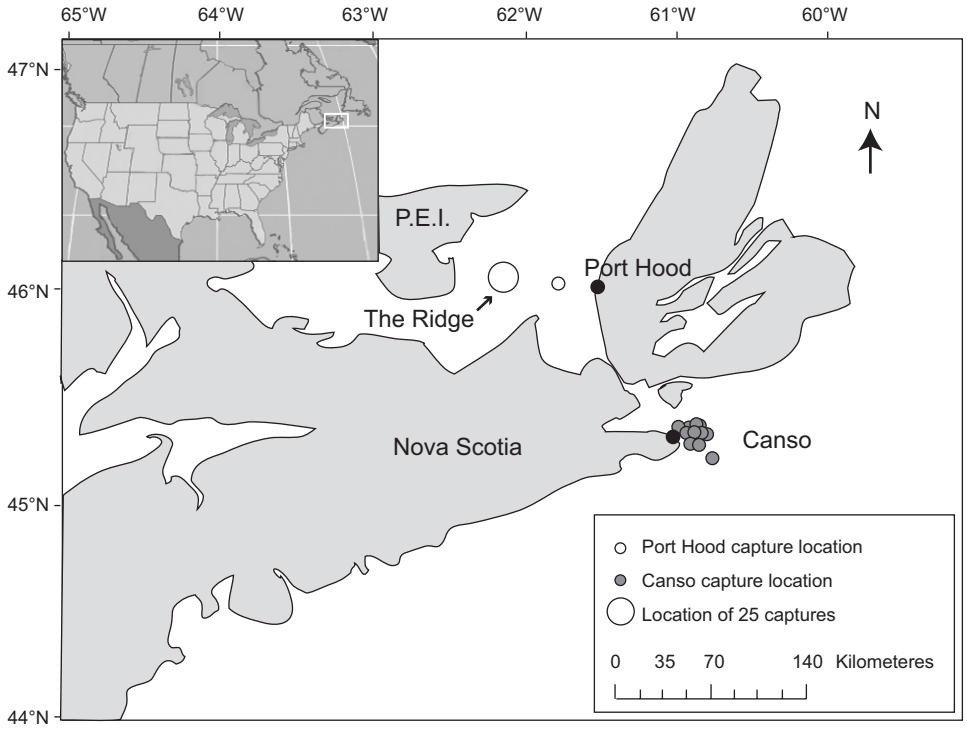

Fig. 1. Reported Atlantic bluefin tuna capture locations (n = 43) and sampling locations (black circles). Capture locations were not reported for 14 samples collected in Canso and 9 samples collected in Port Hood.

were created using Matlab (Student version 2010a, The MathWorks, Inc., Natick, MA). The Student's *t*-test was used to determine if the slope of the least-squares linear regression of the final four stomachs sampled was significantly different from zero. If the slope was not significantly different from zero sample size was considered adequate.

Results

A total of 68 stomachs were collected from the commercial fishery; 33 were collected in Canso and 35 in Port Hood. All fish for which geographic coordinates were provided were caught within approximately 68 km of the sampling port locations (Fig. 1). In Port Hood, 25 of the stomachs were collected from an underwater feature called "The Ridge" (Fig. 1). The mean (± 1s.d.) CFL of all fish collected from Port Hood was 265 ± 22 cm (n = 35) with a mean *RW* of 340 ± 68 kg (n = 35). The mean *RW* for Port Hood includes two sample weights estimated from *DW* using the regression generated from this study's data. The mean CFL of fish sampled in Canso was 144 ± 37 cm (n = 23) and the mean *RW* was 170 ± 87 kg (n = 31), including 17 values estimated from *DW*. Most fish greater than 250 kg *RW* were sampled in Port Hood, whereas most fish less than 250 kg were sampled in Canso (Fig. 2). Both *RW* and CFL differed significantly between sites ($\alpha = 0.05$; $p < 0.001$). Thirty-one (94%) of the stomachs from Canso and 23 (66%) of the stomachs from Port Hood had contents. There were significantly more empty stomachs collected in Port Hood than in Canso (χ^2, $p = 0.01$). A total of 1564 prey items were found; 707 from Canso and 857 from Port Hood. The prey items identified included eleven families of teleosts, consisting of at least twelve species; four families of crustaceans, consisting of at least five species, all of which were found only in Canso samples; two species of bivalve (*Mytilus edulis* and Tellinidae sp.); cephalopods (likely *Illex illecebrosus* and/or *Loligo pealeii*); brown algae (Phaeophyceae sp.); and one starfish (*Leptasterias tenera*) (Table 1). Teleosts dominated the stomach contents in both sampling locations. In the stomachs sampled from Canso, unidentified teleosts occurred most frequently (Fig. 3) and constituted the greatest proportion of prey weight (Fig. 4). The second most important prey item in Canso, both by %O and %W, was herring (*Clupea harengus*), followed by mackerel (*Scomber scombrus*). Of the stomachs sampled at Port Hood, herring was the most important both by %O (Fig. 3) and %W (Fig. 4), followed by unidentified teleosts and mackerel. Unidentified squid occurred in 19% of all stomachs combined, but because their remains consisted exclusively of beaks and pens, their contribution to %W was negligible. Gadid otoliths were moderately frequent in the samples from Canso, but contributed little to %W.

