

Spatial distribution study of Atlantic mackerel (*Scomber scombrus*) and capelin (*Mallotus villosus*) abundance data from winter groundfish surveys in NAFO Divisions 4VW using generalized additive models

Benoît Bruneau and François Grégoire

Department of Fisheries and Oceans
Science Branch
Maurice Lamontagne Institute
P.O. Box 1000, 850 Route de la Mer
Mont-Joli (Quebec)
G5H 3Z4

2011

Canadian Technical Report of
Fisheries and Aquatic Sciences 2930



Pêches
Et Océans

Fisheries
and Oceans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contribute to existing knowledge but that are not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter, and the series reflects the broad interests and policies of the Department of Fisheries and Oceans, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is indexed in the data base *Aquatic Sciences and Fisheries Abstracts*.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and the Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page. Out-of-stock reports will be supplied for a fee by commercial agents.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques du ministère des Pêches et des Océans, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications intégrales. Le titre exact paraît au-dessus du résumé de chaque rapport. Les rapports techniques sont indexés dans la base de données *Aquatic Sciences and Fisheries Abstracts*.

Les numéros 1 à 456 de cette série ont été publiés à titre de rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement d'origine dont le nom figure sur la couverture et la page du titre. Les rapports épuisés seront fournis contre rétribution par des agents commerciaux.

Canadian Technical Report of
Fisheries and Aquatic Sciences 2930

2011

Spatial distribution study of Atlantic mackerel (*Scomber scombrus*) and capelin
(*Mallotus villosus*) abundance data from winter groundfish surveys in
NAFO Divisions 4VW using generalized additive models

Benoît Bruneau and François Grégoire

Department of Fisheries and Oceans
Science Branch
Maurice Lamontagne Institute
P.O. Box 1000, 850 Route de la Mer
Mont-Joli (Quebec)
G5H 3Z4

© Her Majesty the Queen in Right of Canada, 2011
N° de cat. Fs 97-6/2930E-PDF ISSN 1488-5379

Également disponible en français.

N° de cat. Fs 97-6/2930F-PDF ISSN 1488-545X

Correct citation for this publication:

Bruneau, B., and F. Grégoire. 2011. Spatial distribution study of Atlantic mackerel (*Scomber scombrus*) and Capelin (*Mallotus villosus*) abundance data from winter groundfish surveys in NAFO Divisions 4VW using generalized additive models. Can. Tech. Rep. Fish. Aquat. Sci. 2930: vi + 21 pp.

TABLE OF CONTENTS

LIST OF TABLES	iv
LIST OF FIGURES	iv
ABSTRACT	vi
RÉSUMÉ.....	vi
1.0 INTRODUCTION	1
2.0 MATERIAL AND METHODS	1
2.1 Data source	1
2.2 Data processing	2
2.3 Statistical analysis of the data	2
2.3.1 Thermal preferences	2
2.3.2 Generalized additive models (GAM).....	2
3.0 RESULTS	3
3.1 Catches per species.....	3
3.2 Link between abundance and water temperature.....	3
3.3 Generalized additive models (GAM).....	4
3.3.1 Covariate relationships.....	4
3.3.2 Mackerel	4
3.3.3 Capelin.....	4
4.0 DISCUSSION AND CONCLUSION.....	5
5.0 ACKNOWLEDGEMENTS.....	7
6.0 REFERENCES	7

LIST OF TABLES

Table 1.	Date, number of tows, and bottom temperature (°C) for winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.....	10
Table 2.	Results from the generalized additive models tested on Atlantic mackerel and capelin abundance data (log number / tow + 0.1) from the winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003	10

