Fisheries and Oceans Canada
Ecosystems and Oceans Science

Pêches et Océans Canada
Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2022/013

Quebec Region

Preliminary estimates of annual capelin consumption by Atlantic cod and Greenland halibut

Jordan Ouellette-Plante, Hugues P. Benoît, Stéphane Plourde and Denis Chabot

Fisheries and Oceans Canada
Maurice Lamontagne Institute
850, route de la mer P.O. Box 1000
Mont-Joli, Québec, G5H 3Z4

July 2022

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044
ISBN 978-0-660-44198-6 Cat. No. Fs70-5/2022-013E-PDF

Correct citation for this publication:

Ouellette-Plante, J., Benoît, H.P., Plourde, S. and Chabot, D. 2022. Preliminary estimates of annual capelin consumption by Atlantic cod and Greenland halibut. DFO Can. Sci. Advis. Sec. Res. Doc. 2022/013. iv + 48 p.

Aussi disponible en français :

Ouellette-Plante, J., Benoît, H.P., Plourde, S. et Chabot, D. 2022. Estimations préliminaires de consommation annuelle de capelan par la morue franche et le flétan du Groenland. Secr. can. des avis sci. du MPO. Doc. de rech. 2022/013. iv + 50 p.

TABLE OF CONTENTS

ABSTRACT

In order to obtain a fishery-independent index covering a significant portion of the Gulf of St. Lawrence (GSL, NAFO Divisions 4RST) capelin (*Mallotus* spp.) stock area, the stomach contents of Atlantic cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*) collected during the summer nGSL multispecies survey were examined. Using a bioenergetics approach, it was estimated that annual capelin consumption by the two predators continued to be higher than the commercial landings recorded for the GSL. These results support those obtained from previously published ecosystem models. All length classes combined, the percentage of capelin in the mean stomach contents of Atlantic cod shows greater interannual variation compared to the stomach contents of Greenland halibut. The use of capelin by Greenland halibut more closely reflected changes in the average number of capelin caught per tow in the nGSL multispecies surveys in years for which fish stomachs were available. However, several sources of uncertainty were raised regarding the stomach content data used and some of the assumptions in the methodology, and the need to collect samples at other times of the year was pointed out. Since capelin is one of the major forage species in the GSL, considering the population patterns of its predators and assessing their consumption of capelin would be additional aspects of interest to include in the assessment of this species.

1. INTRODUCTION

No scientific surveys to determine the distribution and abundance of the Gulf of St. Lawrence (GSL,[1] NAFO[2] Divisions 4RST) capelin stock (*Mallotus* spp.) have taken place since the surveys by Bailey et al. (1977) in the mid-1970s. Although other surveys have been carried out, these were either exploratory (Grégoire et al. 1999) or focused on non-adult stages (Grégoire et al. 2005, 2006, 2008).

The main indicators used in the assessment of the GSL capelin stock in February 2013 were (Grégoire et al. 2013):

1. commercial landings;
2. the performance index of the purse seine fishery on the west coast of Newfoundland (NAFO Division 4R);
3. mean lengths; and
4. the dispersion index from the multispecies bottom trawl surveys.

With the exception of the last indicator, all of the above are dependent on the commercial fishery. However, given that the commercial fishery is primarily located on the west coast of Newfoundland, little information is available for the other stock Divisions, i.e., 4S and 4T (DFO 2015). It is also well known that fishery-dependent indices can often be disproportional to abundance, remaining high even when abundance is in decline (Hilborn and Walters 1992).

To address this lack of commercial fishery-independent data, other data sources have been used over the years. Additional data sources include the bottom trawl multispecies surveys conducted by Fisheries and Oceans Canada (DFO) in the southern (sGSL) and northern Gulf of St. Lawrence (nGSL[3]). Taking place annually in August (nGSL) and September (sGSL), these surveys are mainly aimed at groundfish, shrimp, and benthic macroinvertebrates. Trawl tow locations are determined based on a stratified-random sampling design in which the study area is divided into strata that share certain common characteristics such as depth, NAFO Divisions, and substrate type (Figure 1a). The reports by Bourdages et al. (2020) and Hurlbut and Clay (1990) may be consulted for more details on the sampling designs used for the nGSL and sGSL surveys, respectively.

Using indicator kriging (Grégoire et al. 2002), both of these surveys were used to produce a dispersion index (occupied proportion of the survey area) for capelin in the GSL in order to describe abundance distributions of capelin and establish relationships between capelin and other species captured in the surveys (Grégoire et al. 2012). Beginning with the January 2018 stock assessment, it was decided that the dispersion index calculated from the multispecies surveys would no longer be used since different environmental factors (predation, water temperature, depth trawled, time of day) could influence the index over time (DFO 2018). However, given the almost complete lack of data on the commercial fishery for capelin in stock Divisions 4S and 4T, it was necessary to consider other sources of data to better understand the dynamics of the stock across its entire range in the GSL.

Thus, in parallel with the recent study by Chamberland et al. (2022), which demonstrated that abundance indices could be produced based on bottom trawl survey data, we examined the

---

[1] For the purposes of this study, the GSL also includes the estuary area of NAFO Division 4T.
[2] Northwest Atlantic Fisheries Organization.
[3] Also includes the estuary area of NAFO Division 4T.

stomach content data collected during the nGSL multispecies survey. We assumed that the proportion of capelin in the stomach contents of the predators examined would reflect capelin abundance in the environment, according to a linear functional relationship.

For this study, our objective was to use Atlantic cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*) as samplers of the environment to describe interannual variations in the use of capelin as a food source. These two predators were selected for the following reasons:

1. They are known to consume large amounts of capelin (Bowering and Lilly 1992; Savenkoff et al. 2004c; Ouellette-Plante et al. 2020). In the event of increased availability of capelin in the system, both Atlantic cod and Greenland halibut prefer to consume capelin over any other type of prey (Lear 1970; Methven and Piatt 1989; Berard and Davoren 2020);
2. They are distributed throughout the nGSL (Bourdages et al. 2020), albeit in different but complementary habitats;
3. They are known to undertake vertical migrations in the water column to forage for food (Groot 1970; Vollen and Albert 2008; Espeland et al. 2010; Le Bris et al. 2013; Boje et al. 2014), thus increasing the probability of observing capelin in their stomach contents; and
4. The available time series for both species is long (1993–2020, Table 1).

Using predators as samplers of the environment is not new. Various studies that have used predators as such have proven their usefulness in:

1. Describing major—or the only—occurrences of some species (Templeman 1970);
2. Providing size classes that are not usually sampled (Gotshall 1969; Parsons et al. 1986). For example, Parsons et al. (1986) used the stomach contents of Atlantic cod to obtain samples of juvenile northern shrimp (*Pandalus borealis*)—which are not normally present in samples from standard scientific surveys—to help develop a growth curve;
3. Tracking abundance trends of prey that are difficult to sample (Mills et al. 2007; Deroba 2018; Eriksen et al. 2018);
4. Comparing age and length composition between species preyed upon and those obtained from commercial sampling (Gotshall 1969; Sunada and Kelly 1981);
5. Evaluating spatiotemporal changes in benthic communities (Frid and Hall 1999; Link 2004) and some families of crustaceans that are difficult to sample (Lasley-Rasher et al. 2015); and
6. Evaluating the geographic distribution of prey (Lilly and Parsons 1991; Hatch and Sanger 1992; Roseneau and Vernon Byrd 1997).

For these reasons, Atlantic cod (Parsons et al. 1986; Lilly and Parsons 1991; Fahrig et al. 1993; Link 2004; Lasley-Rasher et al. 2015; Deroba 2018; Eriksen et al. 2018) and Greenland halibut (Dwyer et al. 2010) are well known as samplers of the environment.

2. MATERIALS AND METHODS

2.1. COLLECTION AND DESCRIPTION OF STOMACHS USED

Details on the at-sea sampling of stomachs and the laboratory analysis are given in Ouellette-Plante et al. (2020). Only stomachs collected during the nGSL multispecies surveys were used in this analysis. Stomachs not from successful random tows, and those for which the associated metadata could not be obtained, were not used. Prey recorded as digestion stage[4] 3, the most advanced stage of digestion, were also not used in this study. This decision was based on the observation that the methods used by stomach content analysts changed over the period 1993–2020. Indeed, it appears that less of an effort was made in terms of identification in the 1990s, when there was an excess of unidentifiable material, and have declined significantly since. Moreover, although retaining occurrences of capelin recorded as stage 3 (often based on the observation of free otoliths in the stomach) would increase the frequency of capelin occurrence, it could result in an underestimation of the true proportion of capelin since most of the ingested prey, unidentifiable, would likely have been recorded as *digested fish*.

Since 1993, 16,769 Atlantic cod stomachs and 19,845 Greenland halibut stomachs have been analyzed (Table 1). Just over 4% of these stomachs contained capelin. No stomachs from either predator were collected during the period 2010–2014. No Greenland halibut stomachs were collected in 2000.

A comparison of the length frequencies of specimens sampled for stomach contents with the length frequencies of fish caught based on the nGSL multispecies survey data showed that the length-stratified sampling used for stomach collection was effective in obtaining representative samples, except for small cod (< 15–20 cm, Figures 2–3). However, the literature shows that these small cod are not piscivorous (Hanson 2011; Ouellette-Plante et al. 2020) and are therefore of less interest for this study.

The spatial distribution of the stomachs collected spans the entire study area (Figures 4–5). In general, using both predators provides more extensive spatial coverage. In areas where using only Atlantic cod stomachs would have led to a data deficit, particularly in the deep channels of the Estuary, the addition of Greenland halibut stomachs increases coverage of the nGSL. However, when the data are broken down by year, it can be seen that this stomach distribution, derived from the predator distribution, was not always optimal. This resulted in some years when the relative proportion of capelin in the diet of capelin predators in some regions of the nGSL could not be estimated (Table 2). For example, the majority of Greenland halibut stomachs collected in the 1990s came from NAFO Division 4R, which reflects the distribution of Greenland halibut at the time.

2.2. PROPORTION OF CAPELIN INGESTED AS A FOOD SOURCE

Once a successful random fishing tow[5] was brought to the surface, the catch was sorted by species. Each species was then weighed, and samples were collected in order to take biological measurements of the fish, e.g., length, mass, sex, maturity, samples such as otoliths, and stomachs. If a given species showed a length distribution with several modes, the catch was then sorted into categories[6] addressed separately. For example, if a catch of Greenland halibut included a large proportion of small individuals, these were separated from the rest. The catch

---

[4] Undigested prey were entered into the database as stage 1, while partially digested prey were entered as stage 2. Very digested or partial prey as well as all other material found were entered as stage 3 (see Appendix B in Ouellette-Plante et al. 2020).

[5] A fishing tow is successful when no damage to the trawl has been reported or when the damage is minor and has not resulted in a biased catch.

[6] In the database, the *category* field records the category(ies) associated with the catch of a given species: 0 (no sorting, so only 1 category), 1 (small specimens), 2 (medium specimens), and 3 (large specimens). For some species including redfish (*Sebastes* spp.), there may be three categories: small, medium, and large. In general, most of the species caught are not sorted.

would then be processed in two categories (small and large). Because a sample was collected from each category in order to take the biological measurements mentioned above, sorting ensures that some of the less frequent size ranges (e.g., small specimens distributed within a substantial catch of large specimens) are still sampled.

In this study, the proportion of capelin in food ingested by the population was adjusted using the approach by Warren et al. (1994), which takes into account the number of fish (cod or Greenland halibut) estimated per survey stratum and per size class. Since a stratum h (h = 1, 2,…, H) was not necessarily sampled in every year g (g = 1993, 1994,…, 2020) for which stomachs were available (Figure 6), a decision was made to remove stomach samples collected from strata that had not been sampled for most of the 1993–2009 and 2015–2020 periods. Strata in Division 3Pn (302 to 305) as well as those added in 2008 in the Estuary (851 to 855) were thus eliminated from the data set used in this part of the analyses. Nevertheless, the strata retained for the analysis still covered 94% of the area sampled during the period 1993–2020.

Three l length classes were created for each predator p:

$$l = \begin{cases} < 30,\ [30\text{-}55[\text{ and } \geq 55 \text{ cm, for Atlantic cod} \\ < 20,\ [20\text{-}40[\text{ and } \geq 40 \text{ cm, for Greenland halibut} \end{cases}$$

These values are the same as those used in Ouellette-Plante et al. (2020) and reflect changes in the food intake of large prey groups[7] by predators as predator length increases. Figure 7 shows that these length classes also appear to be valid when only capelin is considered as prey. Using three length classes also resulted in significant numbers for most g-h-p-l combinations (Figures 8–13).

The first step in order to use the approach by Warren et al. (1994) was to calculate the number of specimens of each predator p caught per length class l in the successful random fishing tows conducted in the strata retained. Since the vessel–gear combination used in the nGSL multispecies survey had changed in 2004 (the CCGS[8] *Alfred Needler*–URI vessel–gear combination was replaced by the CCGS *Teleost*–Campelen), a correction was made to the catch of the CCGS *Alfred Needler*–URI vessel-gear combination using the method described in Bourdages et al. (2007). This was done to make the values equivalent to those of the CCGS *Teleost*–Campelen. For a given tow t, the standardized number in CCGS *Teleost*–Campelen equivalents of category o and length j (e.g., j = 10, 12,…, 90, J. In cm.) specimens caught in the tow was M_{toj}.

For the purposes of clarity and unless otherwise stated, g (year) and p (predator) indices will not be used in the following equations. Therefore, the equations presented will be for a given predator p and year g. All j lengths combined, the standardized number in CCGS *Teleost*–Campelen equivalents of specimens sampled (M_{to}) from category o was, in tow t:

$$M_{to} = \sum_{j}^{J} M_{toj} \tag{1}$$

For a given length class l, the standardized number in CCGS *Teleost*–Campelen equivalents of specimens sampled (M_{tol}) from category o was, in tow t:

---

[7] Fish, crab, shrimp, zooplankton, other invertebrates, and unidentifiable prey.

[8] Canadian Coast Guard Ship.

$$M_{tol} = \sum_{j \geq l_{min}}^{J < l_{max}} M_{toj} \tag{2}$$

where l_{max} and l_{min} are the upper and lower bounds, respectively, of length class l. Their proportion (u_{tol}) in the sample was calculated as follows:

$$u_{tol} = \frac{M_{tol}}{M_{to}} \tag{3}$$

In addition to correcting for differences in catchability between vessel–gear combinations, the data had to be further standardized to align the area trawled in each tow with a standard area *a*. The distance trawled (*b*, in nautical miles [NM]) and the horizontal opening (*d*, in m) for each tow were not always consistent among tows. With respect to the horizontal opening *d*, values specific to each vessel–gear combination were used (Bourdages et al. 2007):

$$d = \begin{cases} \text{13.41 m, with the CCGS } \textit{Alfred Needler}\text{–URI vessel–gear combination} \\ \text{16.94 m, with the CCGS } \textit{Teleost}\text{–Campelen vessel–gear combination} \end{cases}$$

Since it was decided to convert catches to CCGS *Teleost*–Campelen equivalents, the standard area *a* used was obtained by multiplying the target distance trawled of the CCGS *Teleost*–Campelen vessel–gear combination (0.75 NM[9]) by the horizontal opening of the Campelen trawl (16.94 m), i.e., 0.02353 km^2. The number of specimens captured from length class *l* (M_{tl}), all categories *o* combined, in CCGS *Teleost*–Campelen equivalents and standardized for an area *a*, was calculated as follows:

$$M_{tl} = \sum_{o}^{O} \left(M_{tol} \cdot \frac{0.75}{b_t} \cdot \frac{16.94}{d} \cdot u_{tol} \cdot \frac{1}{f_{to}} \right) \tag{4}$$

where f_{to} is the sampled fraction of the catch from category *o* in tow *t*.

For tows with no catches of predator *p* from length class *l*, M_{tl} was assigned a value of 0. Depending on the stomach collection protocols used in each year *g* of the nGSL multispecies surveys, three possible types of successful random fishing tows were observed:

1. tows with catches and stomachs collected;
2. tows with catches, but no stomachs collected; and
3. tows with no catches, hence no stomachs collected.

For each *g*-*h*-*p*-*l* combination at the stratum level, it was possible to observe the following types of tow combinations:

1. only 1;
2. only 2;
3. only 3;

---

[9] Standard tow duration for the CCGS *Teleost*–Campelen vessel–gear combination is 15 min at 3 kt·h^{-1}, corresponding to a trawled distance of 0.75 NM.

4. combination of 1 and 2;
5. combination of 1 and 3;
6. combination of 2 and 3; or
7. combination of 1, 2 and 3.

In cases where no stomachs from length class *l* were sampled in a tow, even though fish of that length class were caught, Warren et al. (1994) suggest omitting this tow and performing the calculations at the stratum level, based on the other non-problematic tows. However, this solution could not be applied in situations 2 and 6, when no stomachs were available in the stratum to infer the proportion of capelin in the stomach contents of captured predators (see pink cells in Figures 8 to 13). To address this lack of data, it was decided that a three-tiered approach would be used to search for stomachs to use in problematic *g-h-p-l* combinations. The objective of this approach was to use stomachs with contents resembling those that would have been observed in the problematic *g-h-p-l* combinations. The three tiers were as follows:

1. adjacent strata (i.e., directly bordering the problematic stratum) that share the same NAFO Division (e.g., 4R) and depth class (e.g., 183–274 m);
2. other strata in the same NAFO Division and depth class; and
3. all stomachs available in year *g*.

For a problematic *g-h-p-l* combination, the search for stomachs would stop at the 1st tier if at least one stomach was available. If no stomachs were available at this tier, the search would proceed to the 2nd tier, using other strata in the same Division and depth class not directly bordering the problematic stratum. If still no stomachs were available, the 3rd and last tier would then use all stomachs available in year *g*. An example of this process is given in Figure 14. Of the 179 problematic *g-h-p-l* combinations for Atlantic cod, tiers 1 to 3 were used 91, 50, and 38 times, respectively. For Greenland halibut, tiers 1 to 3 were used 294, 70, and 83 times, respectively.

Once stomachs had been assigned to all *g-h-p-l* combinations, the rest of the procedure essentially followed what is described in Warren et al. (1994). Let *k* stand for a specimen of predator *p* from length class *l* caught in tow *t* of stratum *h* from which a stomach sample was collected (e.g., *k* = 1, 2,…, *K*). It was possible to calculate the *t* trawl mean, $\overline{y_{tl}}$, as follows:

$$\overline{y_{tl}} = \frac{\sum_{k=1}^{K} y_k}{K} \tag{5}$$

where y_k is the stomach content of the specimen *k* (in g), e.g., capelin content in stomachs or the total stomach content.

The mean stomach content at the stratum level (W_{hl}) was then calculated by weighting each *t* tow of the *T* tows made in stratum *h* by its associated M_{tl} value:

$$w_{hl} = \frac{\sum_{t=1}^{T} M_{tl} \cdot \overline{y_{tl}}}{\sum_{t=1}^{T} M_{tl}} \tag{6}$$

To combine the strata, the number of fish from length class *l* in stratum *h* (F_{hl}) with area A_h (km^2) was first calculated:

$$F_{hl} = \left(\frac{\sum_{t=1}^{T} M_{tl}}{T \cdot a}\right) \cdot A_h \tag{7}$$

The estimate of the total stomach content of all fish from length class *l* (W_{hl}) in stratum *h* was:

$$W_{hl} = F_{hl} \cdot w_{hl} \tag{8}$$

The values of each *H* strata could then be combined to determine the total content at the study area level in a given year *g*:

$$W_l = \sum_{h=1}^{H} W_{hl} \tag{9}$$

The number of fish F_l from length class *l* at the study area level was calculated according to a similar approach:

$$F_l = \sum_{h=1}^{H} F_{hl} \tag{10}$$

Lastly, the mean stomach content at the study area level (C_l) was:

$$C_l = \frac{W_l}{F_l} \tag{11}$$

Since it was difficult to separate empty stomachs from those with contents, but no capelin, equations 5–11 were used in loops to calculate two values:

- capelin in mean stomach content, $C_{l,capelin}$, in g; and
- mean total stomach content, $C_{l,total}$, in g.

The proportion of capelin in the mean stomach content of a specimen from length class *l* in a given year across the study area thus corresponded to the equation below:

$$S_l = \frac{C_{l,capelin}}{C_{l,total}} \tag{12}$$

2.3. CONSUMPTION INDEX

The estimation of both predators' annual consumption is based on the approach presented for Atlantic cod in Benoît and Rail (2016). This method relies on the estimation of the total monthly consumption (i.e., all prey combined) in August, as that was generally the period in the nGSL multispecies survey for which stomachs were available. The monthly consumption in August by a specimen from the 1 cm *q* length class (i.e., c_q) was calculated as follows:

$$c_q = (30.42 \cdot 24) \cdot S_q \cdot R_q \tag{13}$$

where:

- 30.42 is the average number of days in a month;

- 24 is the number of hours in a day;
- S_q is the mean stomach content (g), all prey combined, per length class *q* in August; and
- R_q is the hourly gastric emptying rate in August, which varies depending on the water temperature i_q in the area from which specimens were taken.

To calculate S_q, the mean total stomach content (w_q) per 1 cm *q* length class was estimated using a non-linear model, since not all *q* length classes were present in the stomach data. Only length classes *q* where the sample size *n* was ≥ 5 stomachs and the mean stomach content was > 0 g were retained. For this exercise, data from all years were combined. A GAM (generalized additive model) model using gam(formula = ln[w_q] ~ s[*q*, bs = cs], weights = *n*) was generated using the *R* 4.1.1 free software (R Core Team 2021) with the *mgcv* package (Wood 2011) in order to predict the S_q values.