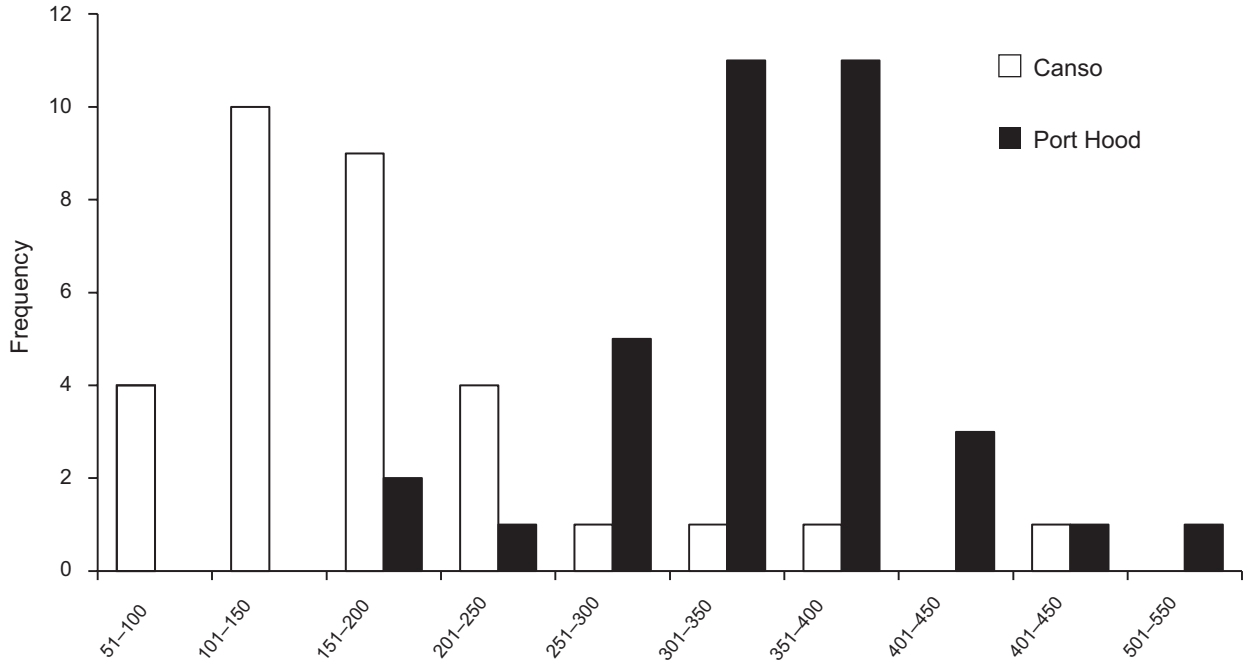

Fig. 2. The frequency of round weights (*RW*) of Atlantic bluefin tuna (*Thunnus thynnus*), in kilograms, sampled in Port Hood (n = 35) and Canso (n = 31), Nova Scotia, during Autumn, 2010. The data includes two values for Port Hood and 17 values for Canso estimated from dressed weight (*DW*) using the regression generated from this study's data (*RW* = (1.2374**DW*) + 7.0754; $r^2 = 0.98$).

Table 1. Number observed, frequency of occurrence, and percent weight of prey taxa found in Atlantic bluefin tuna (*Thunnus thynnus*) stomachs collected in Port Hood and Canso.

		Port Hood (n = 23)*			Canso (n = 31)			Combined (n = 54)		
Family	**Species**	N	% O	% W	N	% O	% W	N	% O	% W
	Teleostei									
	Unidentified	43	39.2	25.6	409	67.7	44.1	452	57.4	0.4
Clupeidae	*Clupea harengus*	46	65.2	39.7	63	48.4	39.7	109	55.6	0.5
Scombridae	*Scomber scombrus*	13	21.7	12.1	60	38.7	13.2	73	31.5	0.1
Merlucciidae	*Merluccius bilinearis*				16	6.5	0.1	16	3.7	<0.1
Scomberesocidae	*Scomberesox saurus*	3	4.3	<0.1				3	1.9	<0.1
Cottidae	*Myoxocephalus octodecemspinosis*	1	4.3	1.6				1	1.9	<0.1
Sebastidae	*Sebastes* spp.				11	6.5	<0.1	11	3.7	<0.1
Gadidae	*Gadus morhua*				5	16.1	<0.1	5	9.3	<0.1
Gadidae	*Melanogrammus aeglefinus*				2	3.2	<0.1	2	1.9	<0.1
Ammodytidae	*Ammodytes* spp.				1	3.2	0.1	1	1.9	<0.1
Osmeridae	*Mallotus villosus*				1	3.2	<0.1	1	1.9	<0.1
Balistidae	*Balistidae* spp.				1	3.2	0.2	1	1.9	<0.1
Labridae	*Tautogolabrus adspersus*	1	4.3	1.4				1	1.9	<0.1
	Crustacea									
Pandalidae	*Pandalus borealis*				53	16.1	2.3	53	9.3	<0.1
Euphausiidae	**Euphausiidae spp.				32	3.2	<0.1	32	1.9	<0.1
Hyperiidae	†Hyperiidae spp.				6	3.2	<0.1	6	1.9	<0.1
	Unidentified crustacean				3	9.7	<0.1	3	5.6	<0.1
	Mollusca									
Mytilidae	*Mytilus edulis*	735	4.3	2.6				735	1.9	<0.1
Tellinidae	Tellinidae spp.				1	3.2	<0.1	1	1.9	<0.1
	Unidentified squid	10	21.7	<0.1	42	16.1	<0.1	10	18.5	<0.1
	Asteroidea									
Asteroidea	*Leptasterias tenera*	1	4.3	0.3				1	1.9	<0.1
	Phaeophyceae									
Phaeophyceae	Unidentified algae	4	17.4	0.2	1	3.2	<0.1	4	9.3	<0.1

*1 bird feather and 2 occurrences of anthropogenic debris - a piece of a plastic bag and pieces of a plastic fish basket, one of which was lodged in the stomach wall, were also found in samples from Port Hood.

**3 individuals were identified as the species *Meganyctiphanes norvegica*

†1 individual was identified as the species *Themisto libellula*

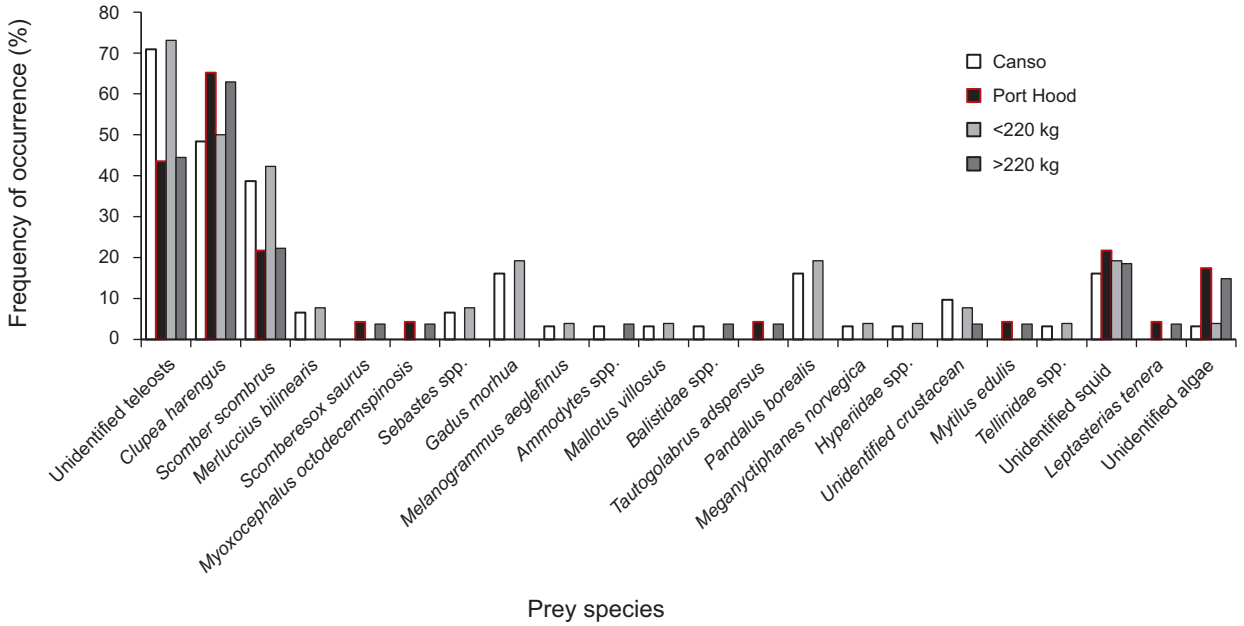

Fig. 3. Percent frequency of occurrence of prey items in Atlantic bluefin tuna (Thunnus thynnus) stomachs grouped by sample port, Port Hood (n = 23) and Canso (n = 31), and by size, <220 kg round weight (*RW*) (n = 26) and >220 kg (n = 27). Samples were collected during Autumn, 2010. The weight classes include 19 values estimated from dressed weight (*DW*) using the regression generated from this study's data ($RW = (1.2374*DW) + 7.0754$; $r^2 = 0.98$).