LIST OF FIGURES

Figure 1.	Map of NAFO Divisions 4VW	11
Figure 2.	Atlantic mackerel and capelin abundance from the winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.....	11
Figure 3.	Atlantic mackerel and capelin abundances and bottom temperatures (°C) from winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003	12
Figure 4.	Atlantic mackerel and capelin cumulative abundance curves according to water temperature for winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.....	14
Figure 5.	Relationships among longitude, latitude, depth, temperature and abundance variables for Atlantic mackerel. The upper right panels show the Spearman correlations and corresponding p values (estimated by permutation). The size of the indicated values is proportionate to the absolute value of the correlations. The diagonal panels contain the frequency histograms and the lower left panels the scatter plots. The grey dots represent the zero abundance values and the black dots the non-zero abundance values.....	16
Figure 6.	Diagnosis of the generalized additive model for log-transformed Atlantic mackerel abundance data: (A) quantile–quantile diagram, (B) frequency histogram of residuals with the mean and median indicated on the right side of the graph and represented by vertical lines (dotted black: mean; grey: median), (C) residuals and linear predictor, and (D) observed and adjusted values.....	17
Figure 7.	Smoothing functions (with standard errors) for geographic positioning (A), temperature (B), and depth (C) for Atlantic mackerel abundance data (log). The vertical lines on the horizontal axis represent the observed values for temperature (B) and depth (C)	18

LIST OF FIGURES (continued)

- Figure 8. Relationships among longitude, latitude, depth, temperature, and abundance variables for capelin. The upper right panels show the Spearman correlations and corresponding p values (estimated by permutation). The size of the indicated values is proportionate to the absolute value of the correlations. The diagonal panels contain the frequency histograms and the lower left panels the scatter plots. The grey dots represent the zero abundance values and the black dots the non-zero abundance values19
- Figure 9. Diagnosis of the generalized additive model for capelin abundance data (log): (A) quantile–quantile diagram, (B) frequency histogram of residuals with the mean and median indicated on the right side of the graph and represented by vertical lines (dotted black: mean; grey: median), (C) residuals and linear predictor, and (D) observed and adjusted values20
- Figure 10. Smoothing functions (with standard errors) for geographic positioning (A), temperature (B), and the linear function of depth (C) for capelin abundance data (log). The vertical lines on the horizontal axis represent the observed values for temperature (B) and depth (C)21

ABSTRACT

Bruneau, B., and F. Grégoire. 2011. Spatial distribution study of Atlantic mackerel (*Scomber scombrus*) and capelin (*Mallotus villosus*) abundance data from winter groundfish surveys in NAFO Divisions 4VW using generalized additive models. Can. Tech. Rep. Fish. Aquat. Sci. 2930: vi + 21 pp.

Generalized additive models (GAM) were studied to describe the possible relationship between the geographic position (km), tow depths (m), bottom water temperature (°C), and abundance (log number / tow + 0.1) of Atlantic mackerel (*Scomber scombrus*) and capelin (*Mallotus villosus*) caught in a series of groundfish surveys conducted on the Scotian Shelf between 1994 and 2003. The selected models were used to determine the factors with a significant influence on Atlantic mackerel and capelin catches. These models also helped describe the thermal preferences of these two species. However, no abundance prediction was made because of the high number of tows without any catches.

RÉSUMÉ

Bruneau, B., et F. Grégoire. 2011. Spatial distribution study of Atlantic mackerel (*Scomber scombrus*) and capelin (*Mallotus villosus*) abundance data from winter groundfish surveys in NAFO Divisions 4VW using generalized additive models. Can. Tech. Rep. Fish. Aquat. Sci. 2930: vi + 21 pp.

Des modèles additifs généralisés (GAM) ont été étudiés afin de décrire les relations possibles entre la position géographique (km), la profondeur (m) des traits, la température (°C) de l'eau au fond et l'abondance (log du nombre / trait + 0.1) de maquereau bleu (*Scomber scombrus*) et de capelan (*Mallotus villosus*) capturés lors d'une série de relevés aux poissons de fond réalisés sur le plateau néo-écossais entre 1994 et 2003. Les modèles sélectionnés ont permis de déterminer les facteurs ayant une influence significative sur les captures de maquereau bleu et de capelan. Ces modèles ont aussi permis de décrire les préférences thermiques de ces deux espèces. Cependant, aucune prédiction d'abondance n'a été réalisée en raison du trop grand nombre de traits n'ayant aucune capture.

1.0 INTRODUCTION

Atlantic mackerel (*Scomber scombrus*) are generally recognized as warm-water fish. Laboratory experiments have shown that they prefer temperatures between 7.3 and 15.8°C (Olla et al. 1976, Overholtz and Anderson 1976). In deep waters, along the U.S. and Canadian coasts, winter catches of Atlantic mackerel have been associated with temperatures around 8°C (Sette 1950, Grégoire 2006). In the northeastern Atlantic, the species' distribution patterns and migration routes are also dependent on water temperature (Molloy 2004). Recently, Atlantic mackerel catches near the Spitzbergen archipelago in the Arctic Ocean were associated with water at 20 m of depth where temperatures were around 6 to 11°C (Nøttestad 2008). Water temperature could also be responsible for the presence of Atlantic mackerel in Iceland and the Faroe Islands (ICES 2008, Jacobsen 2008).