Calculation of the hourly gastric emptying rate is based on the following equation:

$$R_q = 0.004 \cdot e^{0.115 \cdot i_q} \tag{14}$$

where 0.004 and 0.115 are constants derived from the study by Durbin et al. (1983) and later reused by Overholtz et al. (2000) and Benoît and Rail (2016).

For each stratum retained, the average number of individuals from length class *q* caught in a standard tow was calculated ($\overline{M_{htq}}$). Since not all *h* strata were always sampled with ≥ 2 successful random fishing tows (Figure 6) over years *g*, a multiplicative model was used. For problematic *g*-*h* combinations, the value obtained from the multiplicative model was used, calculated from the data available in year *g* and the previous three years (Bourdages et al. 2020). For each $\overline{M_{htq}}$ value, a mean bottom temperature i_{hq} (°C) was determined. To do this, only successful random tows from the strata retained that had a temperature value were selected. For each year–stratum combination, a mean temperature was obtained. A multiplicative model was used to provide values for combinations with < 2 tows with a temperature measurement. Lastly, the mean temperature experienced by specimens from length class *q* was calculated as follows:

$$i_q = \sum_{h}^{H} \left(\overline{M_{htq}} \cdot i_{hq} \cdot \frac{A_h}{\sum_h^H A_h} \right) \tag{15}$$

The mean annual temperatures obtained and used to calculate the gastric emptying rate are given in Figure 15.

Since only stomachs from the nGSL multispecies surveys were available in the analyses (and therefore were collected mainly in August), it was assumed that the stomach contents from this time of year were representative of what would be observed during the rest of the year. It was also assumed that both Atlantic cod and Greenland halibut do not forage for food three months per year. The annual consumption of a C_q specimen was obtained by multiplying the monthly consumption, c_q, by 9. For Atlantic cod, this decision was based on studies by Turuk (1968), Tyler (1971), Fordham and Trippel (1999), and Schwalme and Chouinard (1999), which showed that this species feeds very little in winter in the Northwest Atlantic. The lower feeding intensity of Atlantic cod in winter can also be observed in the data from the fixed gear sentinel fisheries program (Figure 16). For Greenland halibut, the studies by Chumakov and Podrazhanskaya (1983, 1986) and Rodríguez-Marín et al. (1995) showed that the feeding activity of Greenland halibut took place mainly during the summer-fall period.

To estimate total annual consumption across the study area and by length class q ($C_{q,\,tot}$), the mean value of $\overline{M_{tq}}$ was calculated at the study area level:

$$\overline{M_{tq}} = \sum_{h}^{H} \left(\overline{M_{htq}} \cdot \frac{A_h}{\sum_h^H A_h} \right) \tag{16}$$

To estimate a correction of the trawl catchability (Q), the values used were the same as those used by Savenkoff et al. (2005) and derived from Harley et al. (2001), namely:

$$\mathrm{Q} = \begin{cases} \dfrac{0.986 \ \cdot \exp\left(-4.43 + (0.109 \cdot q)\right)}{1 + \exp\left(-4.43 + (0.109 \cdot q)\right)} & \text{for Greenland halibut} \\ \dfrac{0.949 \ \cdot \exp\left(-5.06 + (0.139 \cdot q)\right)}{1 + \exp\left(-5.06 + (0.139 \cdot q)\right)} & \text{for Atlantic cod} \end{cases} \tag{17}$$

The abundance of specimens from length class q in the study area, F_q, could then be calculated:

$$F_q = \overline{M_{tq}} \cdot Q \cdot \sum_{h}^{H} A_h / a \tag{18}$$

where $\sum_h^H A_h / a$ is the number of standard trawlable units of area a located within the study area. The estimated total annual consumption across the study area and by length class q ($C_{q,\,tot}$) was then calculated by multiplying the individual annual consumption (C_q) by the abundance (F_q) in the study area:

$$C_{q,tot} = C_q \cdot F_q \tag{19}$$

Lastly, annual capelin consumption ($C_{capelin}$), all l length classes combined, were calculated as follows:

$$C_{capelin} = \sum_{l}^{L} \left(\sum_{q \geq l_{min}}^{q < l_{min}} C_{q,tot} \right) \cdot S_l \tag{20}$$

2.4. COMPARISON OF RESULTS OBTAINED

To provide an overview of capelin consumption in the nGSL, the results obtained were compared with commercial landings of capelin in NAFO Divisions 4RST. Landings data were obtained from ZIFF files (*Zonal Interchange File Format*, STACAC 1984), which were produced by the standardization of fishery data from various DFO Atlantic regions.

The results were also compared with those obtained from the ecosystem models previously published for the nGSL (Savenkoff et al. 2004 a, 2005, 2009). These mass-balance models used inverse methods to estimate and represent mass—or energy—flows through the ecosystem. In summary, since it is too difficult to make direct estimates of mass flows in an ecosystem of interest, it was assumed that these flows balance each other out—that is, outputs equal inputs, hence the inverse methodology (Vézina and Platt 1988). For example, the consumption by a predator must be balanced by prey production if it is assumed that there is no cannibalism and the system is in equilibrium.

By compartmentalizing the nGSL ecosystem into several *compartments* representing species (e.g., Atlantic cod, Greenland halibut) or functional groupings (e.g., pelagic predators, demersal predators), Savenkoff et al. (2004b) achieved a representation of the trophic chain and potential material flow interactions. This compartmentalization corresponds to their model. Various models were developed for the nGSL, covering specific periods. Three of the models coincided with the period addressed in this study (1993–2020): 1994–1996 (Savenkoff et al. 2004a), 2000–2002 (Savenkoff et al. 2005), and 2003–2005 (Savenkoff et al. 2009). These covered the nGSL, excluding the subtidal zone, and provided fixed values for each period.

Tables in each of the reports associated with these models summarized:

1. the mass contribution of capelin ($\%_{capelin}$, in %) to the diet of the different *compartments* retained[10] to represent the trophic chain of the nGSL; and
2. the total annual consumption per km² ($C_{p\ km^2}$), all prey combined, of these *compartments*.

Knowing that the study area used to calculate the total annual consumption was 116,115.2 km² (the area of the strata retained for stomach content analysis), it was possible to obtain the total annual consumption of capelin for each compartment investigated by the various mass-balance models:

$$C_{gp,capelin} = \%_{capelin} \cdot C_{p\ \mathrm{km}^2} \cdot 116\,115.2 \tag{21}$$

It was then possible to relate, for each period, the consumption of capelin by Atlantic cod and Greenland halibut to the overall consumption by all predators selected in the various mass-balance models (% total consum. column in Table 3).

2.5. LENGTHS OF INGESTED CAPELIN

For ingested capelin with little skin and fin damage from the digestive process, the fork length was sometimes recorded. A summary analysis was conducted to compare the lengths chosen by the two predators with those available from the nGSL multispecies survey. Capelin lengths considered outliers (outside three times the interquartile range) were removed from the analyses.

3. RESULTS

The estimated annual consumption of capelin in years for which stomach content data for both predators were available was consistently higher than the commercial landings in NAFO Divisions 4RST (Figure 17). Given that other predators of capelin were present in the ecosystem (Table 3), the results suggest that fishing mortality (*F*) appears to be lower, or even much lower, than natural mortality. The mass-balance models show that Atlantic cod and Greenland halibut accounted for, on average, ~19% of the total annual consumption of capelin for the periods investigated (Table 3). The annual consumption values estimated by Savenkoff et al. are also significantly higher than those calculated in this study (Figure 17).

Since the annual consumption of both predators is closely linked to the abundance of the three length classes of each predator (Equation 20, Figure 18), it seemed more reasonable to use

---

[10] N.B. The number of *compartments* varied between periods and therefore the different models.

only the proportion of capelin in the mean stomach contents (Figures 19–20). An abundance index was then obtained by weighting the proportions of capelin by year and predator, according to the abundance for each length class and rendered in percentages, resulting in the mean annual percentages of capelin in the mean stomach contents of each predator (Figure 21). However, when comparing the new index with that of the average number of capelin caught per tow in the nGSL bottom trawl multispecies survey, it can be seen that the correlation is consistently weak and non-significant, regardless of the period considered for Atlantic cod (Figure 22). For Greenland halibut, the correlation for the period 1993–2009 was positive, moderate and significant. For both predators, the recent period (2015–2020) shows negative, weak and non-significant correlations. The values for the recent period produce positive weak correlations when used in the full series (1993–2020).

The size of ingested capelin was not influenced by the size of Greenland halibut, but was weakly correlated with the size of cod (Figure 23). Capelin caught in the nGSL multispecies surveys show a size distribution similar to the distributions observed for capelin ingested by Greenland halibut (Figure 24). Capelin ingested by Atlantic cod appear to be smaller than those caught in the surveys.

4. DISCUSSION

The use of stomach content data in this study has yielded some very valuable results. Indeed, they suggest that fishing mortality is much lower than natural mortality, a finding that is supported by previous studies conducted by Savenkoff et al. in the nGSL (2004a; 2005; 2009. Figure 17). However, since both these previous works and the present study used the same stomach contents data, it is questionable why such a difference in consumption is observed. Different explanations could be found in the differences in methodology between the two approaches (Table 4).

By using the mean annual percentage that capelin represents in the mean stomach contents of each predator as an index (Figure 21), it is possible to track variations in catch per unit effort (CPUE; at least for Greenland halibut) in the nGSL multispecies surveys during the period 1993–2009. For Atlantic cod, this relationship is far less clear and may be caused by the more opportunistic nature of its feeding strategy. The question has also been raised as to whether using a reduced size range for predators would help to refine the index produced. For example, Figure 20 shows the range [20–40[cm for Greenland halibut, which appears to better reflect the pattern in CPUE shown in Figure 21. Nevertheless, it should be kept in mind that although the abundance index from the survey is now considered valid (Chamberland et al. 2022), a high level of uncertainty is inherent in its use.

In addition, several sources of uncertainty still need to be clarified. The use of stomach content data brings its own set of challenges, the first being that the identifiability of ingested prey items depends on the extent to which they have been digested. At the time of analysis of some stomachs, it is very likely that some capelin were recorded as *digested fish* in cases where the characteristics enabling identification were no longer present due to digestion. Additional occurrences of capelin will therefore most likely have been overlooked in this study, potentially leading to an underestimation of the consumption results presented.

Although special care was taken at sea to choose only stomachs without signs[11] of regurgitation or ingestion of food in the trawl, it is also possible that empty stomachs were caused by processes besides physiological or behavioural ones. For example, Bernier and Chabot (2013)

---

[11] Stomachs were not collected from fish with a flaccid or evaginated stomach, or a mouth with food in it.

showed that Greenland halibut caught at greater depths had a higher probability of having empty stomachs, potentially caused by the rapid changes in depth and pressure that occur as the trawl is hauled up, which appears to cause regurgitation.

The assumption that stomach contents collected in August are representative of what is observed the rest of the year is another key point. In fact, other studies have shown that both the feeding intensity and the relative proportion of some prey change depending on the season and even sometimes between years. However, for the nGSL region, annual numbers of stomachs outside the period of the multispecies survey (August) are very low, making it difficult to adjust seasonal consumption.

Of the various publications that have described the diet of cod in the nGSL (Minet and Perodou 1978; Fréchet et al. 1995, 2003, 2005; DFO 2004; Ouellette-Plante et al. 2020), three presented results from other months of the year, which mostly yielded limited numbers of stomachs. The first study, conducted by Minet and Perodou (1978), presented the findings obtained from 570 and 194 stomachs collected in the winters of 1975–1976 and the summer of 1975, respectively. According to Minet and Perodou, there was very little seasonal variation in the diet of cod, which was similar between NAFO Divisions in terms of the main species. Their results showed that capelin was the most abundant prey in both summer and winter. However, this abundance of capelin in winter was not observed after the sentinel fisheries program was implemented in fall 1994. After collecting 689 cod stomachs between November 1994 and January 1995, Fréchet et al. (1995) demonstrated that invertebrates made up a greater part of the cod diet (in % of total stomach content mass). Atlantic herring (*Clupea harengus*) accounted for the greatest portion (6.7%), nearly double the contribution of capelin (3.05%). Fréchet et al. (2003) also showed that the variation in feeding intensity across the months of the year decreased from July to August, before increasing again in fall. However, the authors stated that the different vessel–gear combinations used to obtain stomachs could have been a parameter that affected stomach fullness between months. Large discrepancies between these studies have been observed, which are difficult to explain since the stomachs collected did not necessarily cover the same locations or periods, nor were they sampled from comparable surveys.

For Greenland halibut, studies on the diet of the GSL stock are more limited (Tremblay and Axelsen 1981; Morin et al. 1995; Morin and Bernier 2003; Bernier and Chabot 2013; Gauthier et al. 2020; Ouellette-Plante et al. 2020). A review of all data available for the nGSL at the time of publication is provided in Bernier and Chabot (2013), including data from other surveys besides the nGSL summer multispecies survey. Unfortunately, the annual coverage was not complete, with only 79 stomachs available for December through March, which is known as the breeding period for Greenland halibut (Gauthier et al. 2020). Nonetheless, Gauthier et al. observed that the fullness indices for Greenland halibut > 30 cm were higher in spring (after the breeding period) compared to later, near the end of summer.

For both Atlantic cod and Greenland halibut, the current seasonal coverage of the stomach content data is not ideal in terms of the numbers, even though both species are among the most sampled for stomachs in the nGSL. It appears, at first glance, that using the stomach content data from neighbouring stocks could be an interesting alternative. However, the opportunistic nature of both predators should be kept in mind, since their temporal and spatial feeding patterns may vary depending on prey distribution and abundance (Hovde et al. 2002). This means that a pattern observed in one region will not necessarily apply to another region. For example, Atlantic herring has historically been closely linked to cod in the sGSL (Schwalme and Chouinard 1999; NAFO Divisions 4T and 4Vn [November to April], Hanson and Chouinard 2002), whereas capelin is the main prey for northern cod (NAFO Divisions 2J3KL, Lilly 1987).

Should further studies be conducted to explore pelagic fish stocks by studying the stomach contents of their predators, extensive stock-specific data on stomach contents will be necessary to reliably characterize seasonal changes in the diet of the predators studied (Schwalme and Chouinard 1999). Significant effort should be put into collecting stomachs in the winter months to refine our knowledge of the main predators in the GSL, thus making it possible to better assess species that are difficult to sample.

Since capelin is one of the main forage species in the GSL, its assessment would benefit from further taking into account the importance of capelin in the environment as well as the population patterns of other cohabiting species, such as predators of capelin (Winters 1975; Hjermann et al. 2004; Overholtz and Link 2006; Tyrrell et al. 2008).

5. ACKNOWLEDGEMENTS

The authors thank Hugo Bourdages and Caroline Lehoux for their comments and suggestions, which helped to greatly improve this manuscript.

6. REFERENCES CITED

Bailey, R.F.J., Able, K.W., and Leggett, W.C. 1977. Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St. Lawrence Estuary and western Gulf of St. Lawrence. J. Fish. Res. Board Can. 34(11) : 2015–2029.

Benoît, H.P., and Rail, J.-F. 2016. Principal predators and consumption of juvenile and adult Atlantic herring (*Clupea harengus*) in the southern Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/065 : viii + 42 p.

Berard, M.T., and Davoren, G.K. 2020. Capelin (*Mallotus villosus*) availability influences the inshore summer diet of Atlantic cod (*Gadus morhua*) in coastal Newfoundland. Environ. Biol. Fishes 103(6) : 771–782.

Bernier, B., and Chabot, D. 2013. Évaluation de l'état du stock de flétan du Groenland (*Reinhardtius hippoglossoides*) du golfe du Saint-Laurent (4RST) en 2010 et description de son régime alimentaire. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/140: viii + 85 p.

Boje, J., Neuenfeldt, S., Sparrevohn, C.R., Eigaard, O., and Behrens, J.W. 2014. Seasonal migration, vertical activity, and winter temperature experience of Greenland halibut *Reinhardtius hippoglossoides* in West Greenland waters. Mar. Ecol. Prog. Ser. 508 : 211–222.

Bourdages, H., Savard, L., Archambault, D., and Valois, S. 2007. Results from the August 2004 and 2005 comparative fishing experiments in the northern Gulf of St. Lawrence between the CCGS *NGCC Alfred Needler* and the CCGS *NGCC Teleost*. Can. Tech. Rep. Fish. Aquat. Sci. 2750: ix + 57 p.

Bourdages, H., Brassard, C., Desgagnés, M., Galbraith, P., Gauthier, J., Nozères, C., Scallon-Chouinard, P.-M., and Senay, C. 2020. Preliminary results from the ecosystemic survey in August 2019 in the Estuary and northern Gulf of St. Lawrence. DFO Can Sci Advis. Sec. Res. Doc. 2020/009: iv + 93 p.

Bowering, W.R., and Lilly, G.R. 1992. Greenland halibut (*Reinhardtius hippoglossoides*) off Southern Labrador and Northeastern Newfoundland (Northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). Neth. J. Sea Res. 29(1) : 211–222.

Chamberland, J.-M., Plourde, S. and Benoît, H. B. 2022. Biological characteristics, factors affecting catchability, and abundance indices of capelin in the southern and northern Gulf of St. Lawrence multi species bottom trawl surveys. DFO Can. Sci. Advis. Sec. Res. Doc. 2021/077. iv + 41 p.

Chumakov, A.K., and Podrazhanskaya, S.G. 1983. Feeding of Greenland halibut in the northwest Atlantic. NAFO SCR Doc. 83/IX/79 : 22 p.

Chumakov, A.K., and Podrazhanskaya, S.G. 1986. Feeding of the Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic. NAFO Sci. Coun. Studies 10 : 47–52.

Deroba, J.J. 2018. Sources of variation in stomach contents of predators of Atlantic herring in the Northwest Atlantic during 1973–2014. J. Appl. Ichthyol. 75(4) : 1439–1450.

DFO. 2004. The Northern Gulf of St. Lawrence (3Pn, 4RS) cod in 2003. DFO Can. Sci. Advis. Sec. Stock Status Rep. 2004/019.

DFO. 2015. Update of indicators of the status of the estuary and gulf of st. Lawrence (divisions 4RST) capelin stock in 2014. DFO Can. Sci. Advis. Sec., Sci. Resp. 2015/032.

DFO. 2018. Assessment of the Estuary and Gulf of St. Lawrence (Divisions 4RST) Capelin Stock in 2017. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/037.

Durbin, E.G., Durbin, A.G., Langton, R.W., and Bowman, R.E. 1983. Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. Fish. Bull. 81(3) : 437–454.

Dwyer, K.S., Buren, A., and Koen-Alonso, M. 2010. Greenland halibut diet in the Northwest Atlantic from 1978 to 2003 as an indicator of ecosystem change. J. Sea Res. 64(4) : 436–445.

Eriksen, E., Bogstad, B., Dolgov, A., and Beck, I.M. 2018. Cod diet as an indicator of Ctenophora abundance dynamics in the Barents Sea. Mar. Ecol. Prog. Ser. 591 : 87–100.

Espeland, S.H., Thoresen, A.G., Olsen, E.M., Stige, L.C., Knutsen, H., Gjøsæter, J., and Stenseth, N.C. 2010. Diel vertical migration patterns in juvenile cod from the Skagerrak coast. Mar. Ecol. Prog. Ser. 405 : 29–37.

Fahrig, L., Lilly, G.R., and Miller, D.S. 1993. Predator stomachs as sampling tools for prey distribution: Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 50(7) : 1541–1547.

Fordham, S.E., and Trippel, E.A. 1999. Feeding behaviour of cod (*Gadus morhua*) in relation to spawning. J. Appl. Ichthyol. 15(1) : 1–9.

Fréchet, A., Schwab, P., Lambert, Y., Chabot, D., Decker, D., Rowe, G., Nadeau, P., and Collier, F. 1995. The sentinel fisheries of the Northern Gulf of St. Lawrence cod stock (3Pn, 4RS) in 1994. DFO, Atlantic Fisheries Res. Doc. 95/54 : 31 p.

Fréchet, A., Gauthier, J., Schwab, P., Bourdages, H., Chabot, D., Collier, F., Grégoire, F., Lambert, Y., Moreault, G., Pageau, L., and Spingle, J. 2003. The status of cod in the Northern Gulf of St. Lawrence (3Pn, 4RS) in 2002. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/065 : i + 25 p.

Fréchet, A., Gauthier, J., Schwab, P., Pageau, L., Savenkoff, C., Castonguay, M., Chabot, D., Tournois, C., Lussier, J.-F., Spingle, J., and Collier, F. 2005. The status of cod in the Northern Gulf of St. Lawrence (3Pn, 4RS) in 2004. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/060: i + 71 p.

Frid, C.L.J., and Hall, S.J. 1999. Inferring changes in North Sea benthos from fish stomach analysis. Mar. Ecol. Prog. Ser. 184 : 183–188.

Gauthier, J., Marquis, M.-C., Bourdages, H., Ouellette-Plante, J., and Nozères, C. 2020. Gulf of St. Lawrence (4RST) Greenland Halibut Stock Status in 2018: Commercial Fishery and Research Survey Data. Can. Sci. Advis. Sec. Res. Doc 2020/016: v + 127 p.

Gotshall, D.W. 1969. The use of predator food habits in estimating relative abundance of the ocean shrimp, *Pandalus jordani* Rathbun. FAO Fish. Rep. 57 : 667–685.

Grégoire, F., Samson, Y., and Beaulieu, J.-L. 1999. Résultats de la mission exploratoire d'hydroacoustique concernant le capelan (*Mallotus villosus*) de la côte ouest de Terre-Neuve. Secr. can. pour l'éval. des stocks, Doc. de rech. 1999/010 : 20 p.