Northern shrimp (*Pandalus borealis*) also appeared with regularity in the Canso samples, but contributed little to prey biomass. Crustaceans were absent from the samples collected in Port Hood. Notably, the hyperiid amphipod species *Themisto libellula* and a fish from the family Balistidae were also identified in samples from Canso.

In the combined data from both sampling sites, unidentified teleosts occurred 29% more frequently (Fig. 3) and their %W was 16% greater (Fig. 4) in the stomachs of small tuna (<220 kg *RW*, n = 26) than large tuna (>220 kg *RW*, n = 27). Conversely, herring occurred 13% more frequently (Fig. 3) and their %W was 26% greater (Fig. 4) in large tunas than in small tunas.

The CPC for Canso reached an asymptote (p = 0.05, n = 31) (Fig. 5). Neither the CPC for Port Hood nor for the combined data reached an asymptote (Port Hood: p = 0.02, n = 23; combined samples for both ports: p = 0.01, n = 54).

In the plot of frequency of occurrence against P_i (Fig. 6), the data points are distributed in a line from the bottom left to the top right of the plot. The points for herring (Cl), mackerel (Sc), and unidentified teleosts (UF) are clustered in the top right, whereas most other species cluster to the bottom left. Both trends are more pronounced in Canso. The distribution of the points in the plot indicates that the Atlantic bluefin tuna in both sites have dominant prey, herring and mackerel, but also demonstrate generalized feeding on a number of rare species.

The first three principal components were plotted and explained 39%, 19%, and 15% of the variance, respectively (Fig. 7). The observations from each sampling location did not cluster noticeably along any of the axes. Seven species appeared only in the samples from Port Hood and twelve occurred only in the samples from Canso but these occurrences were rare (Fig. 4, Table 1).

Discussion

The results above are consistent with the findings of other feeding studies on Atlantic bluefin tuna diet in the North Atlantic (Dragovich, 1970; Butler, 1971; Eggleston and Bochenek, 1990; Chase, 2002; Butler *et al*., 2010) which characterize Atlantic bluefin tuna as opportunistic, non-specialized predators that feed primarily on schooling teleosts. The presence of demersal prey species in the stomach contents indicates that Atlantic bluefin tuna are foraging not only on pelagic prey above the thermocline, but also on bottom dwelling species. The feeding on demersal species occurred in the GSL despite strong thermal stratification which would often expose the Atlantic bluefin tuna to extremely cold temperatures.

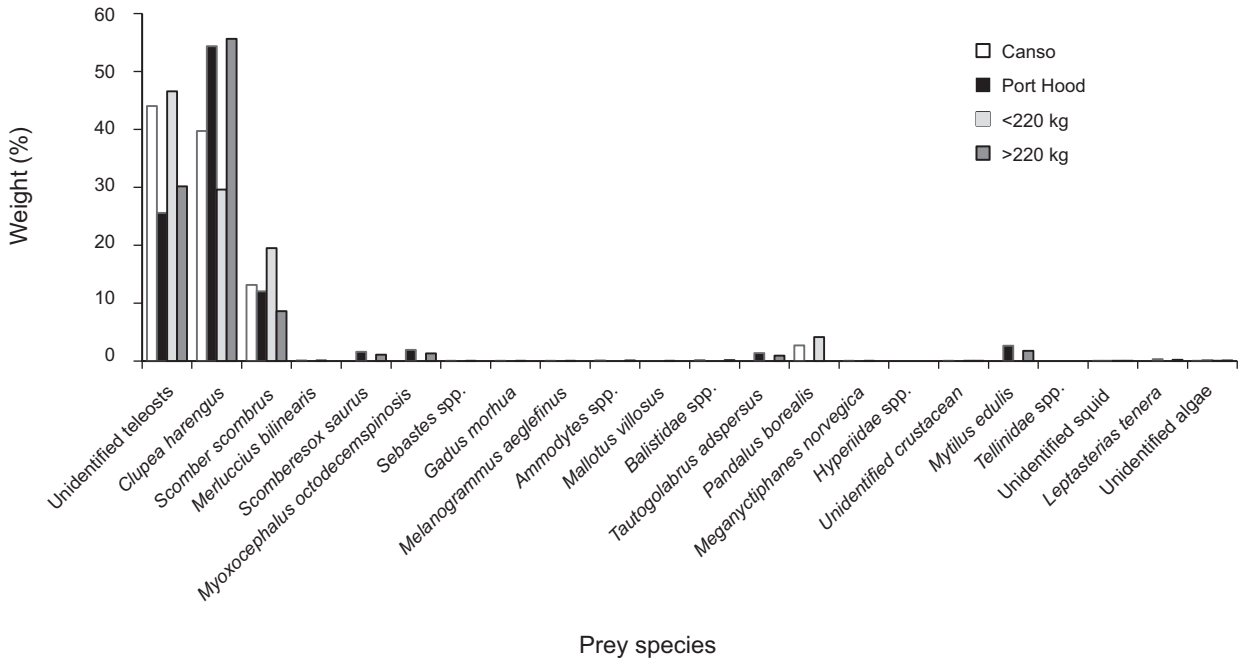

Fig. 4. Percent weight of Atlantic bluefin tuna prey items in Atlantic bluefin tuna (*Thunnus thynnus*) stomachs grouped by sample port, Port Hood (n = 23) and Canso (n = 31), and by size, <220 kg round weight (n = 26) and >220 kg (n = 27). Samples were collected during Autumn, 2010. The weight classes include 19 values estimated from dressed weight (*DW*) using the regression generated from this study's data ($RW = (1.2374*DW) + 7.0754$; $r^2 = 0.98$).

Given the slopes of the last three values of the CPCs for Canso and Port Hood, one can assume that the sample size was adequate to describe the diet of those fish caught in Canso, but too small to fully describe the diet of Atlantic bluefin tuna in the region Port Hood or for the combined data (Fig.5). Nevertheless, the two datasets represent the only data for these two regions and may reasonably be used for an initial description of Atlantic bluefin tuna diet in these places.