Capelin (*Mallotus villosus*) are recognized as cold-water fish. They occur in waters ranging between -1.5 and 14.0°C (Carscadden et al. 1989, Stergiou 1989, Brown 2002) and more particularly between -1.0 and 6.0°C (Rose 2005). The biology of the species, especially migrations associated with spawning activities, is greatly influenced by water temperature (Carscadden et al. 1997, Carscadden et al. 2002, Mowbray 2002). The species is also known to react quickly to temperature changes (Rose 2005).

Atlantic mackerel and capelin are both caught during the winter groundfish surveys conducted on the Scotian Shelf. This region has a temperature range wide enough for these two species to be caught in spite of different thermal preferences. The objective of this study is to use generalized additive models to describe the possible relationships between the abundance of these two species, geographical position, depth, and water temperature in the fishing tows where they were caught.

2.0 MATERIAL AND METHODS

2.1 Data source

Atlantic mackerel and capelin catch data (numbers per standard tow of 1.75 nautical miles) from winter groundfish surveys on the Scotian Shelf were obtained from the Virtual Data Center (VDC) of the Bedford Institute of Oceanography in Nova Scotia. These data included the location (latitude and longitude) and tow depth (m) as well as bottom water temperatures (°C). Surveys conducted between 1994 and 2003 were selected due to the larger catches of Atlantic mackerel and capelin. There were no surveys conducted in 1998 and 2004 and no temperature data is available for the 2005 and 2006 surveys. These groundfish surveys have been conducted since 1986 on the eastern portion of the Scotian Shelf, in NAFO Divisions 4VW (Figure 1).

2.2 Data processing

Data from the surveys conducted between 1994 and 2003 in Divisions 4VW were compiled so as to present all of the Atlantic mackerel and capelin catches.

The temperature data measured at each tow were kriged using the GS+ software (Robertson 1998). Atlantic mackerel and capelin abundances were superimposed on kriged temperature maps. For the GAM models, geographical coordinates (longitude and latitude) in degrees–minutes were converted to km using the Lambert Conformal Conic Projection, and the natural logarithm was used to transform abundances ($\log(\text{Nbr} / \text{tow} + 0.1)$) for each species.

2.3 Statistical analysis

2.3.1 Thermal preferences

Atlantic mackerel and capelin abundance data were studied according to water temperature using an approach similar to that of Perry and Smith (1994). This approach helped qualitatively describe the thermal preferences related to these two species.

2.3.2 Generalized additive models (GAM)

Generalized additive models (GAM) are a semi-parametric and non-linear version of generalized linear models (GLM). The relationship between the dependent variable and independent variables (covariates) of a GAM model is non-parametric and expressed using a smoothing function. For a GAM model, the linear predictor is the sum of the smoothing functions of the covariates. GAM have the same premise as GLM and have the same robustness in terms of non-normality of deviance residuals. The lack of normality in the deviance residuals is important to consider when there is a shift in their distribution.

Different generalized additive models (Hastie and Tibshirani 1990) were studied to describe the possible relationship between Atlantic mackerel and capelin abundances and the following independent variables: (1) geographic position (isotropic smoothing of longitude and latitude), (2) depth, and (3) water temperature at the bottom. For a given GAM model, the choice of independent variables and smoothing functions was made while taking into account the 5% significance level.

In a GAM model, the effect of each independent variable is measured after removing the effect of other covariates from the model. The R software library (R Development Core Team 2008, version 2.12.2) "*mgcv*" (multiple smoothing parameter estimation by gcv; version 1.7-3) (Wood 2006) was chosen to test different models. This library uses the generalized cross-validation (gcv) method amended by Wood (2006) to automatically determine the degree of smoothing to be applied to each independent variable. In R language, the models that were used to describe the relationship between abundance (log-transformed) and the independent variables were expressed as follows:

```
gam (I (log (abundance+0.1)) ~ s(longitude, latitude, bs="ts") + s(temperature,
    bs="ts") + s(depth, bs="ts"), data=inputdata, family=gaussian,
    gamma=1.4)
```

where:

"I" prevents the mathematical operation (+) from being considered as a symbol of the equation of the model, "s" indicates that "*spline*" is the smoothing method used, bs="ts" represents the type of smoothing ("*thin plate regression spline smoothers*"), and family=gaussian indicates that the distribution function of the dependent variable is normal (Gaussian). The link function used is "*identity*" (default). Gamma (1.4) represents an *ad hoc* correction to avoid over-adjustment of the model (Kim and Gu 2004).