Grégoire, F., Bourdages, H., and Roy, J. 2002. Production d'un indice de dispersion pour le capelan (*Mallotus villosus* L.) de l'estuaire et du nord du golfe du Saint-Laurent par le krigeage d'indicatrice. Rapp. tech. can. sci. halieut. aquat. 2418 : vi + 21 p.

Grégoire, F., Barry, W., Barry, J., Lefebvre, C., Lévesques, C., and Hudon, J. 2005. West coast of Newfoundland capelin (*Mallotus villosus* M.) and Atlantic herring (*Clupea harengus harengus* L.) larval survey, part 1: Description of the data collected in partnership with the industry (Barry Group) in July 2004. Can. Data Rep. Fish. Aquat. Sci. 1168 : vi + 32 p.

Grégoire, F., Barry, W., Barry, J., Lefebvre, L., Lévesques, C., and Hudon, J. 2006. West coast of Newfoundland capelin (*Mallotus villosus* M.) and Atlantic herring (*Clupea harengus harengus* L.) larval survey, part 3: Description of the data collected in partnership with the industry (Barry Group) in July 2005. Can. Data Rep. Fish. Aquat. Sci. 1168(3) : vi + 32 p.

Grégoire, F., Barry, W., Barry, J., Lévesques, C., Beaulieu, J.-L., and Gendron, M.-H. 2008. Westcoast of Newfoundland capelin (*Mallotus villosus* M.) and Atlantic herring (*Clupea harengus harengus* L.) larval survey, part 5: Description of the data collected in partnership with the industry (Barry Group) in July 2007. Can. Data Rep. Fish. Aquat. Sci. 1205 : vi + 31 p.

Grégoire, F., Bourdages, H., and Ouellet, J.-F. 2012. Analyses of the capelin (*Mallotus villosus*) abundances from the multidisciplinary groundfish and shrimp surveys conducted in the Estuary and northern Gulf of St. Lawrence from 1990 to 2009. Can. Sci. Advis. Sec. Res. Doc 2011/022: 94 p.

Grégoire, F., Girard, L., Beaulieu, J.-L., Lussier, J.-F., and Bruneau, B. 2013. Capelin (*Mallotus villosus*) in the Estuary and Gulf of St. Lawrence (NAFO Divisions 4RST) in 2012. DFO Can Stock. Assess. Sec. Res. Doc 2013/023: vi + 90 p.

Groot, S.J. de. 1970. Some notes on an ambivalent behaviour of the Greenland halibut *Reinhardtius hippoglossoides* (Walb.) Pisces: Pleuronectiformes. J. Fish Biol. 2(3) : 275–279.

Hanson, J.M. 2011. Ontogenetic diet comparison of Atlantic cod and white hake occurring at historically low population abundances. Trans. Am. Fish. Soc. 140(4) : 1070–1077.

Hanson, J.M., and Chouinard, G.A. 2002. Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959–2000. J. Fish Biol. 60(4) : 902–922.

Harley, S.J., Myers, R., Barrowman, N., Bowen, K., and Amiro, R. 2001. Estimation of research trawl survey catchability for biomass reconstruction of the eastern Scotian Shelf. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/084 : 54 p.

Hatch, S.A., and Sanger, G.A. 1992. Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar. Ecol. Prog. Ser. 80 : 1–14.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, NY.

Hjermann, D.O., Ottersen, G., and Stenseth, N.Chr. 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proc. Natl. Acad. Sci. U.S.A. 101(32) : 11679–11684.

Hovde, S.C., Albert, O.T., and Nilssen, E.M. 2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). ICES J. Mar. Sci. 59(2) : 421–437.

Hurlbut, T., and Clay, D. 1990. Protocols for Research Vessel Cruises within the Gulf Region (Demersal Fish) (1970–1987). Can. Manuscr. Rep. Fish. Aquat. Sci. 2082 : 143 p.

Lasley-Rasher, R.S., Brady, D.C., Smith, B.E., and Jumars, P.A. 2015. It takes guts to locate elusive crustacean prey. Mar. Ecol. Prog. Ser. 538 : 1–12.

Le Bris, A., Fréchet, A., Galbraith, P.S., and Wroblewski, J.S. 2013. Evidence for alternative migratory behaviours in the northern Gulf of St Lawrence population of Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. 70(4) : 793–804.

Lear, W.H. 1970. The biology and fishery of the Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) in the Newfoundland area. mémoire de master, Memorial University.

Lilly, G.R. 1987. Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1567 : vii + 37 p.

Lilly, G.R., et Parsons, D.G. 1991. Distributional patterns of the northern shrimp (*Pandalus borealis*) in the northwest Atlantic as inferred from stomach contents of cod (*Gadus morhua*). ICES C.M. Document 1991/K : 41 : 15 p.

Link, J.S. 2004. Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. Mar. Ecol. Prog. Ser. 269 : 265–275.

Methven, D.A., and Piatt, J.F. 1989. Seasonal and annual variation in the diet of Atlantic cod (*Gadus morhua*) in relation to the abundance of capelin (*Mallotus villosus*) off eastern Newfoundland, Canada. ICES J. Mar. Sci. 45(2) : 223–225.

Mills, K.L., Laidig, T., Ralston, S., and Sydeman, W.J. 2007. Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System. Fish. Oceanogr. 16(3) : 273–283.

Minet, J.P., and Perodou, J.B. 1978. Predation of cod, *Gadus morhua*, on capelin, *Mallotus villosus*, off eastern Newfoundland and in the Gulf of St. Lawrence. ICNAF Res. Bull. 13 : 11–20.

Morin, B., and Bernier, B. 2003. Assessment of Greenland halibut (*Reinhardtius hyppoglossoides*) in the Gulf of St. Lawrence (4RST) in 2002. DFO Can Stock. Assess. Sec. Res. Doc 2003/088: i + 73 p.

Morin, B., Bernier, B., Chabot, D., and Maguire, J.-J. 1995. Évaluation et biologie du flétan du Groenland (*Reinhardiius hippoglosoides*) du golfe du Saint-Laurent (4RST) en 1994. MPO, pêche de l'Atlantique Doc. Rech. 95/59 : 47 p.

Ouellette-Plante, J., Chabot, D., Nozères, C., and Bourdages, H. 2020. Diets of demersal fish from the CCGS *Teleost* ecosystemic surveys in the estuary and northern Gulf of St. Lawrence, August 2015-2017. Can. Tech. Rep. Fish. Aquat. Sci. 3383: v + 121 p.

Overholtz, W.J., and Link, J.S. 2006. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977–2002. ICES J. Mar. Sci. 64(1) : 83–96.

Overholtz, W.J., Link, J.S., and Suslowicz, L.E. 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(4) : 1147–1159.

Parsons, D.G., Lilly, G.R., and Chaput, G.J. 1986. Age and growth of northern shrimp *Pandalus borealis* off northeastern Newfoundland and southern Labrador. Trans. Am. Fish. Soc. 115(6) : 872–881.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rodríguez-Marín, E., Punzón, A., and Paz, J. 1995. Feeding patterns of Greenland halibut (*Reinhardtius hippoglossoides*) in Flemish Pass (Northwest Atlantic). NAFO Sci. Coun. Studies 23 : 43–54.

Roseneau, D.G., and Vernon Byrd, G. 1997. Using Pacific halibut to sample the availability of forage fishes to seabirds. *Dans* Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks. p. 231–241.

Savenkoff, C., Bourdages, H., Castonguay, M., Morissette, L., Chabot, D., and Hammill, M.O. 2004a. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2531 : vi + 93 p.

Savenkoff, C., Castonguay, M., Vézina, A.F., Despatie, S.-P., Chabot, D., Morissette, L., and Hammill, M.O. 2004b. Inverse modelling of trophic flows through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. Can. J. Fish. Aquat. Sci. 61(11) : 2194–2214.

Savenkoff, C., Grégoire, F., and Chabot, D. 2004c. Main prey and predators of capelin (*Mallotus villosus*) in the northern and southern Gulf of St. Lawrence during the mid-1980s and mid-1990s. Can. Tech. Rep. Fish. Aquat. Sci. 2551 : vi + 30 p.

Savenkoff, C., Castonguay, M., Méthot, R., Chabot, D., and Hammill, M.O. 2005. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2000-2002). Can. Tech. Rep. Fish. Aquat. Sci. 2588 : v + 91 p.

Savenkoff, C., Valois, S., Chabot, D., and Hammill, M.O. 2009. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (2003-2005). Can. Tech. Rep. Fish. Aquat. Sci. 2829 : vi+117 p.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence. ICES J. Mar. Sci. 56(3) : 303–319.

STACAC. 1984. Catch & effort computer file structure for zonal interchange - 1984. STACAC Standard Document 3 : 13 p.

Sunada, J.S., and Kelly, P.R. 1981. The brown pelican as a sampling instrument of age group structure in the northern anchovy population. CalCOFI Rep. 22 : 65–68.

Templeman, W. 1970. Distribution of *Anotopterus pharao* in the north Atlantic and comparison of specimens of *A. pharao* from the western north Atlantic with those from other areas. J. Fish. Res. Board Can. 27(3) : 499–512.

Tremblay, C., and Axelsen, F. 1981. Biology and fisheries of Greenland halibut *Reinhardtius hippoglossoides* (Walbaum) of the Gulf of St. Lawrence. MAPAQ. Trav. Pêch. Qué. No 48.

Turuk, T.N. 1968. Seasonal changes of cod feeding in the Labrador and Newfoundland area in 1964-1966. Trudy Pinro 23 : 370–382.

Tyler, A.V. 1971. Monthly changes in stomach contents of demersal fishes in Passamaquoddy Bay, N. B. Fish. Res. Bd. Canada Tech. Rep. 288 : 118 p.

Tyrrell, M.C., Link, J.S., Moustahfid, H., and Overholtz, W.J. 2008. Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem using multispecies virtual population analysis. ICES J. Mar. Sci. 65(9) : 1689–1700.

Vézina, A.F., and Platt, T. 1988. Food web dynamics in the oceans. I. Best-estimates of flow networks using inverse methods. Mar. Ecol. Prog. Ser. 42 : 269–287.

Vollen, T., and Albert, O.T. 2008. Pelagic behavior of adult Greenland halibut (*Reinhardtius hippoglossoides*). Fish. Bull. 106(4) : 457–470.

Warren, W.G., Lilly, G.R., and Shelton, P.A. 1994. Estimating the population mean stomach content weight of cod from a stratified-random trawl survey and length stratified stomach sampling. ICES C.M. Document 1994/D : 13.

Winters, G.H. 1975. Review of capelin ecology and estimation of surplus yield from predator dynamics. ICNAF Res. Doc. 75/2 : 25 p.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Statist. Soc. B 73(1) : 3–36.

7. TABLES

Table 1. Inventory of stomachs available for the analysis, by species and year. The number and percentage of stomachs containing capelin is also provided. No stomachs were available for the period 2010–2014. No Greenland halibut stomachs were available in 2000.

	Atlantic cod			Greenland halibut			Predators combined		
Year	**Nb. total**	**Nb. with**	**% with**	**Nb. total**	**Nb. with**	**% with**	**Nb. total**	**Nb. with**	**% with**
1993	277	72	26.0	503	40	8.0	780	112	14.4
1994	383	47	12.3	566	24	4.2	949	71	7.5
1995	282	15	5.3	1133	68	6.0	1415	83	5.9
1996	604	30	5.0	2202	117	5.3	2806	147	5.2
1997	653	42	6.4	1400	29	2.1	2053	71	3.5
1998	688	30	4.4	782	25	3.2	1470	55	3.7
1999	876	71	8.1	1559	27	1.7	2435	98	4.0
2000	869	23	2.6	0	0	-	869	23	2.6
2001	789	31	3.9	1176	23	2.0	1965	54	2.7
2002	390	8	2.1	852	17	2.0	1242	25	2.0
2003	793	24	3.0	876	17	1.9	1669	41	2.5
2004	1079	69	6.4	665	17	2.6	1744	86	4.9
2005	1342	66	4.9	927	10	1.1	2269	76	3.3
2006	1174	89	7.6	993	19	1.9	2167	108	5.0
2007	1060	41	3.9	1041	17	1.6	2101	58	2.8
2008	1364	100	7.3	1022	43	4.2	2386	143	6.0
2009	1001	54	5.4	818	32	3.9	1819	86	4.7
2015	1060	33	3.1	690	5	0.7	1750	38	2.2
2016	392	17	4.3	378	6	1.6	770	23	3.0
2017	552	18	3.3	386	8	2.1	938	26	2.8
2018	425	31	7.3	576	32	5.6	1001	63	6.3
2019	311	10	3.2	620	32	5.2	931	42	4.5
2020	405	5	1.2	680	7	1.0	1085	12	1.1
Total	**16,769**	**926**	**5.5**	**19,845**	**615**	**3.1**	**36,614**	**1,541**	**4.2**

Table 2. Inventory of stomachs available for the analysis, by species, year and NAFO unit area. See Figure 1b for the location of the unit areas. We observe that unit areas outside the study area of the multi-species survey (Divisions 3Pn–4RST) are shown. This is due to stations which were just outside the study area according to their geographical positions.

Atlantic cod

Year	3Pn	4Ra	4Rb	4Rc	4Rd	4Si	4Ss	4Sv	4Sx	4Sy	4Sz	4Tf	4Tk	4To	4Tq	4Tn	4Tp	3Ka	4Vn
1993	19	66	40	27	14	10	3	5	41	24	13	1	1	10	3	-	-	-	-
1994	-	72	95	23	33	42	22	23	32	15	22	-	4	-	-	-	-	-	-
1995	13	14	53	70	55	6	28	8	5	16	13	-	-	1	-	-	-	-	-
1996	74	36	69	97	102	20	29	2	49	73	42	4	6	-	-	1	-	-	-
1997	82	80	136	134	59	9	24	50	44	14	-	-	18	-	-	3	-	-	-
1998	57	14	102	229	131	7	27	29	51	-	-	22	16	3	-	-	-	-	-
1999	47	112	195	160	172	31	72	23	36	13	-	7	7	1	-	-	-	-	-
2000	36	52	181	212	173	32	71	88	14	2	5	3	-	-	-	-	-	-	-
2001	75	157	260	192	49	8	18	4	1	-	7	18	-	-	-	-	-	-	-
2002	102	107	75	12	8	9	34	18	12	1	-	2	5	-	1	-	4	-	-
2003	26	62	270	111	48	19	113	77	28	8	-	31	-	-	-	-	-	-	-
2004	-	208	191	191	106	41	13	100	32	83	22	51	-	26	-	6	9	-	-
2005	-	222	231	243	226	49	130	113	69	32	15	9	2	1	-	-	-	-	-
2006	-	220	180	156	116	32	126	107	57	103	33	20	3	-	3	1	-	17	-
2007	-	126	95	175	88	58	122	150	78	74	6	52	-	2	15	19	-	-	-
2008	-	210	223	244	57	54	51	81	157	109	25	28	2	1	66	-	34	-	22
2009	-	78	193	188	59	79	83	78	72	55	-	29	5	1	43	-	38	-	-
2015	-	131	152	120	72	63	121	54	145	89	19	5	5	18	43	6	17	-	-
2016	-	40	60	43	10	38	43	21	33	20	16	9	-	13	24	-	22	-	-
2017	-	76	56	83	39	49	53	30	36	54	39	10	1	2	19	1	4	-	-
2018	-	53	62	62	28	23	31	38	31	39	24	17	5	1	4	-	7	-	-
2019	-	53	54	39	-	23	36	12	29	31	4	3	5	-	9	-	13	-	-
2020	-	96	62	79	41	20	15	14	12	51	6	1	-	-	8	-	-	-	-
Total	**531**	**2,285**	**3,035**	**2,890**	**1,686**	**722**	**1,265**	**1,125**	**1,064**	**906**	**311**	**322**	**85**	**80**	**238**	**37**	**148**	**17**	**22**

Greenland halibut

Year	3Pn	4Ra	4Rb	4Rc	4Rd	4Si	4Ss	4Sv	4Sx	4Sy	4Sz	4Tf	4Tk	4To	4Tq	4Tn	4Tp	3Ka	4Vn
1993	2	2	9	7	13	64	70	15	50	5	45	13	18	71	59	9	51	-	-
1994	1	10	5	19	10	48	102	8	47	10	109	14	20	52	92	19	-	-	-
1995	1	-	44	16	2	104	68	53	157	48	103	20	47	179	168	-	123	-	-
1996	3	-	165	63	6	139	126	88	232	149	229	30	113	360	289	35	175	-	-

Year	3Pn	4Ra	4Rb	4Rc	4Rd	4Si	4Ss	4Sv	4Sx	4Sy	4Sz	4Tf	4Tk	4To	4Tq	4Tn	4Tp	3Ka	4Vn
1997	-	-	145	63	20	113	89	73	164	69	45	12	58	206	165	26	152	-	-
1998	-	-	68	30	12	81	32	46	136	-	49	22	33	96	90	3	84	-	-
1999	8	1	137	19	8	156	154	84	194	87	109	59	73	126	216	-	128	-	-
2001	15	-	202	57	3	33	180	53	13	16	120	50	78	123	131	-	102	-	-
2002	-	-	37	40	-	93	65	53	72	28	70	17	63	96	120	-	98	-	-
2003	23	-	121	36	42	48	93	34	65	35	87	44	37	42	86	25	58	-	-
2004	-	-	104	43	17	42	17	69	28	12	67	41	19	79	79	-	48	-	-
2005	-	3	175	65	21	44	133	49	58	34	67	63	60	55	54	-	46	-	-
2006	-	-	111	60	14	71	123	68	59	31	46	44	77	82	87	-	120	-	-
2007	-	-	84	55	16	65	115	51	92	27	60	78	55	104	140	-	99	-	-
2008	-	-	100	43	8	24	86	78	41	41	80	33	69	66	185	36	132	-	-
2009	-	-	82	61	13	30	79	63	60	23	25	18	91	60	142	-	71		-
2015	-	-	51	57	2	61	75	14	81	27	56	53	69	67	55	17	5	-	-
2016	-	-	9	27	8	40	41	6	30	17	39	15	18	40	49	-	39	-	-
2017	-	1	20	2	11	19	62	16	45	34	47	31	19	40	20	-	19	-	-
2018	-	-	59	10	9	47	53	28	53	44	58	27	40	49	57	-	42	-	-
2019	-	5	74	12	14	52	69	14	66	29	57	42	35	50	55	9	37	-	-
2020	-	8	75	22	12	56	87	37	37	53	66	38	56	58	61	-	14	-	-
Total	**53**	**30**	**1,877**	**807**	**261**	**1,430**	**1,919**	**1,000**	**1,780**	**819**	**1,634**	**764**	**1,148**	**2,101**	**2,400**	**179**	**1,643**	**0**	**0**

Table 3. Total annual capelin consumption estimated for the predators selected in the various publications by Savenkoff and collaborators. See section 2.4 for a description of the columns.

1994-1996 (Savenkoff et al. 2004a)

Predator	**$\%_{capelin}$**	**$C_{p\ km^2}$ (t·km^{-2}·year^{-1})**	**$C_{gp,\ capelin}$ (10^3 t·year^{-1})**	**% total consum.**
Cetaceans	56.8	1.514	99.9	32.0
Harp seals	43.0	1.046	52.2	16.7
Hooded seals	0.5	0.056	0.0	0.0
Grey seals	5.9	0.183	1.3	0.4
Harbour seals	7.0	0.024	0.2	0.1
Seabirds	62.6	0.153	11.1	3.6
Large Atlantic cod (> 35 cm)	**36.7**	**0.379**	**16.2**	**5.2**
Small Atlantic cod (≤ 35 cm)	**30.4**	**0.238**	**8.4**	**2.7**
Large Greenland halibut (> 40 cm)	**32.8**	**0.233**	**8.9**	**2.8**
Small Greenland halibut (≤ 40 cm)	**59.9**	**0.412**	**28.7**	**9.2**
American plaice	4.1	1.059	5.0	1.6
Flounders	2.1	0.083	0.2	0.1
Skates	8.5	0.198	2.0	0.6
Redfish	20.8	1.484	35.8	11.5
Large demersal feeders	4.8	0.257	1.4	0.5
Small demersal feeders	1.1	0.402	0.5	0.2
Capelin	1.6	15.486	28.8	9.2
Arctic cod	1.2	0.066	0.1	0.0
Large pelagic feeders	6.1	0.042	0.3	0.1
Piscivorous small pelagic feeders	10.0	0.782	9.1	2.9
Planktivorous small pelagic feeders	0.7	2.293	1.9	0.6
Total	-	-	311.9	-

2000-2002 (Savenkoff et al. 2005)

Predator	**$\%_{capelin}$**	**$C_{p\ km^2}$ (t·km^{-2}·year^{-1})**	**$C_{gp,\ capelin}$ (10^3 t·year^{-1})**	**% total consum.**
Mysticety	86.2	1.501	150.2	35.8
Odontoceti	18.0	0.338	7.1	1.7
Harp / hooded seals	51.0	1.299	76.9	18.3
Grey / harbour seals	16.2	0.298	5.6	1.3
Seabirds	74.6	0.254	22.0	5.2
Large Atlantic cod (> 35 cm)	**7.8**	**1.065**	**9.6**	**2.3**
Small Atlantic cod (≤ 35 cm)	**8.1**	**0.398**	**3.7**	**0.9**
Large Greenland halibut (> 40 cm)	**4.2**	**0.233**	**1.1**	**0.3**
Small Greenland halibut (≤ 40 cm)	**33.5**	**1.608**	**62.5**	**14.9**
American plaice	0.8	2.165	2.0	0.5
Flounders	1.3	0.132	0.2	0.0
Skates	10.2	0.075	0.9	0.2
Redfish	21.1	1.145	28.1	6.7
Large demersal feeders	6.5	0.251	1.9	0.5
Small demersal feeders	0.8	2.653	2.5	0.6
Capelin	0.8	22.010	20.4	4.9
Large pelagic feeders	9.3	0.042	0.5	0.1
Piscivorous small pelagic feeders	17.2	1.088	21.7	5.2
Planktivorous small pelagic feeders	1.1	2.499	3.2	0.8
Total	-	-	420.2	-

2003-2005 (Savenkoff et al. 2009)

Predator	$\%_{capelin}$	$C_{p\ km^2}$ (t·km^{-2}·year^{-1})	$C_{gp,\ capelin}$ (10^3 t·year^{-1})	% total consum.
Mysticety	53.3	1.920	118.8	24.9
Odontoceti	18.5	0.421	9.0	1.9
Harp seals	39.1	1.644	74.6	15.7
Hooded seals	3.4	0.084	0.3	0.1
Grey / harbour seals	34.6	0.407	16.4	3.4
Seabirds	43.7	0.127	6.4	1.4
Large Atlantic cod (> 35 cm)	**11.9**	**1.121**	**15.5**	**3.2**
Small Atlantic cod (≤ 35 cm)	**12.6**	**0.196**	**2.9**	**0.6**
Large Greenland halibut (> 40 cm)	**11.2**	**0.605**	**7.9**	**1.7**
Small Greenland halibut (≤ 40 cm)	**28.2**	**1.762**	**57.7**	**12.1**
American plaice	10.7	0.533	6.6	1.4
Flounders	0.1	0.143	0.0	0.0
Skates	8.9	0.102	1.1	0.2
Redfish	8.0	4.941	45.9	9.6
Large demersal feeders	7.7	0.245	2.2	0.5
Small demersal feeders	2.8	1.540	5.0	1.1
Capelin	1.6	35.118	65.2	13.7
Large pelagic feeders	14.0	0.029	0.5	0.1
Piscivorous small pelagic feeders	14.0	2.141	34.8	7.3
Planktivorous small pelagic feeders	0.8	6.315	5.9	1.2
Total	-	-	476.7	-

Table 4. Different parameters may explain the differences observed in the results of the work of Savenkoff et al. and the present study.