The overall distribution of the data points on the plot of frequency of occurrence against P_i (Fig. 6) from the bottom left to the top right indicates that Atlantic bluefin tuna at both sites display varying degrees of specialization in feeding strategies between individuals, but that few are either extreme specialists or generalists. This plot is useful for displaying the relationship between occurrence and amount. Without data on the relative abundance of prey species in the sampling locations it is not possible to determine whether diet composition is a reflection of prey species availability, feeding strategy, or a combination of the two. A comparison between prey abundance and Atlantic bluefin tuna diet composition at the capture sites is recommended for future investigation.

In the PCA (Fig. 7) the absence of clustering along any of the axes indicates that the main constituents of the diets of the fish at both locations were similar. Larger sample sizes would have a better representation of the frequency of occurrence of these rare species and would produce a more reliable PCA.

Stomach content analysis yields a detailed description of a population's diet at a point in time (Hyslop, 1980) and may also reflect local prey species community composition and abundance (Overholtz *et al*., 2000; Chase, 2002; Link and Garrison, 2002). Yet, despite its convenience in quantifying diet, there are a number of biases inherent to SCA. The rapid digestion rate by Atlantic bluefin tuna as a result of the warming of visceral tissues (Carey *et al*., 1984); differential rates of digestion among food items (Hyslop, 1980; Olson and Boggs, 1986; Chase, 2002); and proneness to regurgitation during capture (Rooker *et al*., 2007) are all problems that likely played a role in biasing the results. Further, as stomachs were collected by commercial fishers, temporal fishing patterns (choosing to fish at dawn versus dusk), fishing quotas, the use of preferred fishing grounds, and capture methods introduce sampling bias (Hyslop, 1980).

The causes of the different proportions of empty stomachs at both sampling sites are unclear. Variability in the availability of prey at the time of capture at the fishing sights is unknown and may have affected the proportions

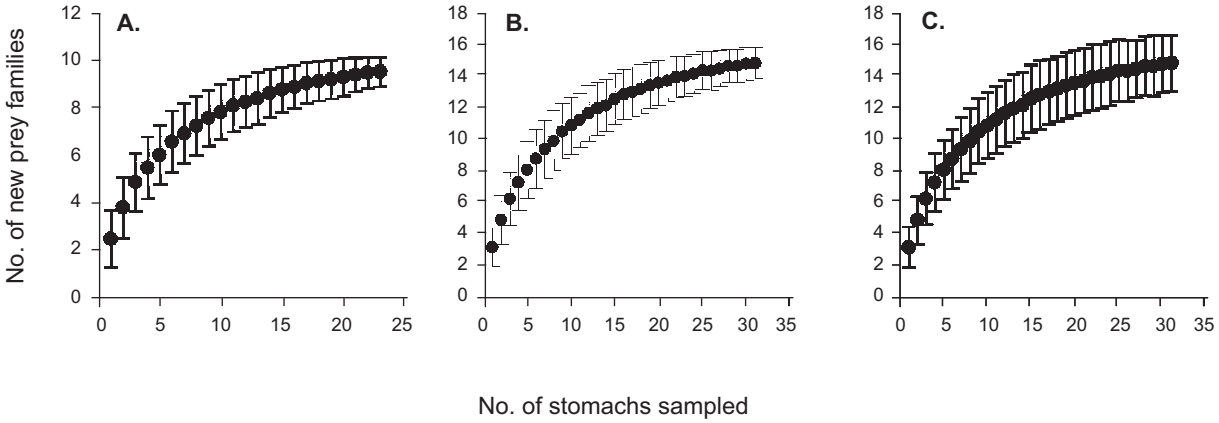

Fig. 5. Cumulative prey curves and standard deviations for Atlantic bluefin tuna (*Thunnus thynnus*) stomach samples collected in (**A**) Port Hood, Nova Scotia (n = 23), (**B**) Canso, Nova Scotia (n = 31), and (**C**) the two ports combined (n = 54), were created using 1000 randomly sampled iterations. The least squares regression of the last four samples of the CPC for Canso reached an asymptote (p = 0.05). The CPCs for Port Hood and the combined did not reach an asymptote (Port Hood: p = 0.02; combined samples for both ports: p = 0.01).

of empty stomachs. Different capture methods at each sample site may also have contributed to the occurrence of empty stomachs. Some fishermen that land their catch at Port Hood are known to pump water into the stomach in an attempt to cool the fish more quickly and may have inadvertently flushed out the contents. There is also anecdotal evidence that fish with a longer fight time may be more likely to regurgitate during that time (D. Cameron, Ceilidh Fishermen's Co-op, 158 Main St., Port Hood, Nova Scotia, B0E 2W0, pers. comm.); however, the authors observed few distended stomachs, which suggests that regurgitation was rare. Although the number of empty stomachs is significantly larger in Port Hood, the sample size is relatively small, as indicated by the CPC analyses, and this difference may simply have been a random occurrence.

The extent to which the findings of this study represent the diet of Atlantic bluefin tuna in these regions may also be limited because sampling was only performed in the Autumn season of one year. Atlantic bluefin tuna diets can vary greatly between years (Chase, 2002; Overholtz, 2006) and seasons (Butler, 1971). Temperature characteristics in the GSL are known to vary between years and may cause changes in prey availability and Atlantic bluefin tuna distribution (Vanderlaan *et al*., 2011). Prey availability also varies throughout the year, as is well documented in the GSL. Mackerel arrive in the GSL in late May and early June (Sette, 1950; D'Amours and Castonguay, 1992) and remain until October (McKay, 1979), whereas herring congregate to spawn in the spring, before the Atlantic bluefin tuna have arrived, and in the Autumn from August to the end of September (Messieh, 1987). The presence of gravid herring in the samples from Port Hood confirms that the Atlantic bluefin tuna in the GSL were feeding on the aggregations of Autumn spawners during sampling. It is likely that the Atlantic bluefin tuna arrive in the GSL in late June and July (Wilson *et al*., 2011) to feed on mackerel and switch to the more plentiful herring later in the summer. For this reason, sampling late in the season may also bias the stomach content results.

The presence of the remains of a balistid in one stomach is surprising, as these are warn-water species. Fish from the family Balistidae and the related Monacanthidae have been reported occasionally in the waters off of Nova Scotia (Scott and Scott, 1988). These occurrences are likely associated with the approach of warm water masses from the Gulf Stream. Sea-surface temperature satellite images indicate that neither the Gulf Stream nor warm-core rings were within 200 km of Canso during the month prior to the capture of the tuna, making the presence of balistids and monacanthids unlikely. It is possible that the tuna had consumed this fish while in the Gulf Stream and the large bones may have resisted digestion and/or expulsion and remained in the stomach as the tuna traveled north. The bones were large and worn, lending credence to the later explanation.