When the degrees of freedom in a covariate smoothing are not significant and tend to match the unit, this covariate can be tested on a strictly linear basis by removing the options "s" and "bs" associated with it.

3.0 RESULTS

3.1 Catches per species

The surveys were conducted from late February or early March to late March. The number of tows carried out between 1994 and 2003 totalled 927 (Table 1). Atlantic mackerel was caught in 92 tows (9.9%) and capelin in 286 tows (30.9%). There were only two tows (0.2%) where both species were caught together. As shown in Figure 2, catch locations of Atlantic mackerel and capelin were distinct.

Atlantic mackerel catches were made in the southwestern portion of the sampled area and capelin catches in the central and northeast portions (Figure 3). The first portion was characterized by warmer water temperatures while colder temperatures were associated with the two other portions. A negative correlation ($r_{\text{Spearman}} = -0.2$, $p < 0.001$) was measured between the abundances of both species.

3.2 Link between abundance and water temperature

Bottom temperatures ranged between -1.44 and 12.96°C (Table 1). The maximum discrepancy was measured in 1994, with minimum and maximum temperatures of -1.36 and 12.09°C , and the minimum range was in 1996, with a minimum of 0.78°C and a maximum of 9.07°C . With the exception of the 1994 and 1999 surveys, $\geq 80\%$ of capelin abundances were associated with temperatures below about 5°C (Figure 4). For Atlantic mackerel, with the exception of the 1995 and 1997 surveys, over 75% of the abundances were measured at temperatures above about 6°C .

3.3 Generalized additive models (GAM)

3.3.1 Covariate relationships

Temperature was inversely related to the longitude and latitude (Figure 5). Longitudes and latitudes had a strong correlation but had a weak correlation with depth. There was a weak positive correlation between temperature and depth.

3.3.2 Mackerel

Atlantic mackerel abundance had a negative correlation with longitude and latitude whereas it had a positive correlation with temperature. Atlantic mackerel abundance was characterized by a large number of negative values (on the logarithmic scale) associated with tows with no catches (Figure 5).

Deviance residuals from the selected model are not normally distributed (Figures 6A, 6B). However, the hypothesis of a centered distribution is not rejected ($mc = -0.119$, $p = 0.3647$) when the "*medcouple*" index (Brys et al. 2004) is applied to the residuals. The large number of zeros makes the residuals distribution leptokurtic (kurtosis = 15.38, $p < 0.0001$). Residuals do not show an increase or a decrease in variance for the high predicted values (Figures 6C, 6D). Residuals that form a distinct line in Figures 6C and 6D are associated with the high number of zero values that are present over all the range of all the independent variables (Figures 5, 6D).

The three independent variables have a significant non-linear relationship ($p < 0.05$) with the dependent variable (Table 2). The coefficient of determination is 0.45, the percentage of deviance explained by the model is 46.6%, and the gcv coefficient is 1.97.

The first smoothing function, geographical position, indicates that the most significant abundances were associated with the southwest portion of the sampled area (Figure 7A). The highest temperatures were also recorded in this area (Figure 3). The second smoothing function indicates that Atlantic mackerel abundance increased rapidly between 7.5 and 11°C and decreased thereafter (Figure 7B). For temperatures below 7.5°C, Atlantic mackerel abundance was low to nil. Finally, abundance declined steadily at depths between 120 m and 275 m (Figure 7C). Standard errors for this smoothing function increased rapidly for depths greater than 275 m due to the low number of observations.

3.3.3 Capelin

Capelin abundance had a positive correlation with longitude and latitude whereas it had a negative correlation with temperature (Figure 8). Capelin abundance was also characterized by a large number of negative values (on the logarithmic scale) associated with tows with no catches.