Parameter	**Studies by Savenkoff et al.**	**This study**
Length classes	≤ or > 35 cm for Atlantic cod, ≤ or > 40 cm for Greenland halibut.	< 30, [30–55[and ≥ 55 cm for Atlantic cod, < 20, [20–40[and ≥ 40 cm for Greenland halibut.
Time periods	1994–1996, 2000–2002, 2003–2005.	Calculated annually.
Predators	Calculated in biomass.	Calculated in abundance.
Stomach data	Combined by period.	Processed by taking into account the sampling design. Stomachs from some strata were not used.
Consumption	Calculated based on Q/B ratios (consumption / biomass).	Calculated using a bioenergetics approach.

8. FIGURES

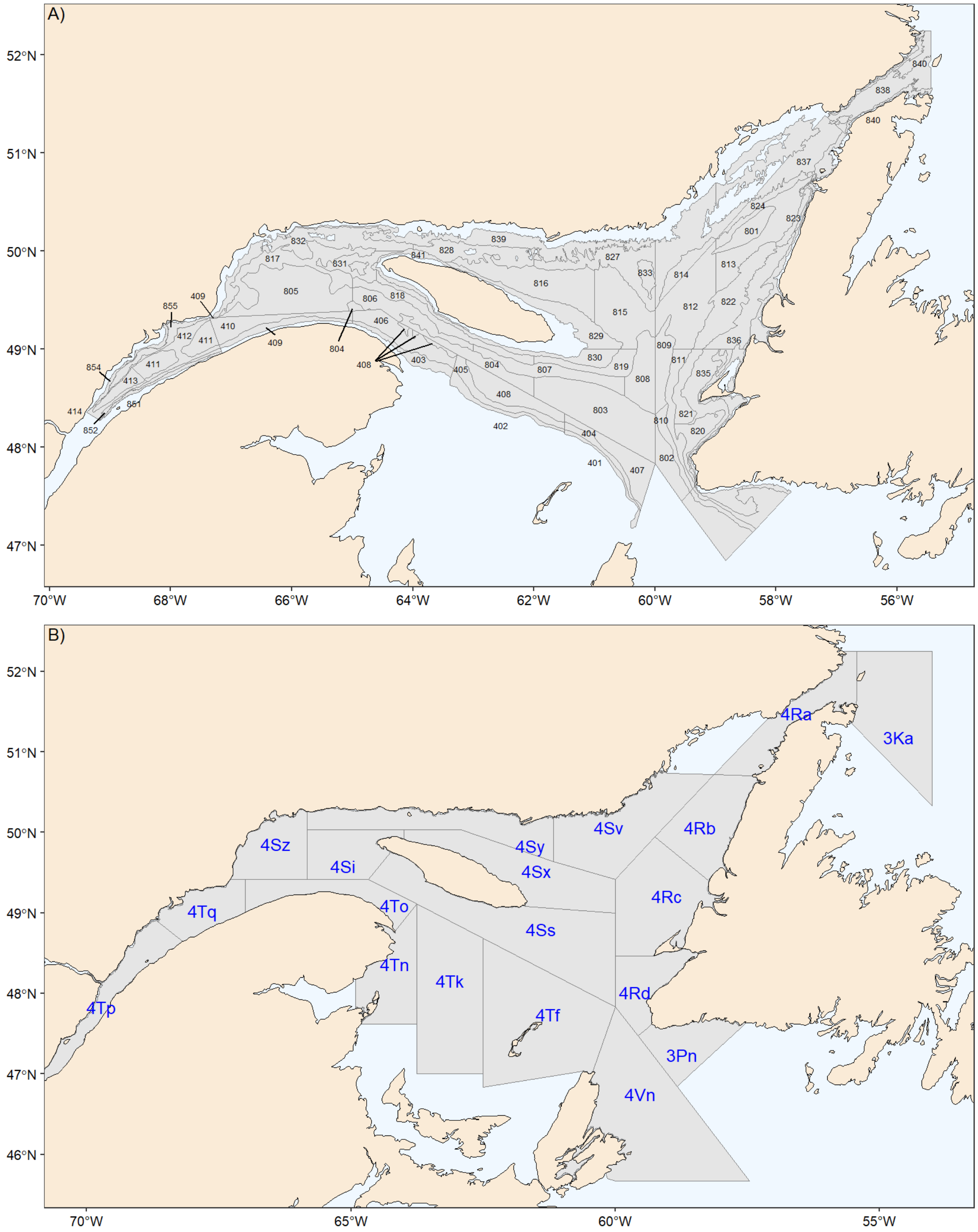


Figure 1. A) Stratification used for the nGSL summer multispecies survey and B) NAFO unit areas mentioned in the document.

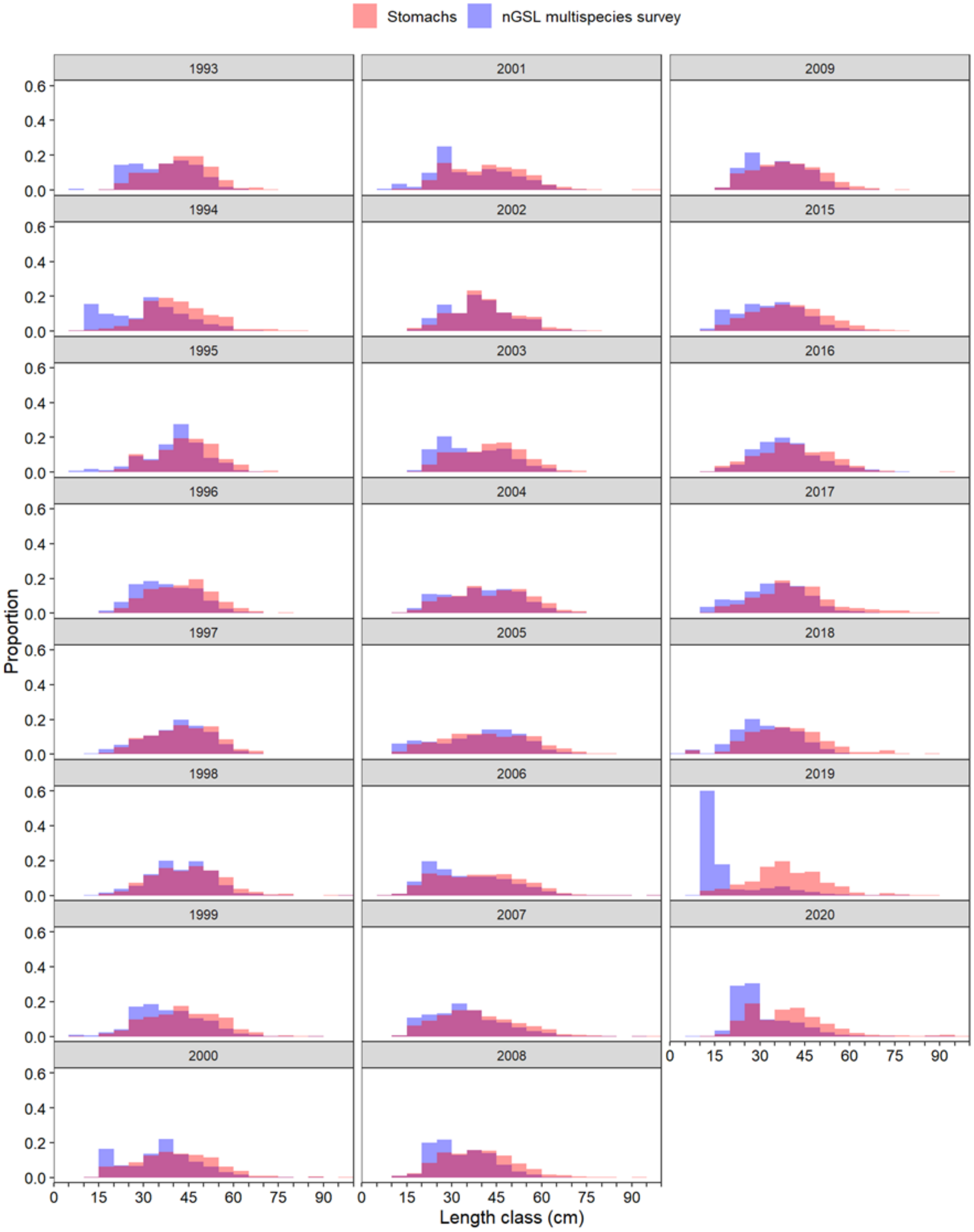


Figure 2. Annual length frequencies of Atlantic cod in groups of 5 cm in length, based on abundance data from the nGSL multispecies survey and stomachs. Only years for which Atlantic cod stomachs are available are shown. The x-axis is truncated to 100 cm, since captures of larger specimens are rare.

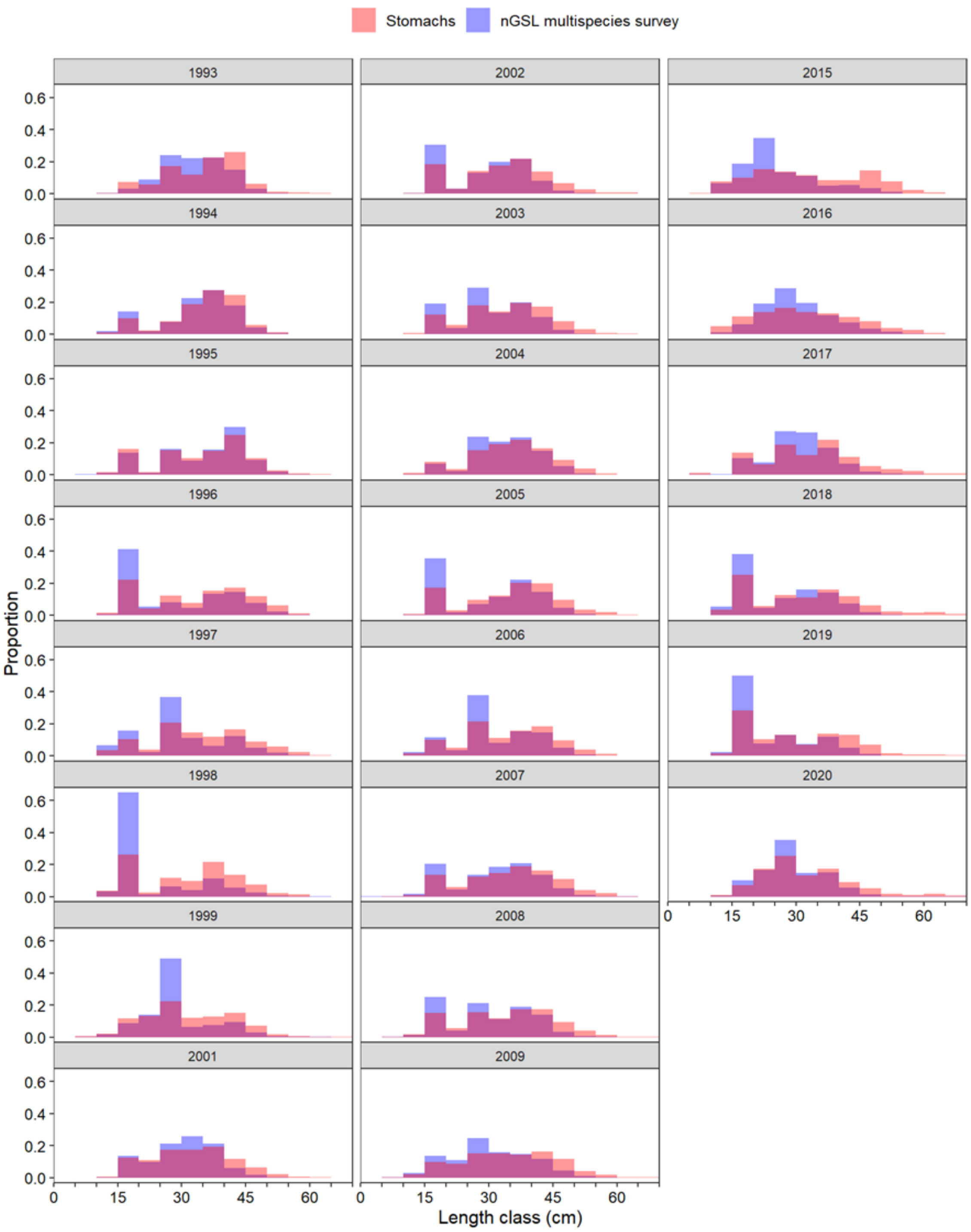


Figure 3. Annual length frequencies of Greenland halibut in groups of 5 cm in length, based on abundance data from the nGSL multispecies survey and stomachs. Only years for which Greenland Halibut stomachs are available are shown. The x-axis is truncated to 70 cm, since captures of larger specimens are rare.

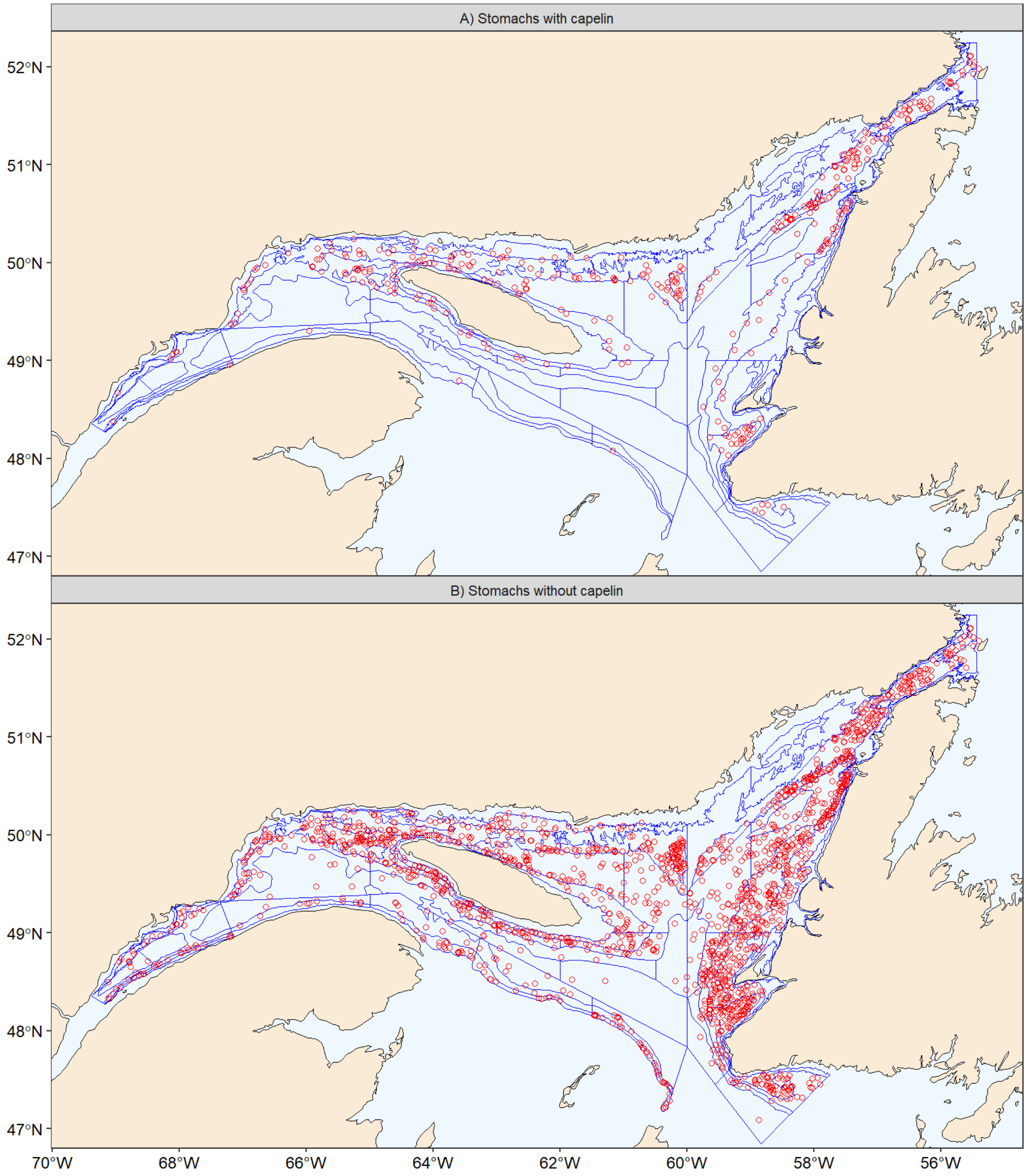


Figure 4. Origin of Atlantic cod stomachs available for analysis A) with and B) without capelin, all years combined. The stratification used for the multispecies nGSL survey is shown in blue.