There appear to be differences in diet between the Atlantic bluefin tuna sampled at each location, although these differences were not statistically significant. The factors contributing to these variations are difficult to determine as Atlantic bluefin tuna size and location are closely correlated in the data. The differences in diet between sampling locations are primarily the occurrences of rare

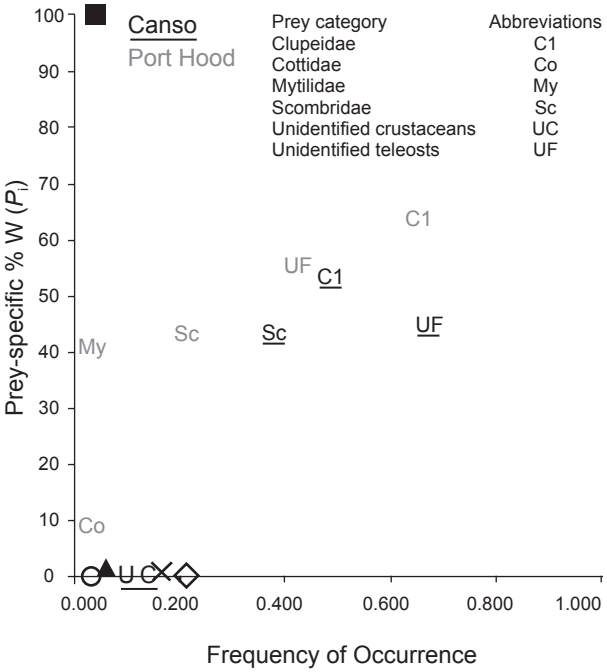

Fig. 6. The relationship between frequency of occurrence and prey species-specific percent weight for the diets of Atlantic bluefin tuna sampled in Port Hood (n = 23) and Canso (n = 31), Nova Scotia. Overlapping prey data were represented by symbols. The black square represents Scomberesocidae and Asteroidea in Port Hood and Balistidae in Canso; the white circle represents Hyperiidae, Osmeridae, Ammodytidae, Euphausiidae, Tellinidae, and algae in Canso; the black triangle represents Merlucciidae and Sebastidae in Canso; the x represents algae in Port Hood and Pandalidae in Canso; and the white diamond represents unidentified squid in Port Hood and Gadidae in Canso.

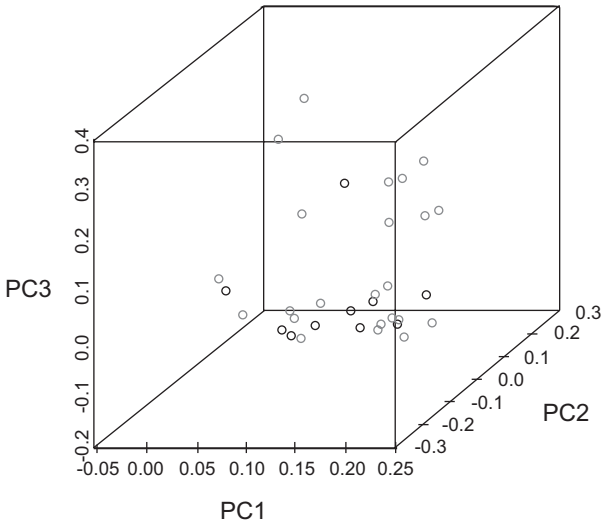

Fig. 7. Principal components (PC) analysis plot of normalized percent frequency of occurrence of prey families in the stomachs of Atlantic bluefin tuna caught in Canso (grey circles) and Port Hood (black circles).The first three principal components explain 39%, 19%, and 15% of the variance, respectively.

prey. The majority of the Atlantic bluefin tuna caught in the GSL were larger than those caught in Canso, with few exceptions (Fig. 2), making it difficult to determine how location and predator size each affect diet. Previous studies provide mixed results as to the relationship between Atlantic bluefin tuna size, prey size, and prey composition, but most authors agree that the relationship is weak (Dragovich, 1970; Young *et al*., 1997; Chase, 2002; Butler *et al*., 2010). Given the results of these previous studies, it is likely that capture location had a greater effect on diet then the predator size. Catch data (Neilson *et al*., 2009) also indicates that larger Atlantic bluefin tuna are foraging in the GSL versus the Scotian Shelf, which raises the question as to why primarily large Atlantic bluefin tuna are found in these waters. It may be that the migration patterns of large individuals are different from smaller individuals and that these large tuna are likely undertaking the migration from the Scotian Shelf to the GSL in order to take advantage of better foraging opportunities.

The results of this study of Atlantic bluefin tuna diet in the GSL and the Scotian Shelf are consistent with other feeding studies in the North Atlantic, which indicate that these fish feed primarily on schooling fish of lower trophic levels and opportunistically on other species. Although the Atlantic bluefin tuna landed in Port Hood were significantly larger than those landed in Canso, the diets at both sites were similar. It would be of interest to determine whether densities of prey and/or the nutritional qualities of prey, such as fat content, are greater in the GSL. Additional sampling years and larger sample sizes are recommended to produce more reliable descriptions of Atlantic bluefin tuna feeding ecology in the sampling areas.

Acknowledgments

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References

AMUNDSEN, P.-A., H.-M. GABLER and F. J. STALDVIK. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *J. Fish Biol.*, **48**: 607–614. http://dx.doi.org/10.1111/j.1095-8649.1996.tb01455.x

BIZZARRO, J. J., H. J. ROBINSON, C. S. RINEWALT and D. A. EBERT. 2007. Comparative feeding ecology of four sympatric skate species off central California, USA. *Env. Biol. Fish.*, **80**: 197–220. http://dx.doi.org/10.1007/s10641-007-9241-6

BLOCK, B. A., J. FINNERTY, A. F. R. STEWART and J. A. KIDD.1993 Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science*, **260**: 210–214.

BLOCK, B. A., S. L. H. TEO, A. WALLI, A. BOUSTANY, M. J. W. STOKESBURY, C. J. FARWELL, K. C. WENG, H. DEWAR and T. D. WILLIAMS. 2005. Electronic tagging and population structure of Atlantic Bluefin Tuna. *Nature*, **434**: 1121–1127. http://dx.doi.org/10.1038/nature03463
PMid:15858572

BUTLER, M. J. A. 1971. Biological investigations on aspects of the life history of the bluefin tuna, 1970–1971. Newfoundland and Labrador Tourism Development Office, Canada, 169 p.

BUTLER, C. M., P. J. RUDERSHAUSEN and J. A. BUCKEL, 2010. Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in North Carolina: diet, daily ration, and consumption of Atlantic menhaden (*Brevoortia tyrannus*). *Fish. Bull.*, **108**: 56–69.

CAREY, F. G. and J. M TEAL. 1969. Regulation of body temperature by bluefin tuna. *Comp. Biochem. Physiol.*, **28**: 205–213. http://dx.doi.org/10.1016/0010-406X(69)91336-X

CAREY, F. G., J. W. KANWISHER and E. D. STEVENS. 1984. Bluefin tuna warm their viscera during digestion. *J. Exp. Biol.,* **109**: 1–20.

CHASE, B. C. 2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. *Fish. Bull.*,**100**: 168–180.