Deviance residuals from the selected model are not normally distributed (Figures 9A, 9B). However, they are considered centered ($mc = -0.005$, $p = 0.9711$) when the "*medcouple*" shift index is used. Residuals present a leptokurtic distribution (kurtosis = 5.03, $p < 0.0001$) due to the high number of zeros. In addition, they do not show an increase or a decrease in variance for the high predicted values (Figures 9C, 9D). Residuals that form distinct lines in Figures 9C and 9D are associated with the high number of zero values that, as with Atlantic mackerel, are present over all the range of all independent variables (Figures 8, 9D).

The geographic position and temperature covariates have a significant non-linear relationship ($p < 0.05$) with the dependent variable whereas depth presents a weak linear significant ($p < 0.05$) relationship (slope = 0.004) with the dependent variable (Table 2). The coefficient of determination is 0.47, the percentage of deviance explained by the model is 49.1%, and the gcv coefficient is 5.72 (Table 2).

The first smoothing function, geographical position, indicates that the most significant abundances were associated with the northeast portion of the sampled area (Figure 10A). This area was characterized by lower temperatures (Figure 3). The second smoothing function indicates that capelin abundance increased for temperatures between 0 and 3.5°C and decreased thereafter (Figure 10B). For temperatures below 0°C and above 7.5°C, capelin abundance was low to nil. Finally, a slight increase in abundance was recorded according to depth (Figure 10C). Standard errors associated with this relationship presented a steady increase due to the low number of observations at great depths.

4.0 DISCUSSION AND CONCLUSION

The results of this study indicate that Atlantic mackerel and capelin abundances from the winter groundfish surveys were strongly related to bottom temperature. The geographical position and depth of tows also had a significant non-linear influence on Atlantic mackerel abundance. Atlantic mackerel abundances were measured at an average depth of 116.5 m compared to 130.2 m for tows with zero catch. These mean depths were significantly different from one another (Welch t test, $p < 0.01$).

Capelin abundances were also related to position, bottom temperature, and tow depth. However, the influence of depth on capelin abundance was weak and linear, whereas location had a strong and non-linear influence. Capelin abundances were measured at an average depth of 129.3 m compared to 128.3 m for tows with zero catch. These mean depths were not significantly different (Welch t test, $p > 0.05$), which corroborates the results of the model. The optimum temperature for capelin was found at greater depths (CV: 51%) than that of Atlantic mackerel (CV: 34%). Although these species are found only in portions of the study area where temperature was optimal for each species, the model indicates that the geographical position had a significant effect even after the effects of temperature and depth were removed. The geographical position takes into account other sources of variation that were not included in the model.

GAM models have the advantage of using multiple covariates. In this case, these models have helped to refine the relationship between the abundance of both species and temperature, including geographical position and depth. The use of a GAM model is advantageous when the relationship between the covariates and the dependent variable is not linear. This approach is more flexible than a parametric non-linear model because it allows the use of a model without having to define the formulation of the parametric relationship between variables.

Atlantic mackerel and capelin abundance data included a large number of zeros. This means that there are probably more zeros than would be expected for a Poisson or a negative binomial distribution (Borchers et al. 1997, Augustin et al. 1998). However, ignoring their presence could cause a bias in estimating a GAM model's parameters (Zuur et al. 2009). Data with many zeros can be analyzed using ZINB (Zero-Inflated Negative Binomial) and ZIP (Zero-Inflated Poisson) models (Zuur et al. 2009) from "*pscl*" (Zeileis et al. 2008) and "*gamlss*" (Rigby and Stasinopoulos 2005) models. ZINB and ZIP models are considered as mixed models since the zeros are considered to come from two different processes, namely (1) probability calculations of obtaining false zeros according to the values of one or more independent variables and (2) abundance data calculations (which could include zeros) according to one or more independent variables (Zuur et al. 2009). False zeros can be defined as the absence of a species at some sites even if habitat conditions are suitable. Unfortunately, models based on zero-inflated distributions could not be used in this case because these models did not converge.

The thermal preferences of Atlantic mackerel and capelin were defined for a data set covering several years. These preferences could be compared to those obtained from other databases to verify whether they remain the same, and if so, to determine potential habitats. Other variables describing the biological characteristics of a stock could be incorporated to new models. For example, length, age and sexual maturity of catches could be used in conjunction with environmental variables to describe the role of these variables in year-class recruitment.