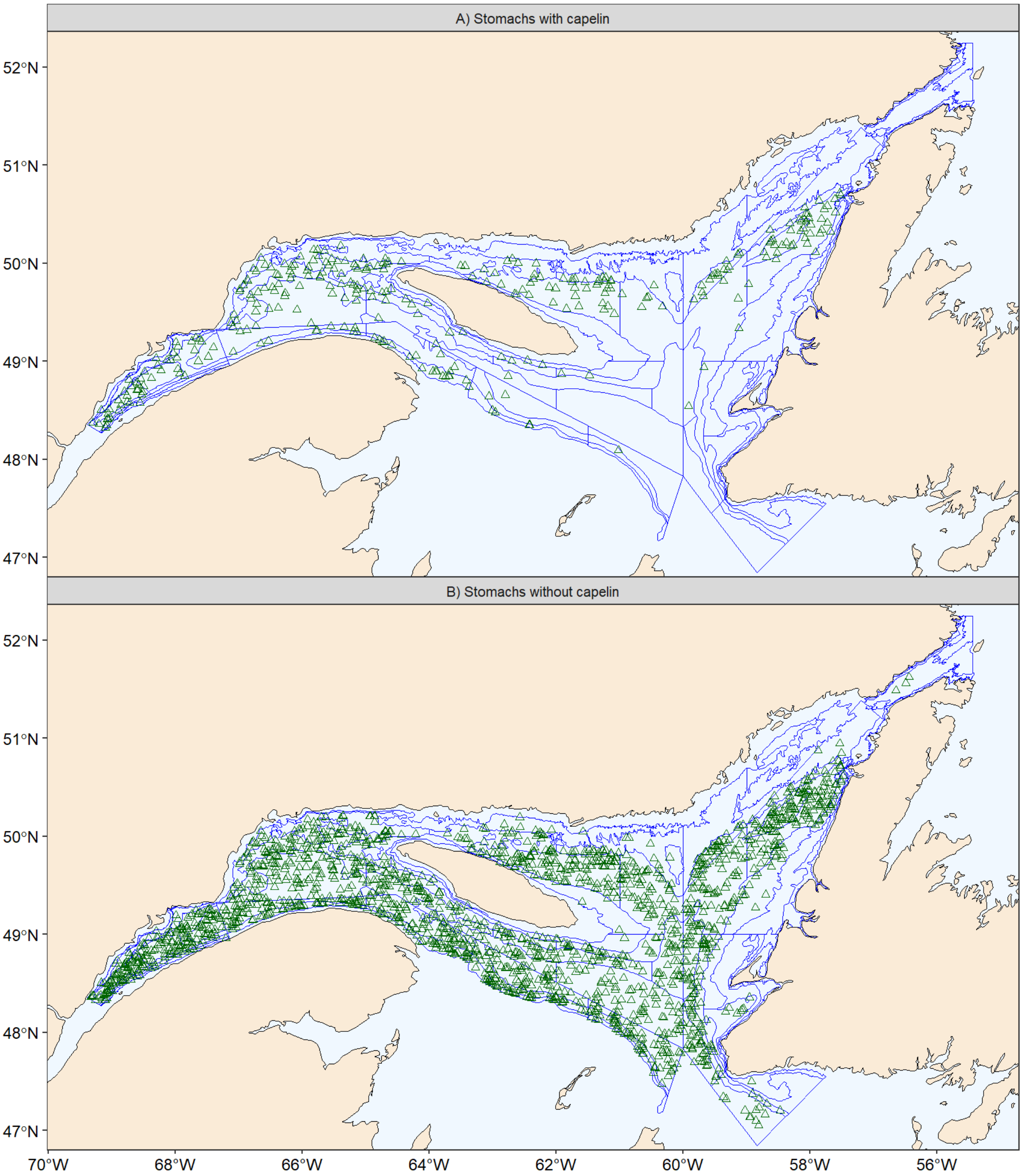
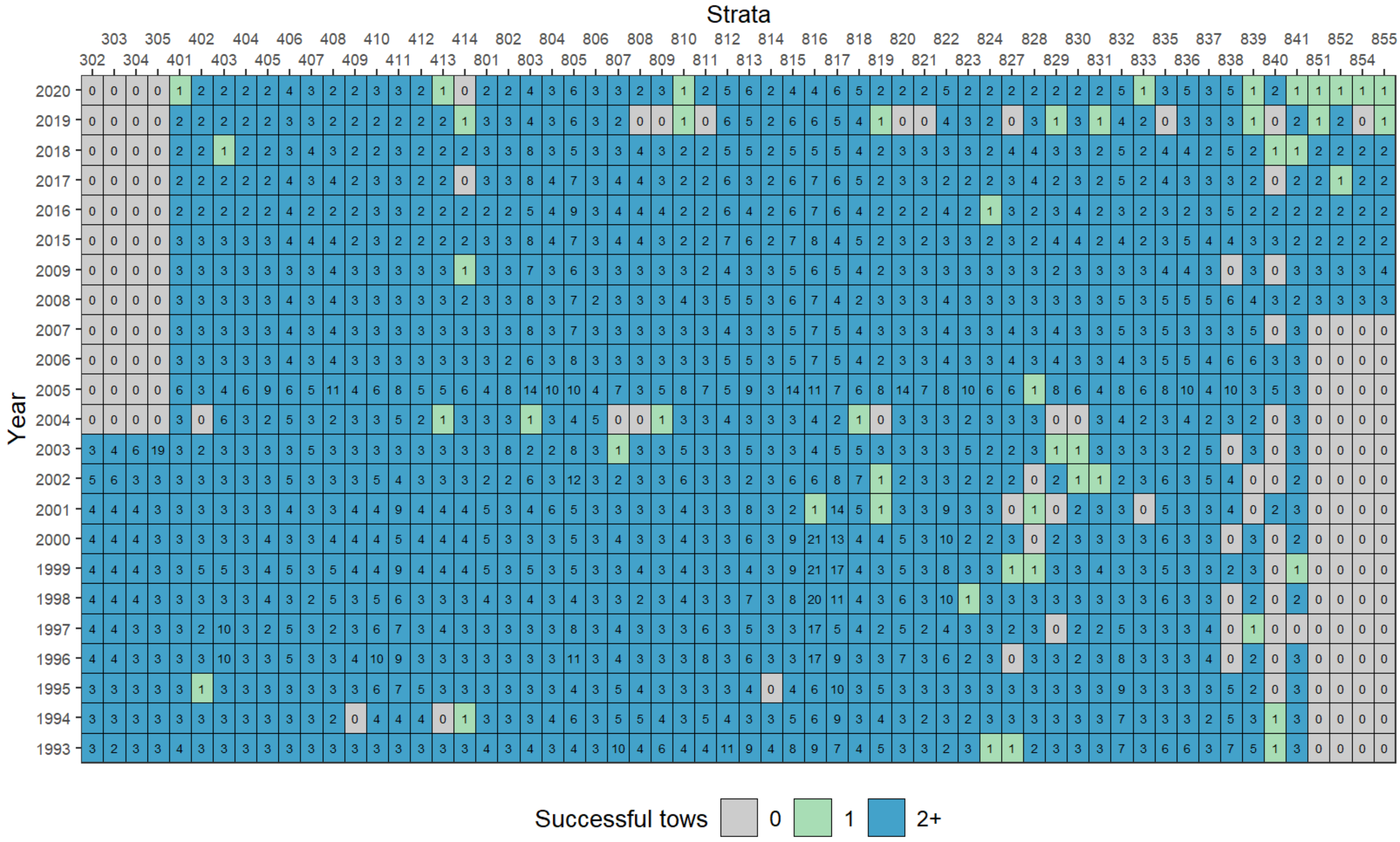


Figure 5. Origin of Greenland halibut stomachs available for analysis A) with and B) without capelin, all years combined. The stratification used for the multispecies nGSL survey is shown in blue.



Year	302	303	304	305	401	402	403	404	405	406	407	408	409	410	411	412	413	414
2020	0	0	0	0	1	2	2	2	2	4	3	2	2	3	3	2	1	0
2019	0	0	0	0	2	2	2	2	2	3	3	2	2	2	2	2	2	1
2018	0	0	0	0	2	2	1	2	2	3	4	3	2	2	3	2	2	2
2017	0	0	0	0	2	2	2	2	2	4	3	4	2	3	3	2	2	0
2016	0	0	0	0	2	2	2	2	2	4	2	2	2	3	3	2	2	2
2015	0	0	0	0	3	3	3	3	3	4	4	4	2	3	2	2	2	2
2009	0	0	0	0	3	3	3	3	3	3	3	4	3	3	3	3	3	1
2008	0	0	0	0	3	3	3	3	3	4	3	4	3	3	3	3	3	2
2007	0	0	0	0	3	3	3	3	3	4	3	4	3	3	3	3	3	3
2006	0	0	0	0	3	3	3	3	3	4	3	4	3	3	3	3	3	3
2005	0	0	0	0	6	3	4	6	9	6	5	11	4	6	8	5	5	6
2004	0	0	0	0	3	0	6	3	2	5	3	2	3	3	5	2	1	3
2003	3	4	6	19	3	2	3	3	3	3	5	3	3	3	3	3	3	3
2002	5	6	3	3	3	3	3	3	3	5	3	3	3	5	4	3	3	3
2001	4	4	4	3	3	3	3	3	3	4	3	3	4	4	9	4	4	4
2000	4	4	4	3	3	3	3	3	4	3	3	4	4	4	5	4	4	4
1999	4	4	4	3	3	5	5	3	4	5	3	5	4	4	9	4	4	4
1998	4	4	4	3	3	3	3	3	4	3	2	5	3	5	6	3	3	3
1997	4	4	3	3	3	2	10	3	2	5	3	2	3	6	7	3	4	3
1996	4	4	3	3	3	3	10	3	3	5	3	3	4	10	9	3	3	3
1995	3	3	3	3	3	1	3	3	3	3	3	3	3	6	7	5	3	3
1994	3	3	3	3	3	3	3	3	3	3	3	2	0	4	4	4	0	1
1993	3	2	3	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3

Year	801	802	803	804	805	806	807	808	809	810	811	812	813	814	815	816	817	818	819	820	821	822	823	824
2020	2	2	4	3	6	3	3	2	3	1	2	5	6	2	4	4	6	5	2	2	2	5	2	2
2019	3	3	4	3	6	3	2	0	0	1	0	6	5	2	6	6	5	4	1	0	0	4	3	2
2018	3	3	8	3	5	3	3	4	3	2	2	5	5	2	5	5	5	4	2	3	3	3	3	2
2017	3	3	8	4	7	3	4	4	3	2	2	6	3	2	6	7	6	5	2	3	3	2	2	2
2016	2	2	5	4	9	3	4	4	4	2	2	6	4	2	6	7	6	4	2	2	2	4	2	1
2015	3	3	8	4	7	3	4	4	3	2	2	7	6	2	7	8	4	5	2	3	2	3	3	2
2009	3	3	7	3	6	3	3	3	3	3	2	4	3	3	5	6	5	4	2	3	3	3	3	3
2008	3	3	8	3	7	2	3	3	3	4	3	5	5	3	6	7	4	2	3	3	3	4	3	3
2007	3	3	8	3	7	3	3	3	3	3	3	4	3	3	5	7	5	4	3	3	3	4	3	3
2006	3	2	6	3	8	3	3	3	3	3	3	5	5	3	5	7	5	4	2	3	3	4	3	3
2005	4	8	14	10	10	4	7	3	5	8	7	5	9	3	14	11	7	6	8	14	7	8	10	6
2004	3	3	1	3	4	5	0	0	1	3	3	4	3	3	3	4	2	1	0	3	3	3	2	3
2003	3	8	2	2	8	3	1	3	3	5	3	3	5	3	3	4	5	5	3	3	3	3	5	2
2002	2	2	6	3	12	3	2	3	3	6	3	3	2	3	6	6	8	7	1	2	3	3	2	2
2001	5	3	4	6	5	3	3	3	3	4	3	3	8	3	2	1	14	5	1	3	3	9	3	3
2000	5	3	3	3	5	3	4	3	3	4	3	3	6	3	9	21	13	4	4	5	3	10	2	2
1999	5	3	5	3	5	3	3	4	3	4	3	3	4	3	9	21	17	4	3	5	3	8	3	3
1998	4	3	4	3	4	3	3	2	3	4	3	3	7	3	8	20	11	4	3	6	3	10	1	3
1997	3	3	3	3	8	3	4	3	3	3	6	3	5	3	3	17	5	4	2	5	2	4	3	3
1996	3	3	3	3	11	3	4	3	3	3	8	3	6	3	3	17	9	3	3	7	3	6	2	3
1995	3	3	3	3	4	3	5	4	3	3	3	3	4	0	4	6	10	3	5	3	3	3	3	3
1994	3	3	3	4	6	3	5	5	4	3	5	4	3	3	5	6	9	3	4	3	2	3	2	3
1993	4	3	4	3	4	3	10	4	6	4	4	11	9	4	8	9	7	4	5	3	3	2	3	1

Year	827	828	829	830	831	832	833	835	836	837	838	839	840	841	851	852	854	855
2020	2	2	2	2	2	5	1	3	5	3	5	1	2	1	1	1	1	1
2019	0	3	1	3	1	4	2	0	3	3	3	1	0	2	1	2	0	1
2018	4	4	3	3	2	5	2	4	4	2	5	2	1	1	2	2	2	2
2017	3	4	2	3	2	5	2	4	3	3	3	2	0	2	2	1	2	2
2016	3	2	3	4	2	3	2	3	2	3	5	2	2	2	2	2	2	2
2015	3	2	4	4	2	4	2	3	5	4	4	3	3	2	2	2	2	2
2009	3	3	2	3	3	3	3	4	4	3	0	3	0	3	3	3	3	4
2008	3	3	3	3	3	5	3	5	5	5	6	4	3	2	3	3	3	3
2007	4	3	4	3	3	5	3	5	3	3	3	5	0	3	0	0	0	0
2006	4	3	4	3	3	4	3	5	5	4	6	6	3	3	0	0	0	0
2005	6	1	8	6	4	8	6	8	10	4	10	3	5	3	0	0	0	0
2004	3	3	0	0	3	4	2	3	4	2	3	2	0	3	0	0	0	0
2003	2	3	1	1	3	3	3	3	2	5	0	3	0	3	0	0	0	0
2002	2	0	2	1	1	2	3	6	3	5	4	0	0	2	0	0	0	0
2001	0	1	0	2	3	3	0	5	3	3	4	0	2	3	0	0	0	0
2000	3	0	2	3	3	3	3	6	3	3	0	3	0	2	0	0	0	0
1999	1	1	3	3	4	3	3	5	3	3	2	3	0	1	0	0	0	0
1998	3	3	3	3	3	3	3	6	3	3	0	2	0	2	0	0	0	0
1997	2	3	0	2	2	5	3	3	3	4	0	1	0	0	0	0	0	0
1996	0	3	3	2	3	8	3	3	3	4	0	2	0	3	0	0	0	0
1995	3	3	3	3	3	9	3	3	3	3	5	2	0	3	0	0	0	0
1994	3	3	3	3	3	7	3	3	3	2	5	3	1	3	0	0	0	0
1993	1	2	3	3	3	7	3	6	6	3	7	5	1	3	0	0	0	0

Figure 6. Strata sampled for years in which Atlantic cod and/or Greenland halibut stomachs are available in the nGSL multispecies survey. No stomachs of the 2 species were collected from 2010 to 2014. The value in each cell corresponds to the number of successful random tows. Strata 302–305, 851–852, 854–855 were not retained for the analyses.

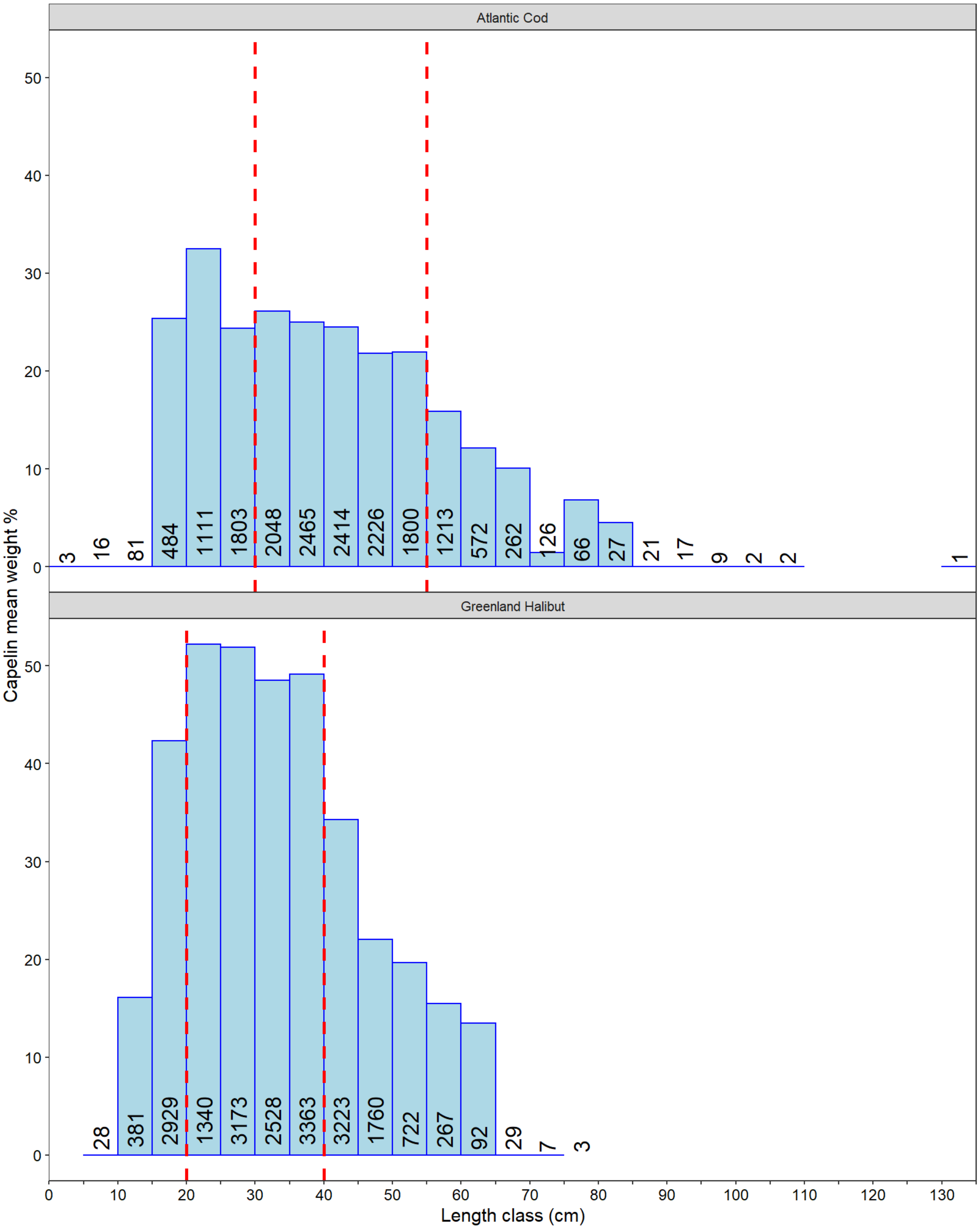


Figure 7. Average percentage of the total stomach content consisting of capelin in the stomachs of Atlantic cod and Greenland halibut collected during the 1993–2020 period, by length classes of 5 cm. The number of stomachs is shown for each length class. The vertical dotted lines delimit the 3 length classes used by predator in the calculation of the average proportion that capelin represents at the scale of the study area.

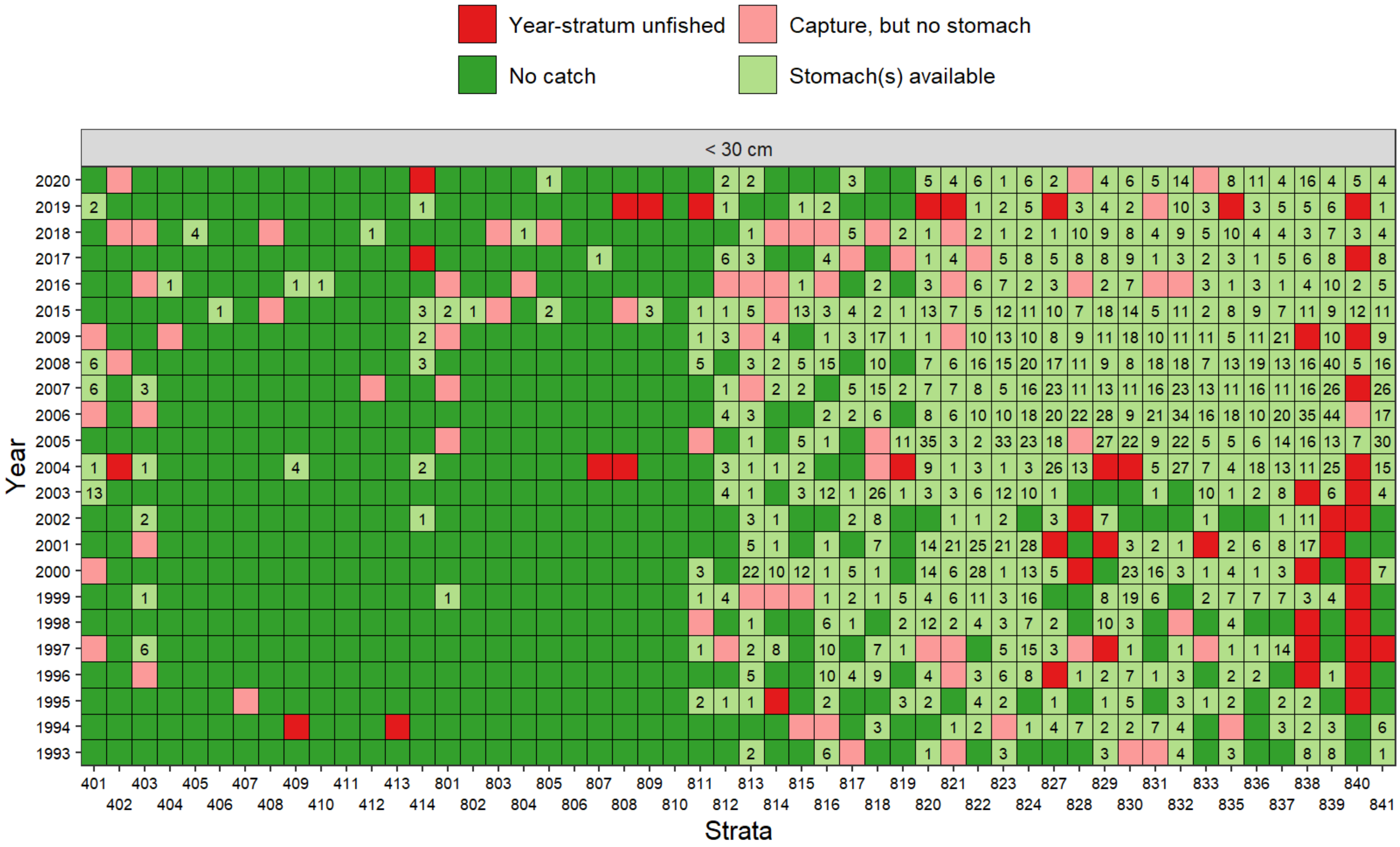


Figure 8. Situation for each of the year–stratum combinations retained for Atlantic cod < 30 cm. The number of stomachs is shown in each cell.