COLLETTE, B. B. and C. E. NAUEN. 1983. FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. *FAO Fish.Synop.*, **2**: 91.

COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA (COSEWIC). 2011. COSEWIC assessment and status report in the Atlantic bluefin tuna *Thunnus thynnus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, 2011. 30 pp.

D'AMOURS, D. and M. CASTONGUAY. 1992. Spring migration of Atlantic mackerel, *Scomber scombrus*, in relation to water temperature through Cabot Strait (Gulf of St. Lawrence). *Enviro. Biol. Fishes,* **34**: 393–399. http://dx.doi.org/10.1007/BF00004743

DE CRESPIN DE BILLY, V., S. DOLEDEC and D. CHESSEL. 2000. Biplot presentation of diet composition data: an alternative for fish stomach contents analysis. *J. Fish Biol.*, **56**: 961–973. http://dx.doi.org/10.1111/j.1095-8649.2000.tb00885.x

DFO, 2010. 2009 Value of Atlantic Coast Commercial Landings, by Region. http://www.dfo-mpo.gc.ca/stats/commercial/land-debarq/sea-maritimes/s2009av-eng.htm

DRAGOVICH, A. 1970. The food of bluefin tuna (*Thunnus thynnus*) in the Western North Atlantic Ocean. *T. Am. Fish. Soc.*, **99**: 726–731. http://dx.doi.org/10.1577/1548-8659(1970)99<726:TFOBTT>2.0.CO;2

EGGLESTON, D. B. and E. A. BOCHENEK. 1990. Stomach contents and parasite infestation of school bluefin tuna *Thunnus thynnus* collected from the Middle Atlantic Bight, Virginia. *Fish. Bull.*, **88**: 389–395.

FERRY, L. A. and G. M. CAILLIET. 1996. Sample size and data: Are we characterizing and comparing diet properly? *In:* Feeding ecology and nutrition in fish; proceedings of the symposium on feeding ecology and nutrition in fish; Int. Congress Biology of Fishes. D. Makinlay and K. Shearer, (eds.), p. 70–81. American Fisheries Society, San Francisco, CA.

GALUARDI, B., F. ROYER, W. GOLET, J. LOGAN, J. NEILSON and M. LUTCAVAGE. 2010. Complex migration routes of Atlantic bluefin tuna question current population structure paradigm. *Can. J. Fish. Aquat. Sci.,* **67**: 966–976. http://dx.doi.org/10.1139/F10-033

GRAHAM, J. B. and DICKSON, K. A. 2004. Evolution and consequences of endothermy in fishes. *Physiol. Biochem. Zool.*, **77**: 998–1018. http://dx.doi.org/10.1086/423743
PMid:15674772

HYSLOP, E.J. 1980. Stomach contents analysis – a review of methods and their application. *J. Fish Biol.*, **17**: 411–429. http://dx.doi.org/10.1111/j.1095-8649.1980.tb02775.x

ICCAT (International Commission for the Conservation of Atlantic Tunas). 2011. Report of the Standing Committee on Research and Statistics 2010–2011. Madrid.

LANDEIRA-FERNANDEZ, A. M., P. C. CASTILHO and B. A. BLOCK. 2012. Thermal dependence of cardiac SR Ca^{2+}-ATPase from fish and mammals. *J. Therm. Biol.*, **37**: 217–223. http://dx.doi.org/10.1016/j.jtherbio.2012.01.003

LAWSON, G. L., M. R. CASTLETON and B. A. BLOCK.2010. Movements and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) in relation to water column structure in the Northwestern Atlantic. *Mar. Ecol. Prog. Ser.*, **400**: 245–265. http://dx.doi.org/10.3354/meps08394

LOGAN, J. M., E. RODRIGUEZ-MARÍN, N. GOÑI, H. ARRIZABALAGA, W. GOLET and M. E. LUTCAVAGE. 2011. Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Mar. Biol.*, **158**: 73–85.

MacKAY, K. T. 1979. Synopsis of biological data of the northern population Atlantic mackerel (*Scomber scombrus*). *Fish. Mar. Serv. Tech. Rep.,* **885**. http://dx.doi.org/10.1007/s00227-010-1543-0. Erratum: http://dx.doi.org/10.1007/s00227-011-1758-8

MESSIEH, S. N. 1987. Some characteristics of Atlantic herring (*Clupea harengus*) spawning in the Southern Gulf of St. Lawrence. *NAFO Sci. Coun. Studies,* **11**: 53–61.

NRC (National Research Council). 1994. An Assessment of Atlantic Bluefin Tuna. National Academy Press, Washington DC.

NEILSON, J. D., S. SMITH, M. ORTIZ and B. LESTER. 2009. Indices of stock status obtained from the Canadian bluefin tuna fishery. *Collect.Vol. Sci. Pap. ICCAT*, **64**: 380–404.

OLSON, R. J. and C. H. BOGGS. 1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Can. J. Fish.*

Aquat. Sci., **43**: 1760–1775. http://dx.doi.org/10.1139/f86-220

OVERHOLTZ, W. J. 2006. Estimates of consumption of Atlantic herring (*Clupea harengus*) by bluefin tuna (*Thunnus thynnus*) during 1970–2002: an approach incorporating uncertainty. *J. Northwest Atl. Fish. Sci.*, **36**: 55–63. http://dx.doi.org/10.2960/J.v36.m572

OVERHOLTZ, W. J., J. S. LINK and L. E. SUSLOWICZ. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. *ICES J. Mar. Sci.*, **57**: 1147–1159. http://dx.doi.org/10.1006/jmsc.2000.0802

ROOKER, J. R., J. R. ALVARADO BREMER, B. A. BLOCK, H. DEWAR, G. DE METRIO, A. CORRIERO, R. T. KRAUS, E. D. PRINCE, E. RODRÍGUES-MARÍN and D. H. SECOR. 2007. Life history and stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). *Rev. Fish. Sci.*, **15**: 265–310. http://dx.doi.org/10.1080/10641260701484135

SETTE, O. E. 1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 2: Migrations and habits. *U. S. Fish. Bull.,* **51**: 251 –358.

SCOTT, W. B. and M. G. SCOTT. 1988. Atlantic Fishes of Canada. *Can. Bull. Fish. Aquat. Sci.,* **219**: 562–564.

VANDERLAAN, A. S. M., B. A. BLOCK, J. CHASSÉ, M. E. LUTCAVAGE, A. HANKE, S. G. WILSON and J. D. NEILSON. 2011. Initial investigations of environmental influences on Atlantic bluefin tuna catch rates in the Southern Gulf of St. Laurence. *Collect. Vol. Sci. Pap. ICCAT*, **66**: 1204–1215.