Until now, generalized additive models helped to describe complex and non-linear relationships between variables (Daskalov 1999). However, their use with fisheries data or abundance surveys is relatively recent (Swartzman et al. 1995, Daskalov 1999, Cardinale and Arrhenius 2000). The possible processing of the many zeros that characterize these data could lead to greater use of these models. In this study, no prediction was calculated from the models selected because of the great number of zeros. Their presence would bias predictions (Figures 6D, 9D).

Although groundfish surveys were conducted in winter, Atlantic mackerel and capelin could have been located near the bottom when they were caught, and not only on the bottom, which would reduce their catchability in a bottom trawl. Pelagic fish biomass index calculations using this type of survey should also be done with caution. It has recently been suggested that increases in pelagic fish biomass measured in recent years from bottom trawl surveys might simply reflect a greater presence of these fish in the suprabenthic habitat abandoned by the decreasing groundfish populations (McQuinn

2009). For this reason, the objective of this study was only to describe possible relationships between the abundances and environmental variables and not to calculate abundances that would be used as biomass indices.

5.0 ACKNOWLEDGEMENTS

Very sincere thanks are expressed to Ms. Louise Savard, Dr. Denis Chabot, and Dr. Stephane Plourde for revising the document.

6.0 REFERENCES

- Augustin, N. H., Borchers, D. L., Clarke, E. D., Buckland, S. T., and Walsh, M. 1998. Spatiotemporal modelling for the annual egg production methods of stock assessment using generalized additive models. *Can. J. Fish. Aquat. Sci.* 55: 2608–2621.
- Borchers, D. L., Buckland, S. T., Priede, I. G., and Ahmadi, S. 1997. Improving the precision of the daily egg production method using generalized additive models. *Can. J. Fish. Aquat. Sci.* 54: 2727–2742.
- Brown, E. D. 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. *ICES J. Mar. Sci.* 59: 983–996.
- Brys, G., Hubert, M., and Struyf, A. 2004. A robust measure of skewness. *J. Comput. Graph. Statist.* 13(4): 996–1017.
- Cardinale, M., and Arrhenius, F. 2000. The relationship between stock and recruitment: are the assumptions valid? *Mar. Ecol. Prog. Ser.* 196: 305–309.
- Carscadden, J. E., Frank, K. T., and Miller, D. S. 1989. Capelin (*Mallotus villosus*) spawning of the southeast shoal: influence of physical factors past and present. *Can. J. Fish. Aquat. Sci.* 46: 1743–1754.
- Carscadden, J. E., Nakashima, B. S., and Frank, K. T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 54: 781–787.
- Carscadden, J. E., Montevecchi, W. A., Davoren, G. K., and Nakashima, B. S. 2002. Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. *ICES J. Mar. Sci.* 59: 1027–1033.

- Daskalov, G. 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. *Fish. Res. (Amst.)*, 41: 1–23.
- Grégoire, F. 2006. Distribution verticale des captures de maquereau bleu (*Scomber scombrus* L.) au chalut pélagique en relation avec la température de l'eau / *Vertical distribution of the midwater trawl catches of Atlantic mackerel (Scomber scombrus L.) in relation with water temperature*. Secr. can. de consult. sci. du MPO, Doc. de rech. / *DFO Can. Sci. Advis. Sec. Res. Doc.* 2006/097. 44 pp.
- Hastie, T. J., and Tibshirani, R. J. 1990. *Generalized Additive Models*. Chapman & Hall. New York. Monographs on Statistics and Applied Probability. Volume 43. 335 pp.
- ICES. 2008. Report of the planning group on Northeast Atlantic pelagic ecosystem surveys (PGNAPES), 19–22 August 2008, Hirsthals, Denmark. ICES CM 2008/RMC:05. 87 pp.
- Kim, Y. J., and Gu, C. 2004. Smoothing spline gaussian regression: more scalable computation via efficient approximation. *J. Roy. Statist. Soc. Ser. B* 66:337–356.
- Jacobsen, J. A. 2008. Wide distribution of mackerel. Working document to ICES Working Group on Widely Distributed Stocks in September 2008. ICES Headquarters Copenhagen. 691 pp.
- McQuinn, I. H. 2009. Pelagic fish outburst or suprabenthic habitat occupation: legacy of the Atlantic cod (*Gadus morhua*) collapse in eastern Canada. *Can. J. Fish. Aquat. Sci.* 66: 2256–2262.
- Molloy, J. 2004. The Irish mackerel fishery and the making of an industry. Marine Institute. Galway. 245 pp.
- Mowbray, F. 2002. Changes in vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. *ICES J. Mar. Sci.* 59: 942–949.
- Nøttestad, L. 2008. Mapping the northerly distribution of NEA mackerel (*Scomber scombrus*) in summer 2008. Working document to ICES Working Group on Widely Distributed Stocks in September 2008. ICES Headquarters Copenhagen. 691 pp.
- Olla, B. L., Bejda, A. J., and Stuholme, A. L. 1976. Swimming speeds of Atlantic mackerel, *Scomber scombrus* L., under laboratory conditions: relation to capture by trawling. *ICNAF Res. Doc.* 76/XII/143. 6 pp.