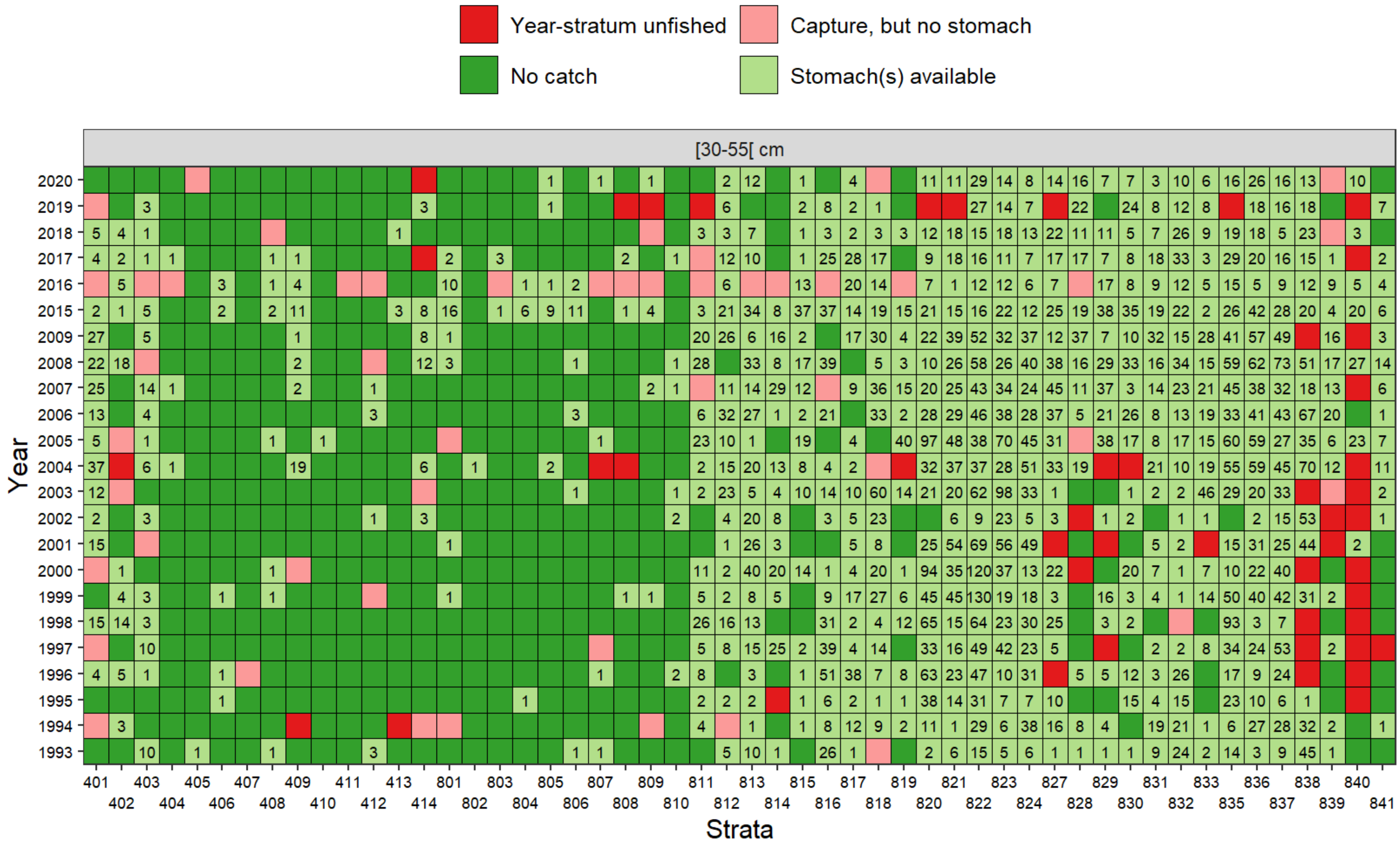


Figure 9. Situation for each of the year–stratum combinations retained for Atlantic cod [30-55[cm. The number of stomachs is shown in each cell.

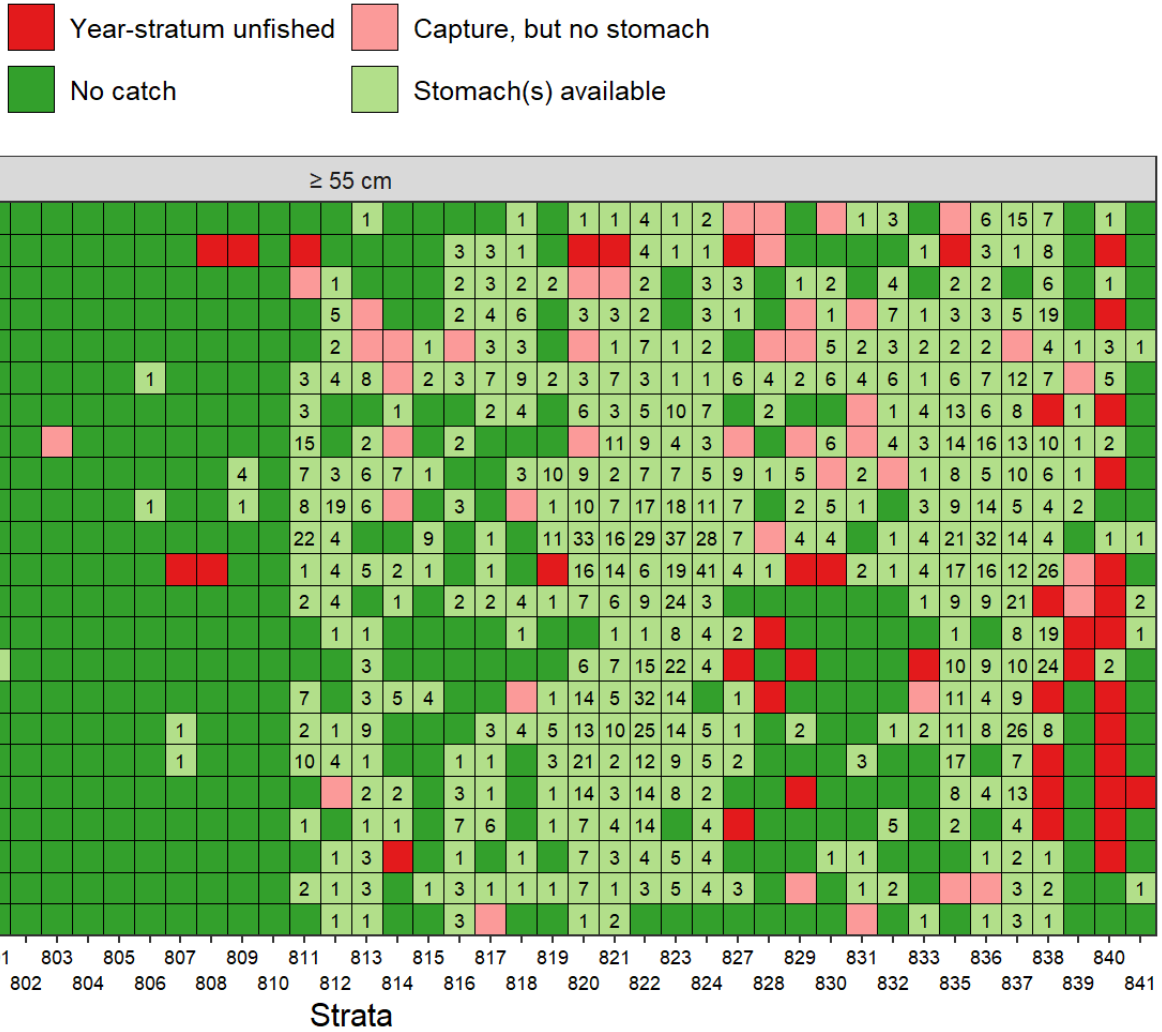


Figure 10. Situation for each of the year–stratum combinations retained for Atlantic cod ≥ 55 cm. The number of stomachs is shown in each cell.

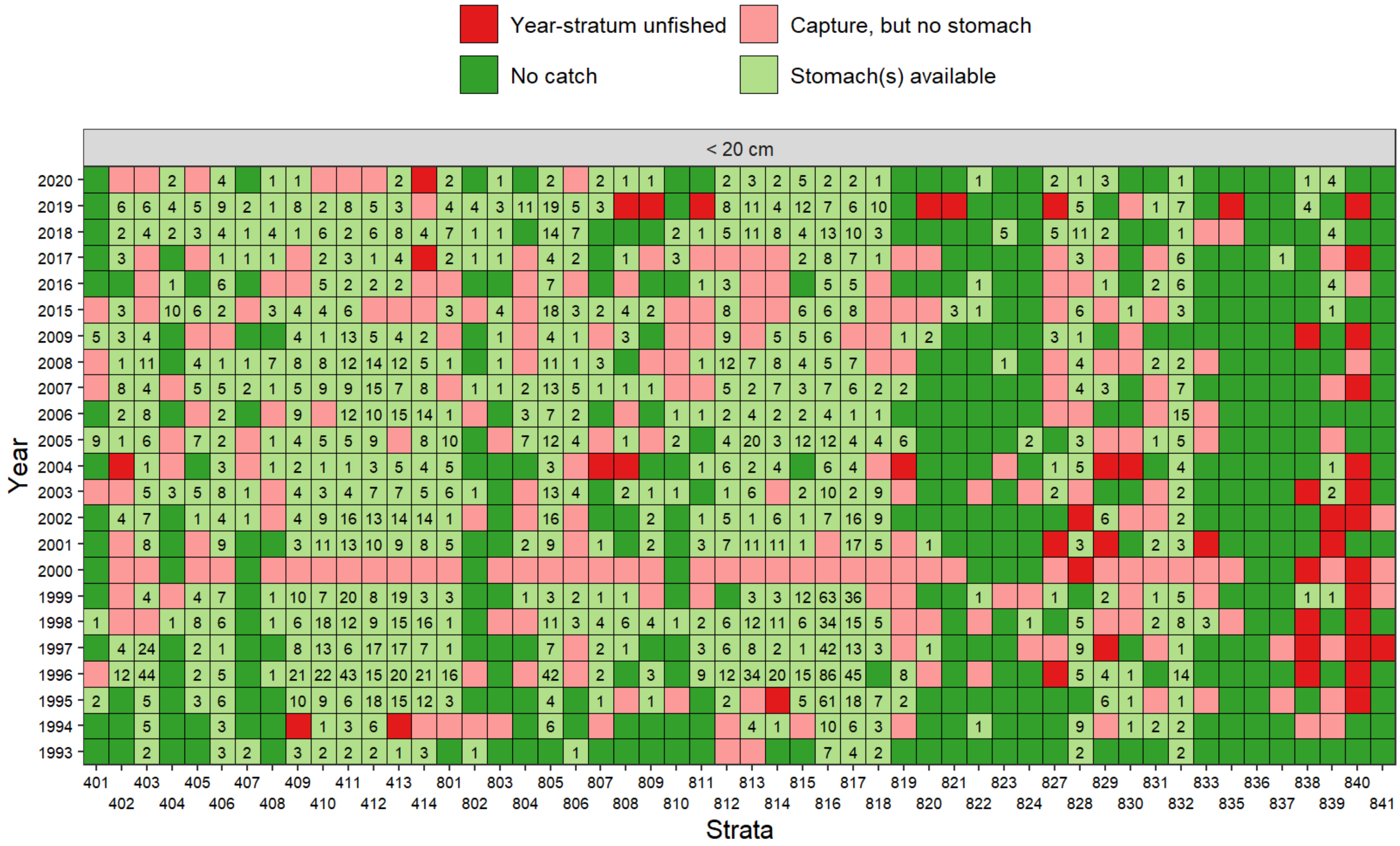
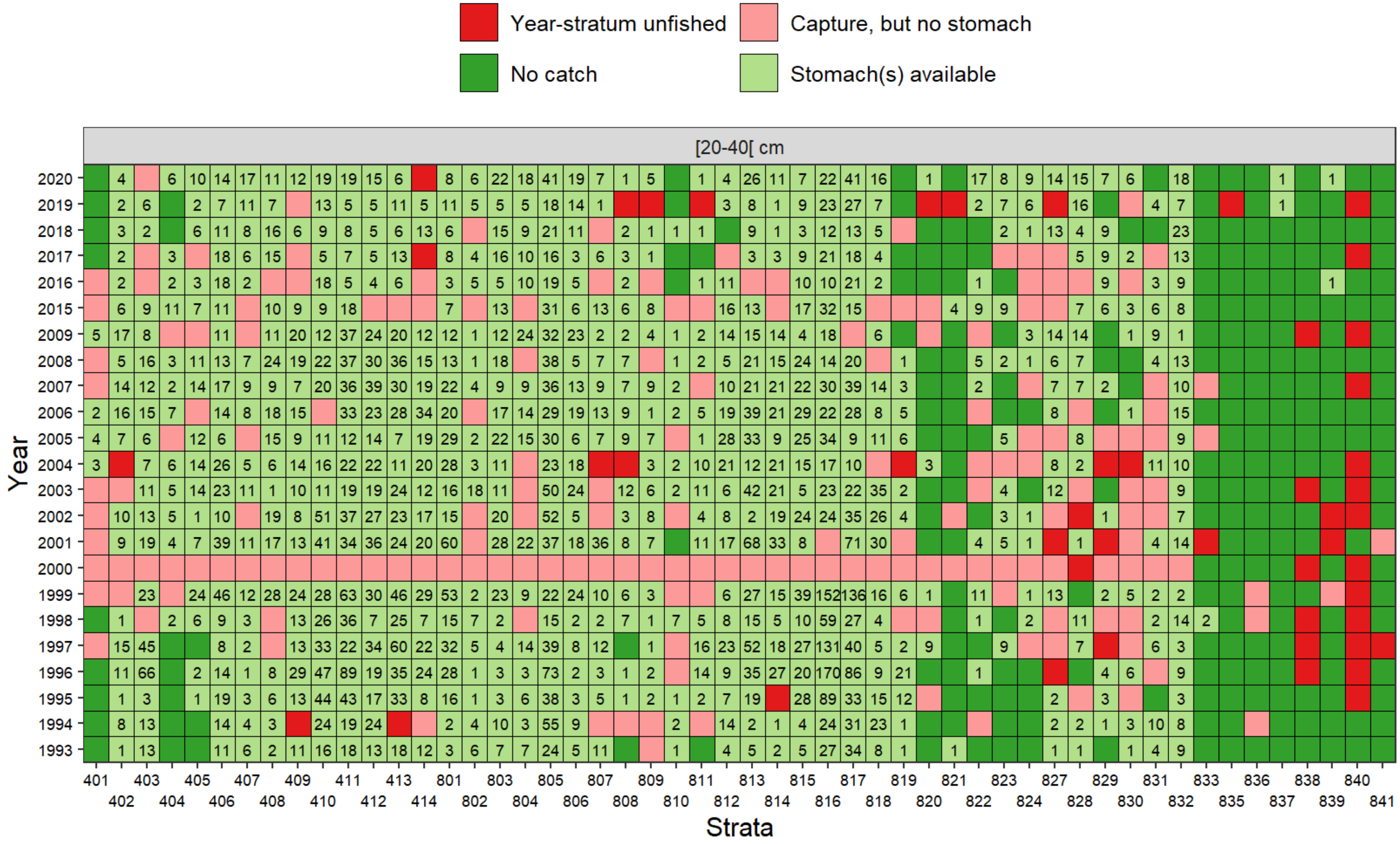


Figure 11. Situation for each of the year–stratum combinations retained for Greenland halibut < 20 cm. The number of stomachs is shown in each cell. No Greenland halibut stomachs were collected in 2000.



🟥 Year-stratum unfished
▨ Capture, but no stomach
🟩 No catch
▢ Stomach(s) available

[20-40[cm

Year	401	402	403	404	405	406	407	408	409	410	411	412	413	414	801	802	803	804	805	806	807	808	809	810	811	812	813	814	815	816	817	818	819	820	821	822	823	824	827	828	829	830	831	832	833	835	836	837	838	839	840	841
2020	🟩	4	▨	6	10	14	17	11	12	19	19	15	6	🟥	8	6	22	18	41	19	7	1	5	🟩	1	4	26	11	7	22	41	16	🟩	1	🟩	17	8	9	14	15	7	6	🟩	18	🟩	🟩	🟩	1	🟩	1	🟩	🟩
2019	🟩	2	6	🟩	2	7	11	7	▨	13	5	5	11	5	11	5	5	5	18	14	1	🟥	🟥	🟩	🟥	3	8	1	9	23	27	7	🟩	🟥	🟥	2	7	6	🟥	16	🟩	▨	4	7	🟩	🟥	🟩	1	🟩	🟩	🟥	🟩
2018	🟩	3	2	🟩	6	11	8	16	6	9	8	5	6	13	6	▨	15	9	21	11	▨	2	1	1	1	🟩	9	1	3	12	13	5	▨	🟩	🟩	🟩	2	1	13	4	9	🟩	🟩	23	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
2017	🟩	2	▨	3	▨	18	6	15	▨	5	7	5	13	🟥	8	4	16	10	16	3	6	3	1	🟩	🟩	▨	3	3	9	21	18	4	🟩	🟩	🟩	🟩	▨	▨	▨	5	9	2	▨	13	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩
2016	▨	2	▨	2	3	18	2	▨	▨	18	5	4	6	▨	3	5	5	10	19	5	▨	2	▨	🟩	1	11	▨	▨	10	10	21	2	🟩	🟩	🟩	1	🟩	▨	▨	▨	9	▨	3	9	🟩	🟩	🟩	🟩	🟩	1	🟩	🟩
2015	▨	6	9	11	7	11	▨	10	9	9	18	▨	▨	▨	7	▨	13	▨	31	6	13	6	8	▨	▨	16	13	▨	17	32	15	▨	▨	▨	4	9	9	▨	▨	7	6	3	6	8	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
2009	5	17	8	▨	▨	11	▨	11	20	12	37	24	20	12	12	1	12	24	32	23	2	2	4	1	2	14	15	14	4	18	▨	6	🟩	▨	🟩	▨	🟩	3	14	14	🟩	1	9	1	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟩
2008	▨	5	16	3	11	13	7	24	19	22	37	30	36	15	13	1	18	▨	38	5	7	7	▨	1	2	5	21	15	24	14	20	▨	1	🟩	🟩	5	2	1	6	7	🟩	🟩	4	13	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
2007	▨	14	12	2	14	17	9	9	7	20	36	39	30	19	22	4	9	9	36	13	9	7	9	2	▨	10	21	21	22	30	39	14	3	🟩	🟩	2	🟩	▨	7	7	2	🟩	▨	10	▨	🟩	🟩	🟩	🟩	🟩	🟥	🟩
2006	2	16	15	7	▨	14	8	18	15	▨	33	23	28	34	20	▨	17	14	29	19	13	9	1	2	5	19	39	21	29	22	28	8	5	🟩	🟩	▨	🟩	🟩	8	▨	🟩	1	▨	15	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
2005	4	7	6	▨	12	6	▨	15	9	11	12	14	7	19	29	2	22	15	30	6	7	9	7	▨	1	28	33	9	25	34	9	11	6	🟩	🟩	🟩	5	▨	▨	8	▨	▨	▨	9	▨	🟩	🟩	🟩	🟩	🟩	🟩	🟩
2004	3	🟥	7	6	14	26	5	6	14	16	22	22	11	20	28	3	11	▨	23	18	🟥	🟥	3	2	10	21	12	21	15	17	10	▨	🟥	3	🟩	▨	▨	▨	8	2	🟥	🟥	11	10	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩
2003	▨	▨	11	5	14	23	11	1	10	11	19	19	24	12	16	18	11	▨	50	24	▨	12	6	2	11	6	42	21	5	23	22	35	2	🟩	🟩	▨	4	🟩	12	▨	🟩	▨	▨	9	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟩
2002	▨	10	13	5	1	10	▨	19	8	51	37	27	23	17	15	▨	20	▨	52	5	▨	3	8	▨	4	8	2	19	24	24	35	26	4	🟩	▨	🟩	3	1	▨	🟥	1	▨	▨	7	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩
2001	▨	9	19	4	7	39	11	17	13	41	34	36	24	20	60	▨	28	22	37	18	36	8	7	🟩	11	17	68	33	8	▨	71	30	▨	🟩	🟩	4	5	1	🟥	1	🟥	▨	4	14	🟥	🟩	🟩	🟩	🟩	🟥	🟩	▨
2000	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	🟥	▨	▨	▨	▨	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟩
1999	▨	▨	23	▨	24	46	12	28	24	28	63	30	46	29	53	2	23	9	22	24	10	6	3	▨	▨	6	27	15	39	152	136	16	6	1	🟩	11	▨	1	13	🟩	2	5	2	2	🟩	🟩	▨	🟩	🟩	▨	🟥	🟩
1998	🟩	1	▨	2	6	9	3	▨	13	26	36	7	25	7	15	7	2	▨	15	2	2	7	1	7	5	8	15	5	10	59	27	4	▨	▨	🟩	1	🟩	2	▨	11	▨	▨	2	14	2	🟩	▨	🟩	🟥	🟩	🟥	🟩
1997	▨	15	45	🟩	🟩	8	2	▨	13	33	22	34	60	22	32	5	4	14	39	8	12	🟩	1	▨	16	23	52	18	27	131	40	5	2	9	🟩	🟩	9	▨	▨	7	🟥	▨	6	3	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟥
1996	🟩	11	66	🟩	2	14	1	8	29	47	89	19	35	24	28	1	3	3	73	2	3	1	2	▨	14	9	35	27	20	170	86	9	21	🟩	🟩	1	🟩	🟩	🟥	🟩	4	6	▨	9	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟩
1995	🟩	1	3	🟩	1	19	3	6	13	44	43	17	33	8	16	1	3	6	38	3	5	1	2	1	2	7	19	🟥	28	89	33	15	12	▨	🟩	🟩	🟩	🟩	2	▨	3	▨	🟩	3	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩
1994	🟩	8	13	🟩	🟩	14	4	3	🟥	24	19	24	🟥	▨	2	4	10	3	55	9	▨	▨	▨	2	▨	14	2	1	4	24	31	23	1	🟩	🟩	▨	🟩	🟩	2	2	1	3	10	8	🟩	🟩	▨	🟩	🟩	🟩	🟩	🟩
1993	🟩	1	13	🟩	🟩	11	6	2	11	16	18	13	18	12	3	6	7	7	24	5	11	🟩	▨	1	🟩	4	5	2	5	27	34	8	1	🟩	1	🟩	🟩	🟩	1	1	🟩	1	4	9	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩

Figure 12. Situation for each of the year–stratum combinations retained for Greenland halibut [20-40[cm. The number of stomachs is shown in each cell. No Greenland halibut stomachs were collected in 2000.