WALLI, A., H. TEO, A. BOUSTANY, C. J. FARWELL, T. WILLIAMS, H. DEWAR, E. PRINCE and B. A. BLOCK. 2009. Seasonal movements, aggregations and diving behaviour of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. PLoS ONE **4**:e6151. http://dx.doi.org/10.1371/journal.pone.0006151

WILSON, S. G., G. L. LAWSON, M. J. W. STOKESBURY, A. SPARES, A. M. BOUSTANY, J. D. NEILSON and B. A. BLOCK. 2011. Movements of Atlantic bluefin tuna from the Gulf of St. Lawrence to their spawning grounds. *Collect. Vol. Sci. Pap. ICCAT*, **66**: 1247–1256.

YOUNG, J. W., T. D. LAMB, D. LE, R. W. BRADFORD and A. W. WHITELAW. 1997. Feeding ecology and interannual variations in diet of southern bluefin tuna *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. *Environ. Biol. Fishes*, **50**: 275–291.

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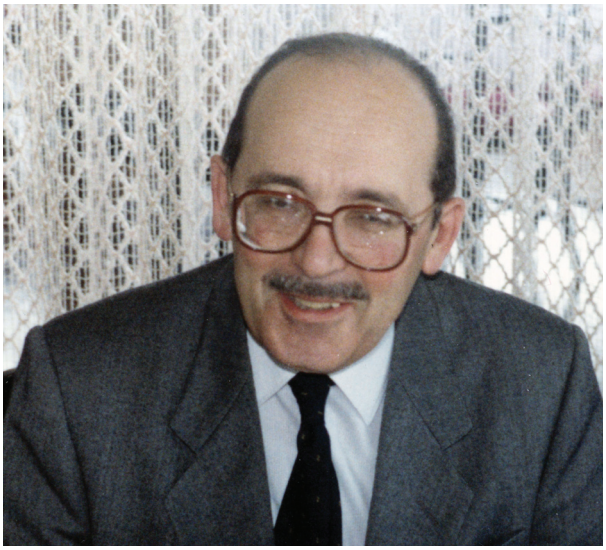
Manuel Gómez Larrañeta

(1924–2012)



Dr. Larrañeta was born in Tolosa, Spanish Basque Country; he boasted about that to justify his tenacious and tireless character. With a degree in Natural Sciences from the University of Barcelona (1946) and a PhD from the same university (1965), he joined the Fisheries Research Institute when it was founded in 1949, and contributed greatly to its development, sharing the enthusiasm and the efforts of a handful of pioneers. He was laboratory director of Castellon (1954–1967) and Vigo (1967–1979).

Dr. Larrañeta was the only Spaniard attending the international seminar sponsored by FAO in Lowestoft (England, 1957) where the most advanced analytical methods of the time on fish population dynamics were presented. He applied this methodology in the Mediterranean Castellón Experimental Trawling Plan (1961–1967), showing that it allowed improving fishing yields. This made Dr. Larrañeta a passionate scholar and eventually a master of fisheries science and management, pioneering their implementation and dissemination in Spain and then to Latin America, beginning with Chile, where he taught for one year at the Pontifical Catholic University in Santiago. After his retirement in 1989 he continued to attend the Institute for ten years, preparing his more complete theoretical work, which deals with the stock-recruitment relationship in fish.

In 1969, shortly after arriving in Vigo, Dr. Larrañeta initiated his participation in the ICNAF Scientific Council, making efforts for the Spanish contribution to be appropriate, as much in the scientific field, where he tried to maintain the highest level, as in defense of the Spanish fishing sector, of which he felt a server. Until retirement in 1989 Dr. Larrañeta was the reference in Spain for NAFO fisheries; one of his articles triggered the Spanish fishery for Greenland halibut in NAFO waters; his theory on two equilibrium states in production curve was a noble attempt to explain cod fisheries evolution. The now established consolidated annual routine of sampling and analysis he developed was one step towards a better monitoring of these fisheries; maintaining it required fighting one battle every year, not always won, but he never gave up.

Antonio Vázquez,
Vigo, Spain,
December 2012

In Spanish:
El Dr. Larrañeta había nacido en Tolosa, en el País Vasco, y siempre hacía gala de ello para justificar su carácter tenaz e infatigable. Licenciado en Ciencias Naturales por la Universidad de Barcelona (1946) y doctor por esa misma universidad (1965), se incorporó al Instituto de Investigaciones Pesqueras en el momento de su fundación, en 1949, y contribuyó notablemente a su desarrollo, compartiendo el entusiasmo y los esfuerzos de un puñado de pioneros. Fue director de laboratorio de Castellón (1954–1967) y de Vigo (1967–1979).

El Dr. Larrañeta fue el único español que asistió al curso internacional patrocinado por la FAO en Lowestoft (Inglaterra, 1957) en el que se presentaron los métodos analíticos más avanzados en dinámica de poblaciones de peces. Aplicó esa metodología en el Plan Experimental de Pesca de Arrastre de Castellón (1961–1967), demostrando que ello permitía ciertamente mejorar los rendimientos pesqueros. Esto lo convirtió en un apasionado, un estudioso y, finalmente, un maestro en la ciencia y gestión de las pesquerías, siendo pionero en su aplicación y divulgación en España, también en Hispanoamérica, comenzando por Chile, donde impartió clases durante un curso en la Pontificia Universidad Católica, en Santiago. Tras su jubilación el Dr. Larrañeta aún continuó diez años más asistiendo al Instituto donde preparó su obra teórica más completa, que versa sobre la relación stock-reclutamiento en peces.

En 1969, poco después de su llegada a Vigo, el Dr. Larrañeta comenzó su participación en el Consejo Científico de la ICNAF y desde entonces se esforzó en que la aportación española fuese la adecuada, tanto a nivel científico, ámbito en el que trató de mantenerse siempre al más alto nivel, como en defensa del sector pesquero español, del cual se sentía servidor. Hasta su jubilación en 1989 el Dr. Larrañeta fue el referente en España para las pesquerías NAFO; un artículo suyo de divulgación fue el detonante para el comienzo de la pesquería española de fletán negro en NAFO; su teoría de dos estados de equilibrio de la curva de producción fue un noble intento para explicar la evolución de las pesquerías de bacalao. La rutina anual de muestreo y análisis que él creó, hoy consolidada, fue un gran paso adelante para el seguimiento de estas pesquerías; mantenerla exigió librar una batalla cada año, no siempre ganada, que no le hicieron desistir.

Scientific Publications of the Northwest Atlantic Fisheries Organization

In efforts to reduce paper usage and ensure publications are accessible to all, most publications are available FREE electronically at *www.nafo.int* or *http://journal.nafo.int*

The NAFO publications listed below are available through the NAFO Secretariat. Prices include postage and handling.

Please note: Pricing for volumes shipped overseas is higher due to increased postage costs.