- Overholtz, W. J., and Anderson, E. D. 1976. Relationship between mackerel catches, water temperature, and vessel velocity during USA spring bottom trawl surveys in SA 5-6. ICNAF Res. Doc. 76/XII/170. 7 pp.
- Perry, R. I., and Smith, S. J. 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 51: 589-602.
- R Development Core Team. 2008. R Foundation for Statistical Computing. Vienna, Austria.
- Rigby, R. A., and Stasinopoulos, D. M. 2005. Generalized additive models for location, scale and shape. *J. Roy. Statist. Soc. Ser. B.*, 54(2): 507–554.
- Robertson, G. P. 1998. GS+: Geostatistics for the Environmental Sciences. Gamma Design Software. Plainwell, Michigan, USA. 152 pp.
- Rose, G. A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change. *ICES J. Mar. Sci.* 62: 1524–1530.
- Sette, O. E. 1950. Biology of the Atlantic mackerel (*Scomber scombrus* L.). Part 2: Migration and habits. *U.S. Wild. Serv., Fish. Bull.* 49 (51): 251–358.
- Stergiou, K. I. 1989. Capelin *Mallotus villosus* (Pisces: Osmeridae), glaciations, and speciation: a nomothetic approach to fisheries ecology and reproductive biology. *Mar. Ecol. Prog. Ser.* 56: 211–224.
- Swartzman, G., Silverman, E., and Williamson, N. 1995. Relating trends in walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to environmental factors. *Can. J. Fish. Aquat. Sci.* 52: 369–380.
- Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman & Hall/CRC. Chapman & Hall/CRC. 416 pp.
- Zeileis, A., Kleiber, C., and Jackman, S. 2008. Regressions models for count data in R. *J. Stat. Soft.* 27: 1–25
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York. 524 pp.

Table 1. Date, number of tows, and bottom temperature (°C) for winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.

YEAR	DATE		NUMBER OF TOWS				TEMPERATURE (°C)		
	Start (day-month)	End (day-month)	Mackerel	Capelin	Mackerel and Capelin	Total	Min.	Average	Max.
1994	27-02	10-03	18	20	1	95	-1.36	5.13	12.09
1995	27-02	12-03	12	35	0	121	-0.59	3.31	11.06
1996	03-03	10-03	1	14	0	52	0.78	3.83	9.07
1997	07-03	24-03	14	47	0	115	0.06	4.48	10.45
1999	02-03	21-03	13	44	1	109	-0.15	4.41	10.89
2000	01-03	16-03	12	41	0	116	1.22	5.15	12.96
2001	27-02	14-03	9	28	0	90	-0.16	3.88	10.40
2002	05-03	19-03	2	34	0	121	0.52	3.88	9.41
2003	04-03	20-03	11	23	0	108	-1.44	3.52	10.57
Min.:			1	14	0	52			
Average			10	32	0	103			
Max.:			18	47	1	121			
TOTAL			92	286	2	927			
(%)			(9.9)	(30.9)	(0.2)				

Table 2. Results from the generalized additive models tested on Atlantic mackerel and capelin abundance data (log number / tow + 0.1) from the winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.