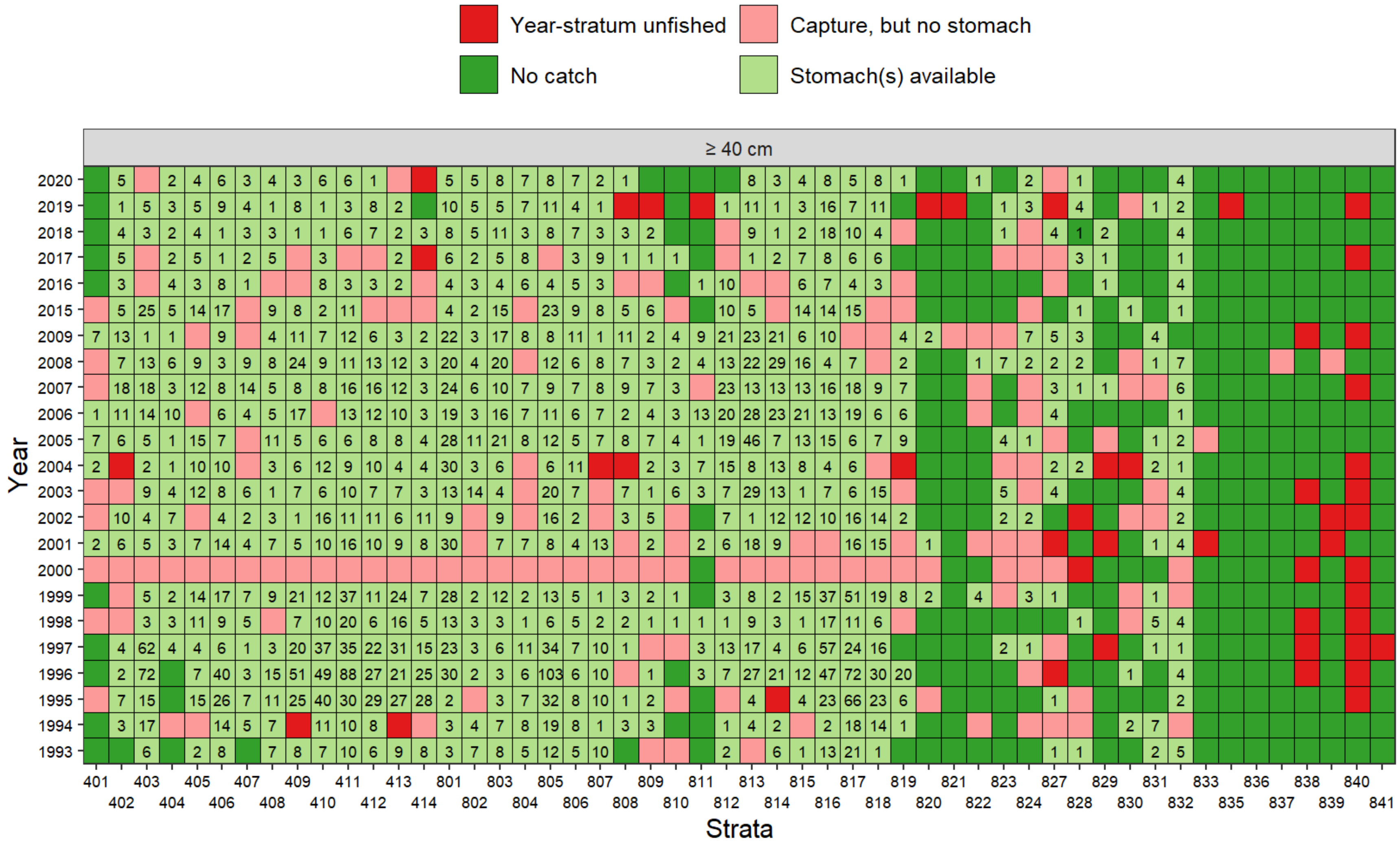


Figure 13. Situation for each of the year–stratum combinations retained for Greenland halibut ≥ 40 cm. The number of stomachs is shown in each cell. No Greenland halibut stomachs were collected in 2000.

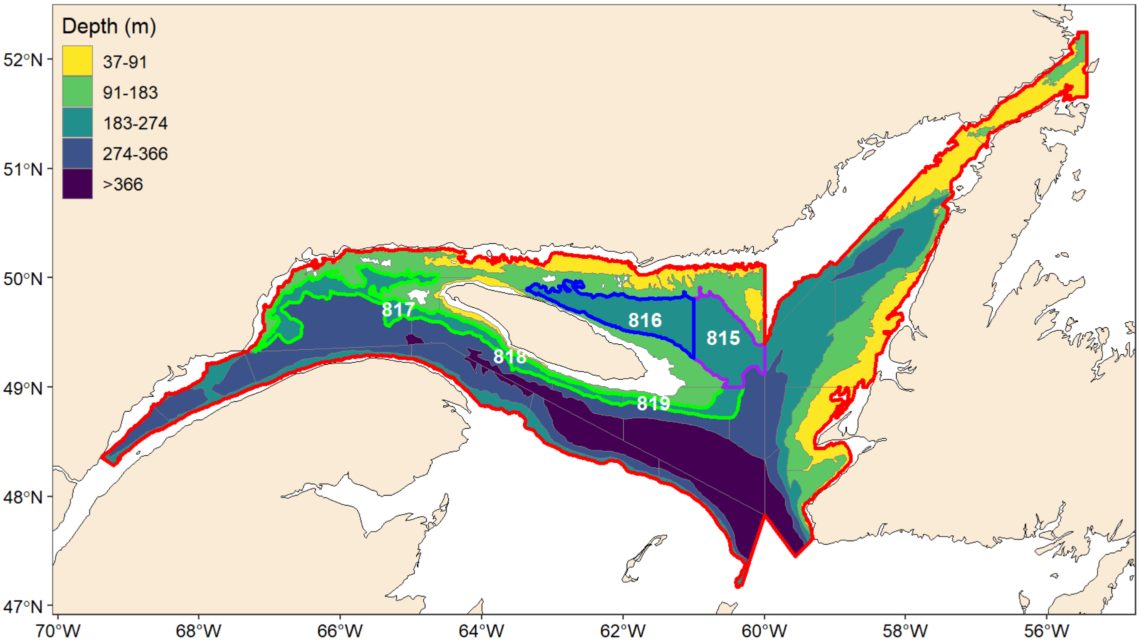


Figure 14. Strata retained in the analysis. The fill color corresponds to the depth class associated with each stratum. An example where the diet of a problematic year–stratum cell is inferred from a three-tiered approach is presented. At Figure 8, we find that although catches of cod < 30 cm were reported in 2016 for stratum 816, no stomach from cod < 30 cm was available that year to characterize their diet. To overcome this lack of data, an initial search in the adjacent strata (i.e. directly bordering the problematic stratum) that share the same NAFO Division and depth class was carried out (here only stratum 815, purple outline). If stomachs < 30 cm were available in this stratum in 2016, then they were used to infer feeding at stratum 816. If no cod stomach < 30 cm was available, the other strata of the same NAFO Division and depth class were used (strata 817–819, green outline). In the event that no cod stomach < 30 cm was still available for 2016, all cod stomachs < 30 cm in the study area selected (red outline) in 2016 were then used.

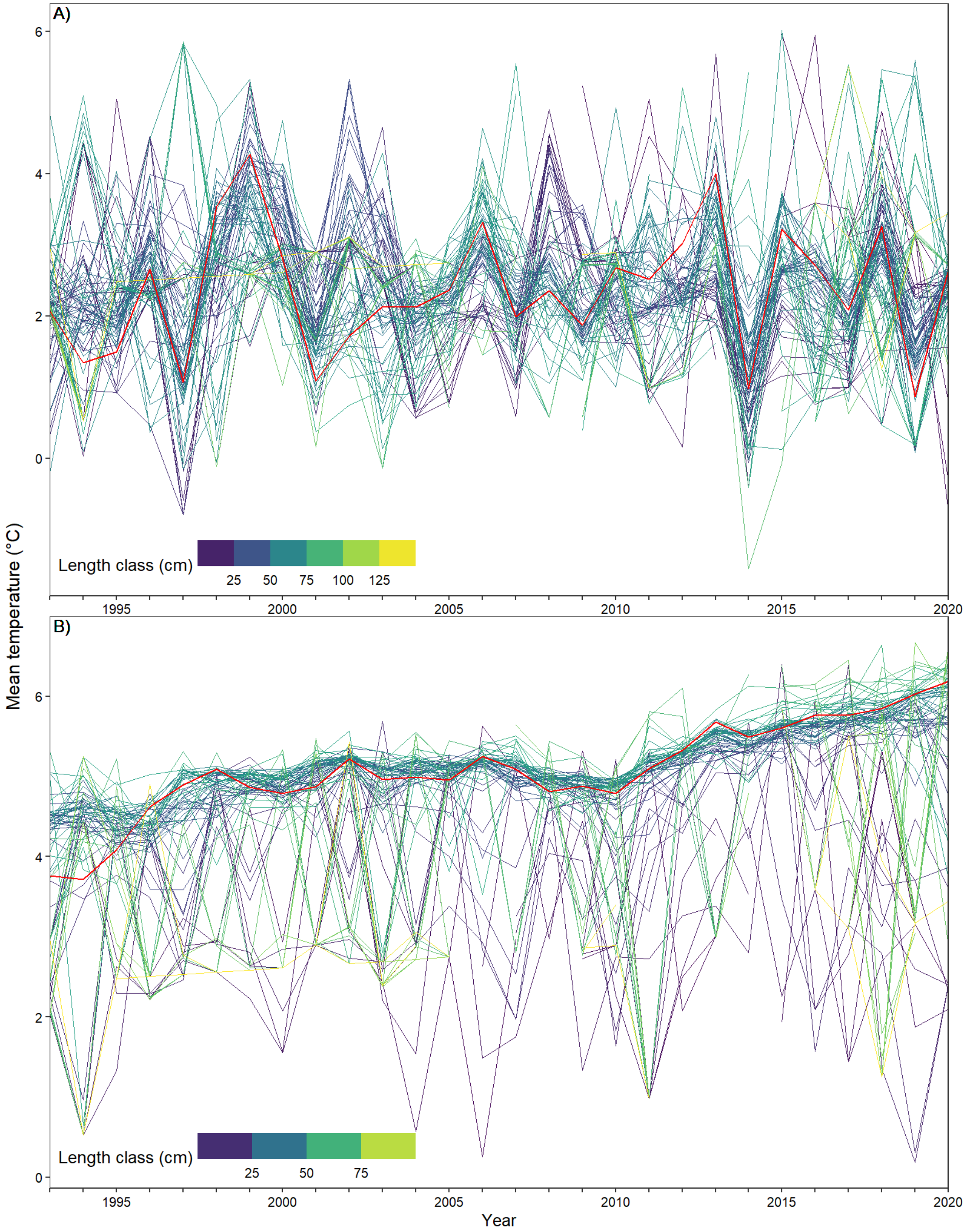


Figure 15. Average temperature (°C) measured while trawling by 1 cm length class for a) Atlantic cod and b) Greenland halibut at the scale of the area covered by the strata selected in the analyses. Each colored line going from purple to yellow represents the evolution of the annual average temperatures by 1 cm length class. The red line represents the evolution of mean temperatures for specimens of a) 50.0 to 50.9 and b) 40.0 to 40.9 cm.

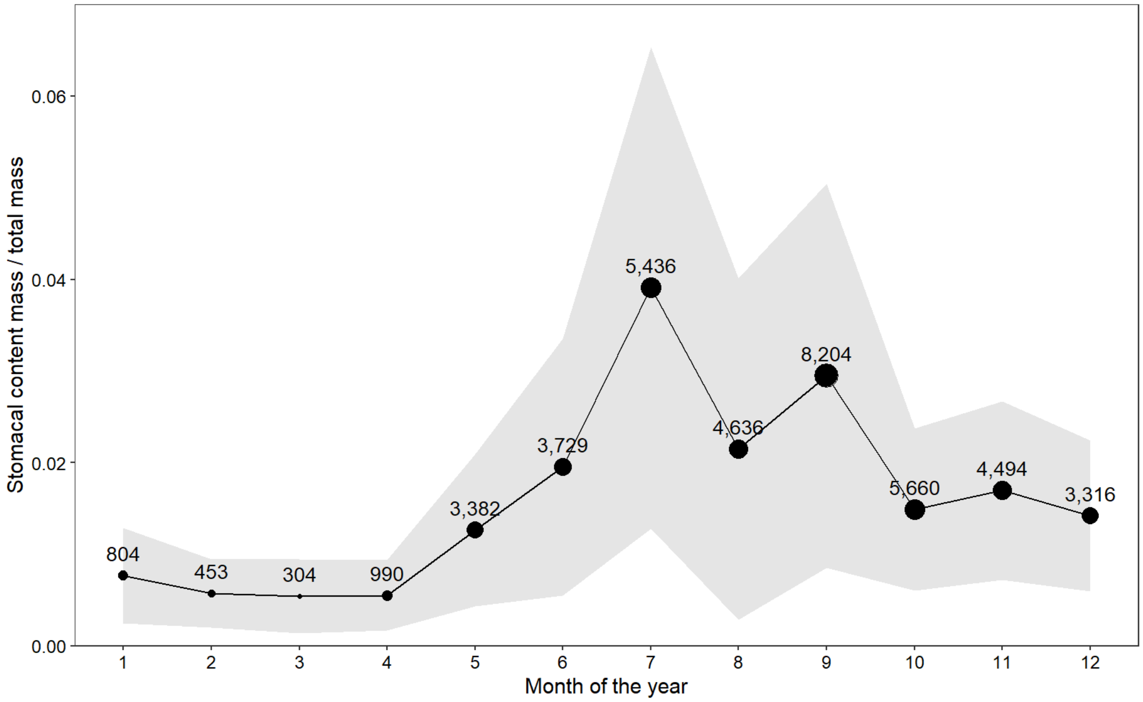


Figure 16. Average proportion represented by the stomach content of Atlantic cod over its total mass, depending on the month of the year. The shaded area extends ± 0.5 standard deviation around the mean. Monthly cod numbers are provided. Data source: Sentinel Fisheries Program using fixed gear.

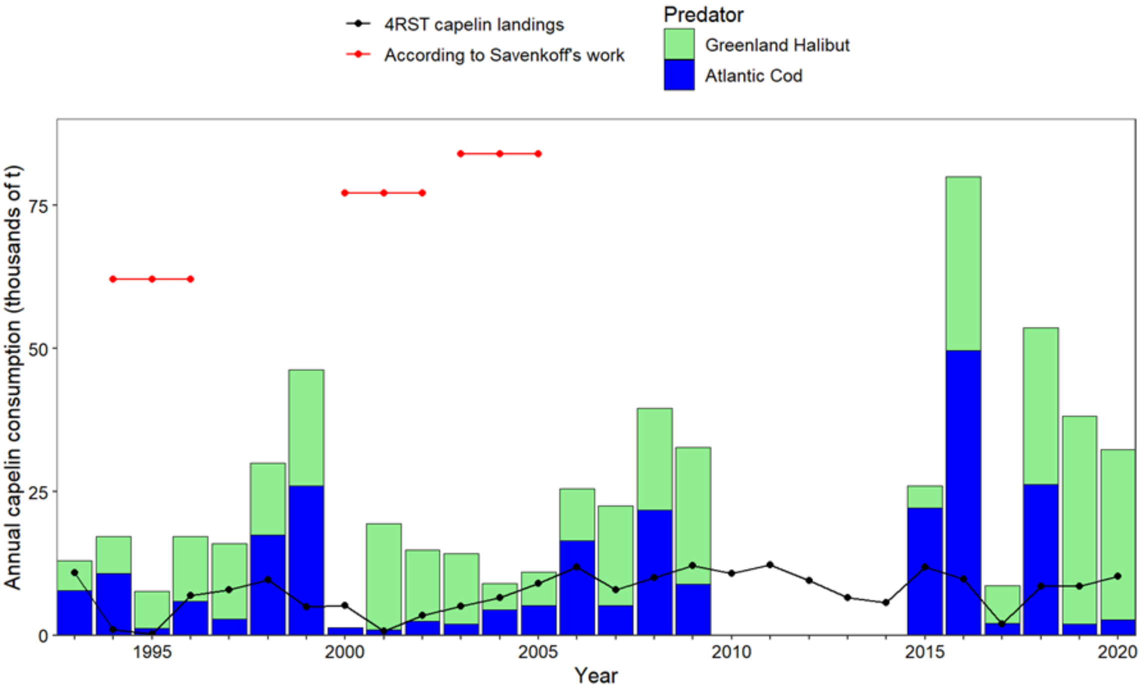


Figure 17. Annual capelin consumption estimated for Greenland halibut and Atlantic cod over the entire study area selected. Capelin landings in NAFO Divisions 4RST are shown, as are consumption estimates for the two predators from the work carried out by Claude Savenkoff and collaborators for different periods (see Table 3). No stomachs were harvested during the 2010–2014 period (two predators) and in 2000 (Greenland halibut).

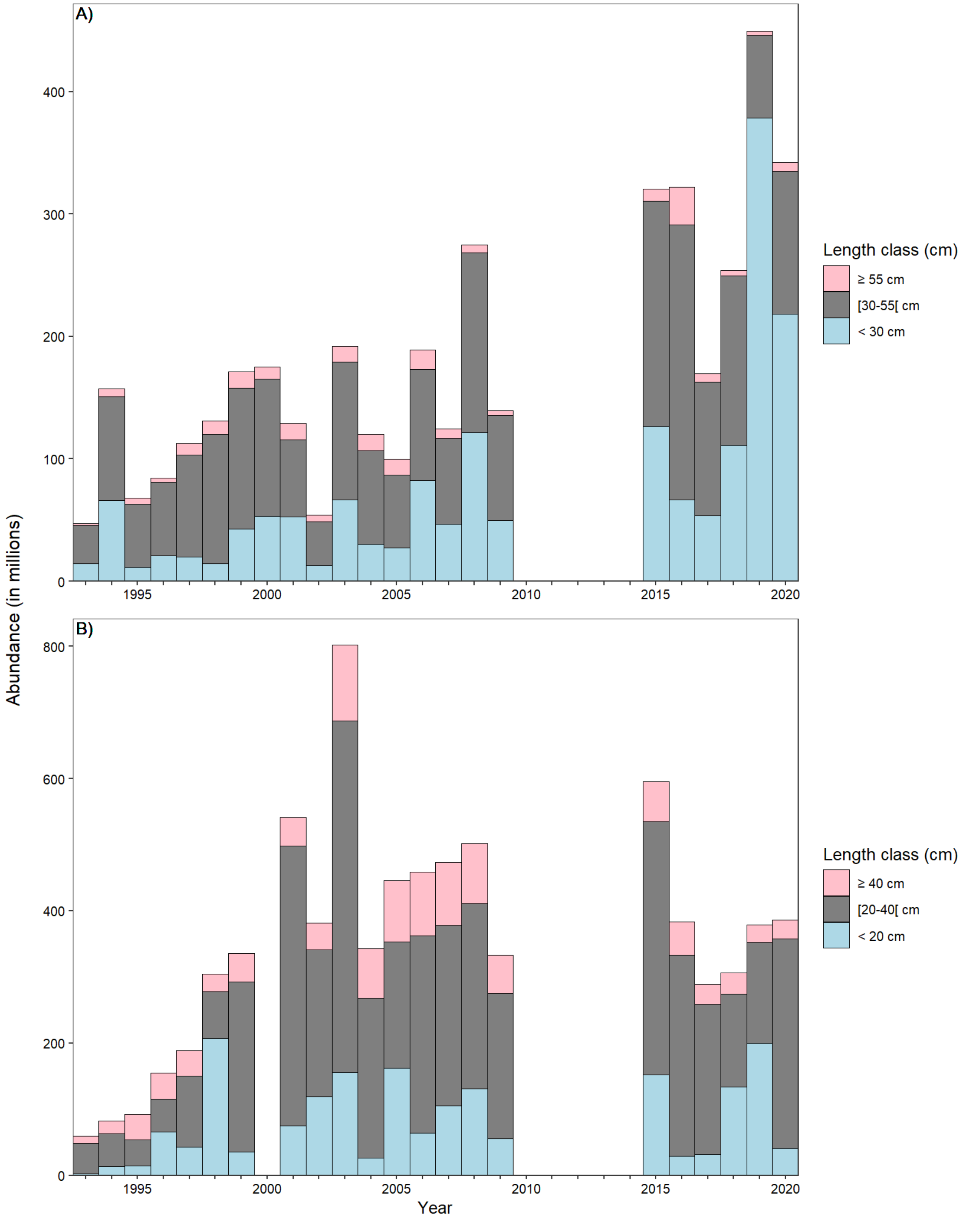


Figure 18. Trawlable abundance of a) Atlantic cod and b) Greenland halibut broken down into the three length classes specific to each predator. Since no stomachs were collected during the 2010–2014 period (two predators) and in 2000 (Greenland halibut), abundances are not shown.