	Price North America (CAD $)	Price Overseas (CAD $)
Early Stages of Fishes in the Western North Atlantic Ocean (Davis Strait, Southern Greenland and Flemish Cap to Cape Hatteras)		
This comprehensive scientific publication is the only up-to-date textbook providing detailed descriptions and accurate drawings of the early life-history stages of the fishes from the Northwest Atlantic Ocean north of 35°N and west of 40°W. The region covers the world's most famous fishing grounds and includes the Davis Strait, southern Greenland, Flemish Cap, Georges Bank, northern Sargasso Sea and Middle Atlantic Bight to Cape Hatteras.		
Hardcover 2-Volume Edition by Michael. P. Fahay	120.00	135.00
Identification of Wolffish, Hake and Rockling in the Northwest Atlantic		
1-page Identification Guide produced in full-colour on laminated stock	10.00	15.00
Sponge Identification Guide NAFO Area		
Coral Identification Guide NAFO Area (full-colour on waterproof stock)	30.00	35.00
Coral Identification Guide NAFO Area		
Coral Identification Guide NAFO Area (full-colour on waterproof stock)	25.00	30.00
Journal of Northwest Atlantic Fishery Science - *Available FREE online at www.journal.nafo.int*		
This publication provides an international forum for the primary publication of original research papers on fisheries science in the Northwest Atlantic, with emphasis on environmental, biological, ecological and fishery aspects of the living marine resources and ecosystems.		
Please note: Scientific publications during ICNAF times (1949–1979) are available at the Secretariat in print format and also available online at www.nafo.int		
Vol. 44, 2012 (Regular Issue)	40.00	45.00
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1998 (issued January 1999)	26.00	31.00
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1996 (issued January 1997)	23.00	28.00
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1994 (issued January 1995)	21.00	26.00
1993 (issued January 1994)	21.00	26.00
1992 (issued December 1992)	18.00	23.00
1991 (issued December 1991)	16.00	21.00
1990 (issued December 1990)	14.00	19.00
1989 (issued December 1989)	14.00	19.00
1988 (issued December 1988)	12.00	17.00
1987 (issued December 1987)	12.00	17.00
1986 (issued December 1986)	12.00	17.00
1985 (issued December 1985)	12.00	17.00
1984 (issued December 1984)	12.00	17.00
1983 (issued December 1983)	12.00	17.00
1982 (issued December 1982)	12.00	17.00
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NAFO Scientific Council Studies - *Available FREE online at www.nafo.int*

This publication includes papers of topical interest and importance to the current and future activities of Scientific Council.

No. 44, 2012 (Report of the Workshop on Implementation of Stock Reproductive Potential into Assessment and Management Advice for Harvested Marine Species)	Online only	
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No. 42, 2009 (Coral Identification Guide - NAFO Area)	Online only	
No. 41, 2008 (Report of the Greenland Halibut (*Reinhardtius hippoglossoides*) Age Determination Workshop)	Online only	
No. 40, 2007 (Identification of Wolffish, Hake and Rockling in the Northwest Atlantic)	Online only	
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No. 5, 1982 (Symposium on Environmental Conditions in the Northwest Atlantic During 1970–79, September 1981)	14.00	19.00
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No. 2, 1982 (Manual on Groundfish Surveys in the Northwest Atlantic)	11.00	16.00
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Information for Preparing Manuscripts for NAFO Scientific Publications

Journal of Northwest Atlantic Fishery Science

The Journal is for the primary publication of original practical and theoretical research that is unpublished and is not being submitted for publication elsewhere. While it is intended to be regional in scope, papers of general applicability and methodology may be considered. Space is also provided for notes, letters to the editor and notices. Each paper is assigned to an Associate Editor of the Journal's Editorial Board, and is normally reviewed by two referees regarding suitability as a primary publication.

NAFO Scientific Council Studies

The Studies publishes papers which are of topical interest and importance to the current and future activities of the Scientific Council, but which do not meet the high standards or general applicability required by the Journal. Such papers have usually been presented as research documents at Scientific Council meetings and nominated for publication by the Standing Committee on Publications. Studies papers are not peer reviewed.

Content of Paper

The paper should be in English. The sequence should be: Title, Abstract, Text, References, Tables and Figures.

Title

The paper should start with the title, followed by the name(s), address(es) and emails of the author(s) including professional affiliation, and any related footnotes.

Abstract

An informative concise abstract should be provided along with key words listed alphabetically.

Text

In general, the text should be organized into Introduction, Materials and Methods, Results, Discussion, and Acknowledgements. Authors should be guided by the organization of papers that have been published in the NAFO Journal or Studies.

Introduction should be limited to the purpose and rationale of the study.

Materials and Methods should describe in sufficient detail the materials and methods used, so as to enable other scientists to evaluate or replicate the work.

Results should answer the questions evolving from the purpose of the study in a comprehensive manner and in an orderly and coherent sequence, with supporting tables and figures.

Discussion should explain the main contributions from the study, with appropriate interpretation of the results focusing on the problem or hypothesis. Comparisons with other studies should be included here.

Acknowledgements should be limited to the names of individuals who provided significant scientific and technical support, including reviewers, during the preparation of the paper, and the names of agencies which provided financial support.

References

The references cited in the text should be listed alphabetically. References should be mainly restricted to significant published literature. Unpublished documents and data, papers in preparation, and papers awaiting acceptance to other journals, may be cited with full contact addresses as unpublished or personal communications.

Examples:

KING, M. 1995. Fisheries biology, assessment and management. Fishing News Books, UK, 341 p.

CROWDER, L. B., and S. A. MURAWSKI. 1998. Fisheries bycatch: implications for management. *Fisheries*, **23**: 8–16. doi:10.1577/1548-8446(1998)023<0008:FBIFM>2.0.CO;2

ÁVILA DE MELO, A. M., D. POWER, and R. ALPOIM. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc.*, No. 52, Serial No. N5138, 19 p.

Text citations of the above would be (King, 1995; Crowder and Murawski, 1998; Ávila de Melo *et al.*, MS 2005). The surnames of two authors may be used in a citation, but *et al.* should be used for more than two authors. The citation of mimeographed reports and meeting documents should contain the abbreviation "MS". Abbreviations of periodicals can be found ftp://ftp.fao.org/fi/asfa/Monitoring_List/MASTER.txt . The Digital Object Identifier (doi) should be included if available. http://www.crossref.org/freeTextQuery/ can be used to checked this.

Tables and Figures

All Tables and Figures must be cited in the text. Tables and Figures must be numbered consecutively and correspond with the order of presentation in the text. Figure captions should be included as a separate page. Each table and figure should have a complete concise descriptive caption. Figures should always be submitted in black and white. Colour plots and photographs are acceptable only if colour is essential to the content. Preferably, all figures should be submitted as separate files in .eps or .ps format. Photographs, maps and contour plots can also be submitted in high quality .jpg format.

If using excel, open the files in R and save the graphs by right clicking and saving as metafiles or postscript files. If using SlideWrite copy the files as Metafiles (WMF). Do not save them as bitmap files. They are not editable.

Paper Submission

Papers should be submitted by email to Dr. Neil Campbell, General Editor, at journal@nafo.int or ncampbell@nafo.int