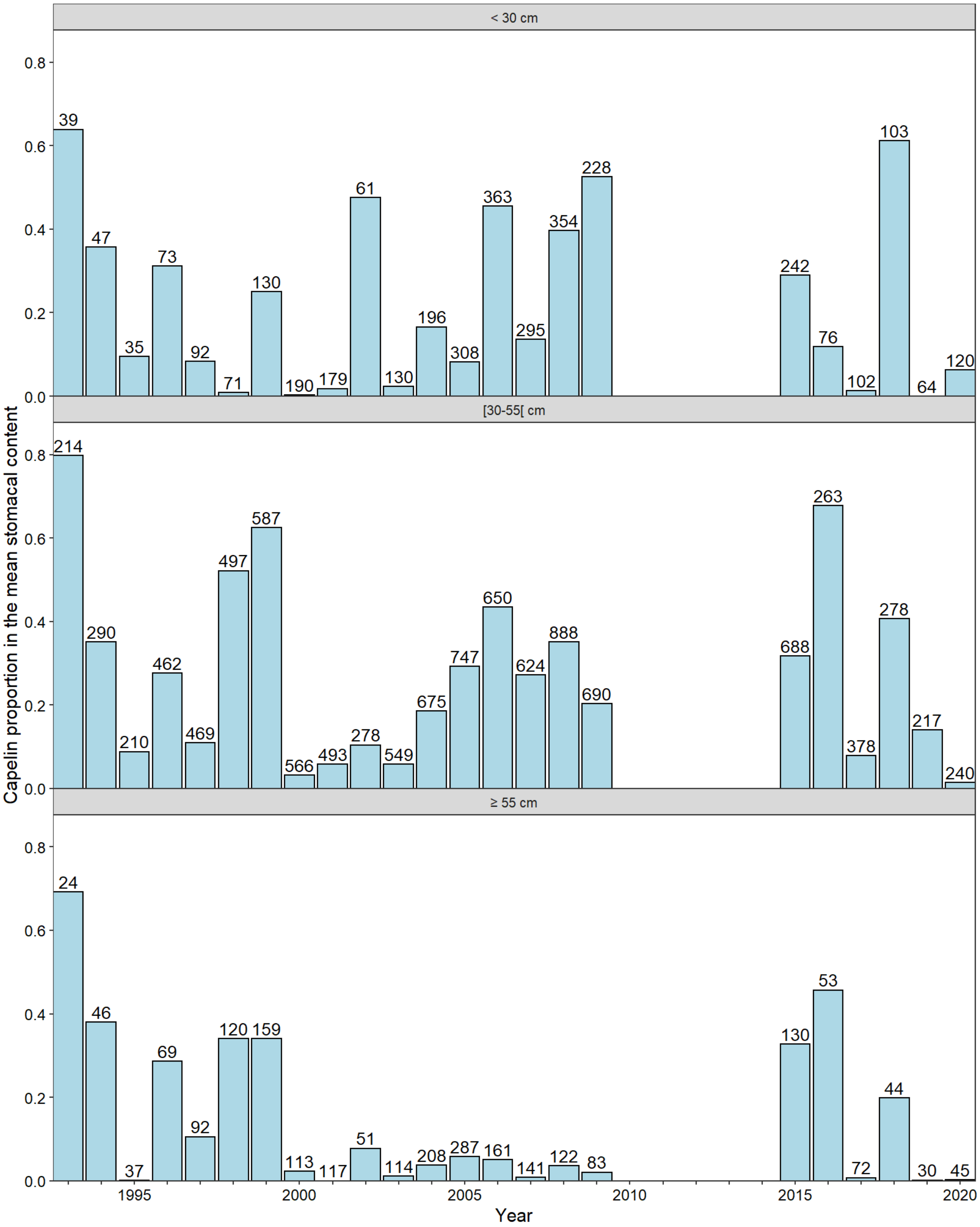


Figure 19. Proportion of capelin in the average stomach content of Atlantic cod for each of the three length classes selected. Values above bars represent the number of stomachs used for the method of Warren et al. (1994). No stomachs were available for the 2010–2014 period.

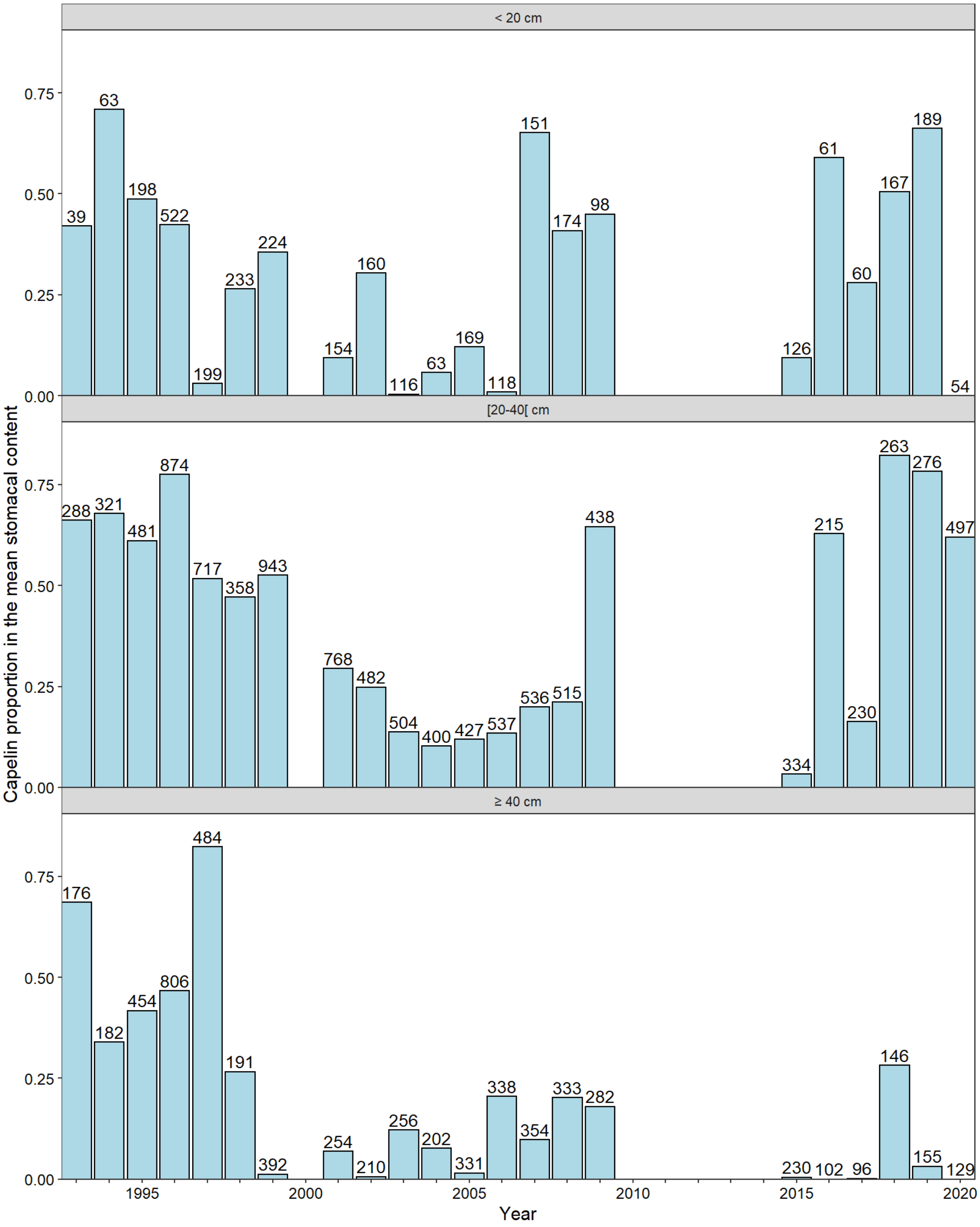


Figure 20. Proportion of capelin in the average stomach content of Greenland halibut for each of the three length classes selected. Values above bars represent the number of stomachs used for the method of Warren et al. (1994). No stomachs were available for the year 2000 and the 2010–2014 period.

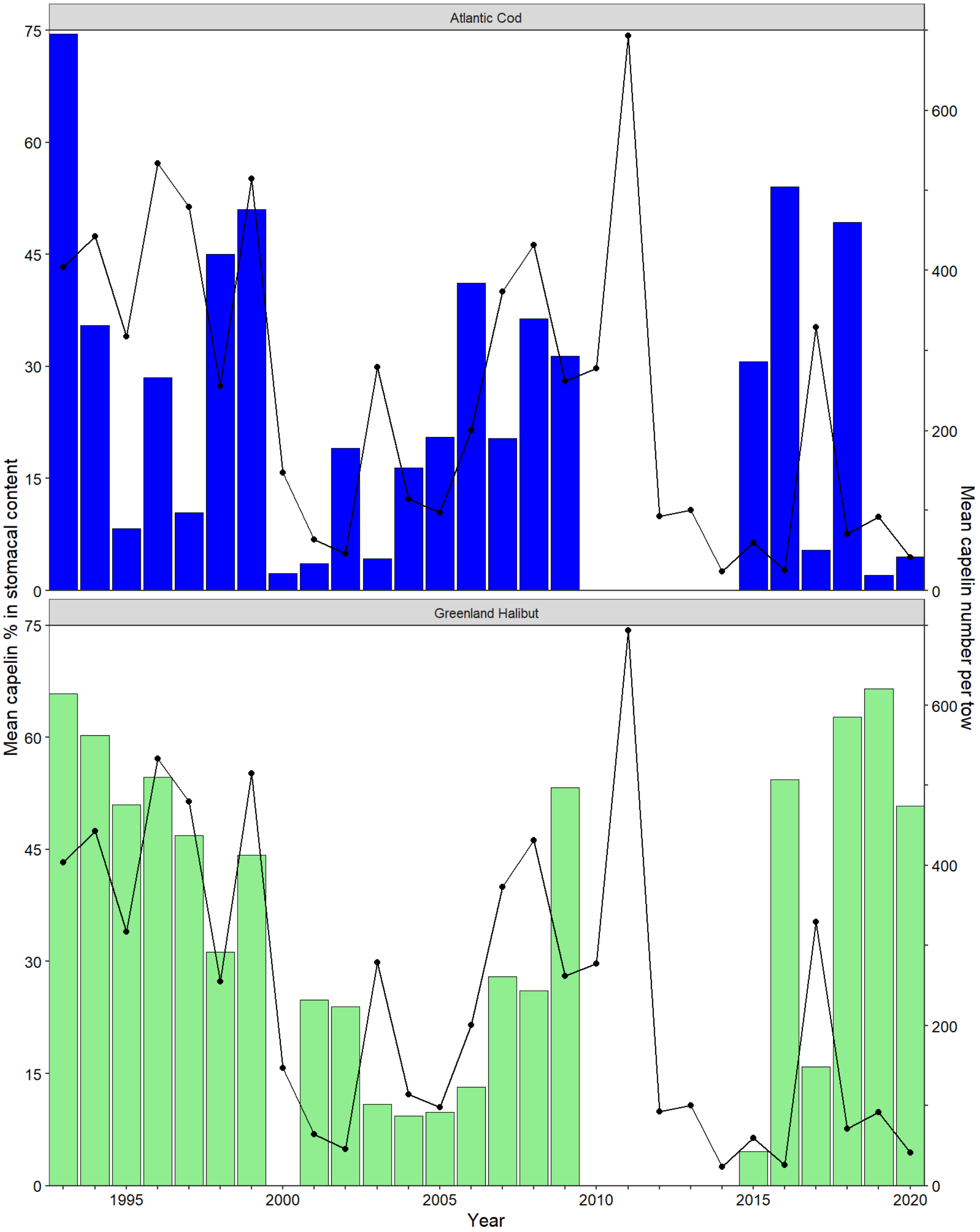


Figure 21. Percentage of capelin in the average stomach contents of Atlantic cod and Greenland halibut, all length classes combined. No stomachs were harvested during the 2010–2014 period (two predators) and in 2000 (Greenland halibut). The black line corresponds to the average number of capelin caught per tow in the nGSL survey.

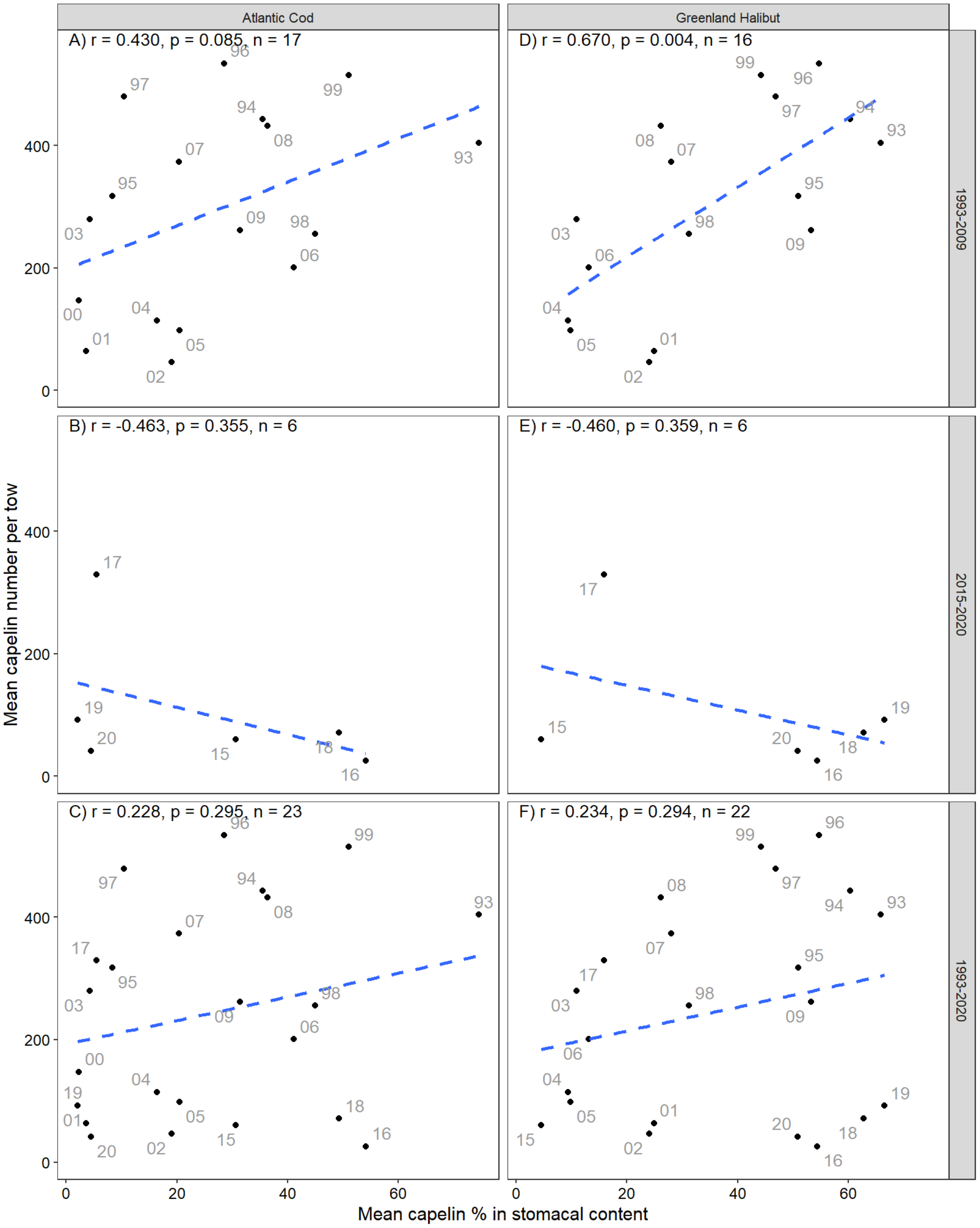


Figure 22. Relationship between the average % that capelin represents in the stomach contents of one of the two predators studied and the average number of capelin per tow obtained during the nGSL multispecies bottom trawl survey, for the 1993–2009, 2015–2020 and 1993–2020 (full series) periods. The last two digits of the year are displayed for each point. The correlation coefficient (r), the probability (p) and the sample size (n) are provided in each panel. No stomachs were available for the year 2000 (Greenland halibut) and the 2010–2014 period (two predators). The blue hatched line in each panel shows the simple linear regression.

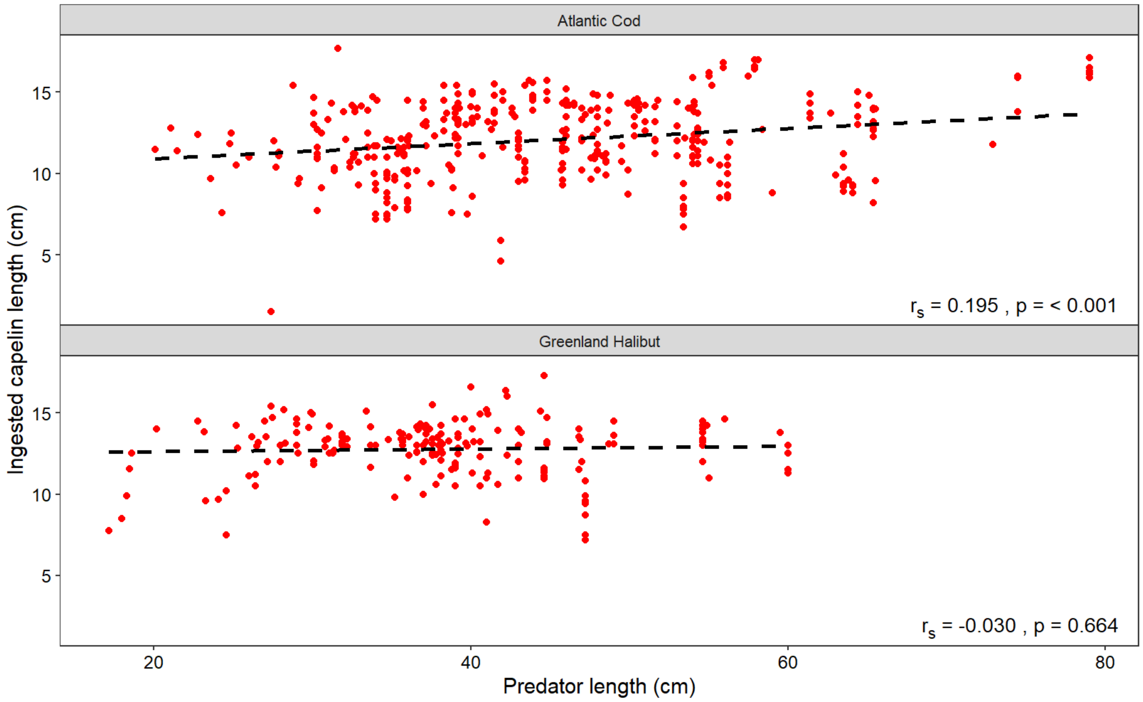


Figure 23. Relationship between the size of the predator and that of the ingested capelin. For each predator, the value of the Spearman correlation coefficient (r_S) is provided along with the associated probability (p).

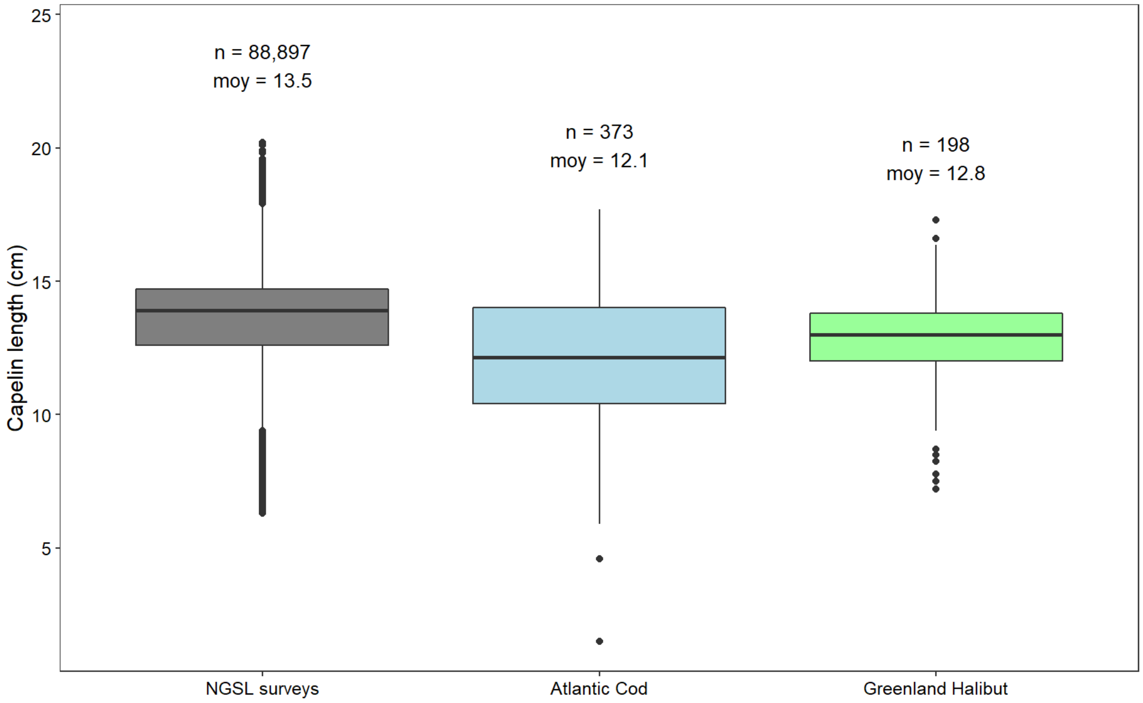


Figure 24. Boxplots showing the lengths of capelin ingested by predator and according to catches made during the multispecies nGSL survey of the years for which stomachs of both predators are available. The bottom, middle, and top horizontal lines of the boxplots represent the 25th, 50th (median), and 75th percentiles, respectively. The upper mustache extends from the box to the highest value not exceeding 1.5 times the interquartile range. The lower mustache follows the same principle, but with the lower values. The number of capelin measured as well as the average length are provided.