SPECIES	FAMILY	LINK FUNCTION	VARIABLE AND SMOOTHING FUNCTION	d.f. or coefficient	F	p	R ² (adjusted)	DEVIANCE EXPLAINED (%)	GCV* Score
Mackerel	Gaussian	Identity	s(longitude,latitude)	19.955	3.21	< 0.0001	0.45	46.6	1.97
			s(temperature)	7.678	18.56	< 0.0001			
			s(depth)	2.538	3.86	0.0077			
Capelin	Gaussian	Identity	s(longitude,latitude)	22.119	15.78	< 0.0001	0.47	49.1	5.72
			s(temperature)	3.026	3.86	0.0175			
			depth**	0.004	4.72	0.0184			

* Generalized cross validation

** Covariate not smoothed

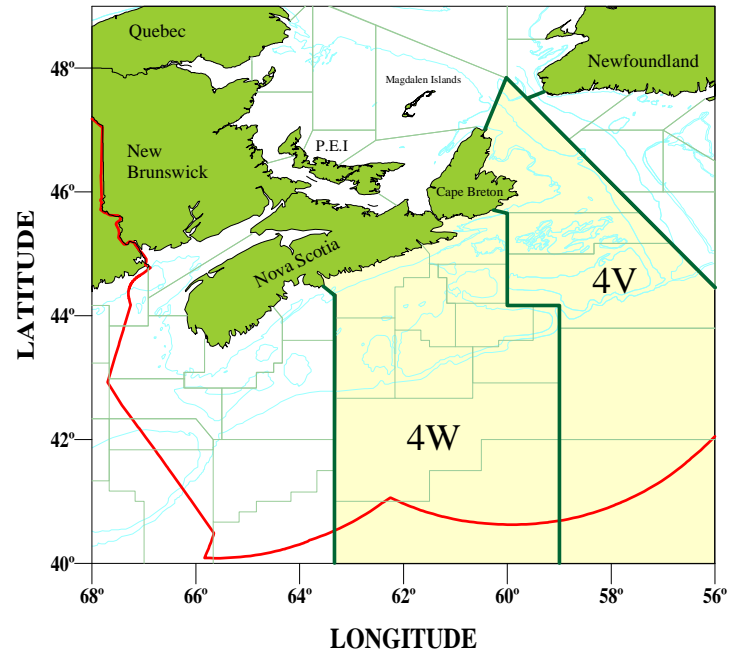


Figure 1. Map of NAFO Divisions 4VW.

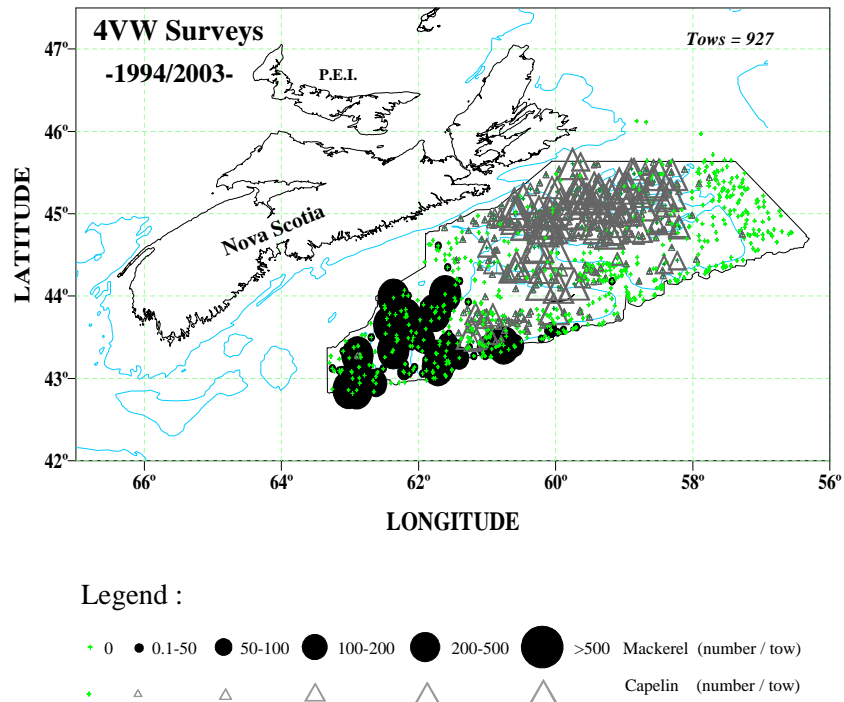


Figure 2. Atlantic mackerel and capelin abundances from the winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.

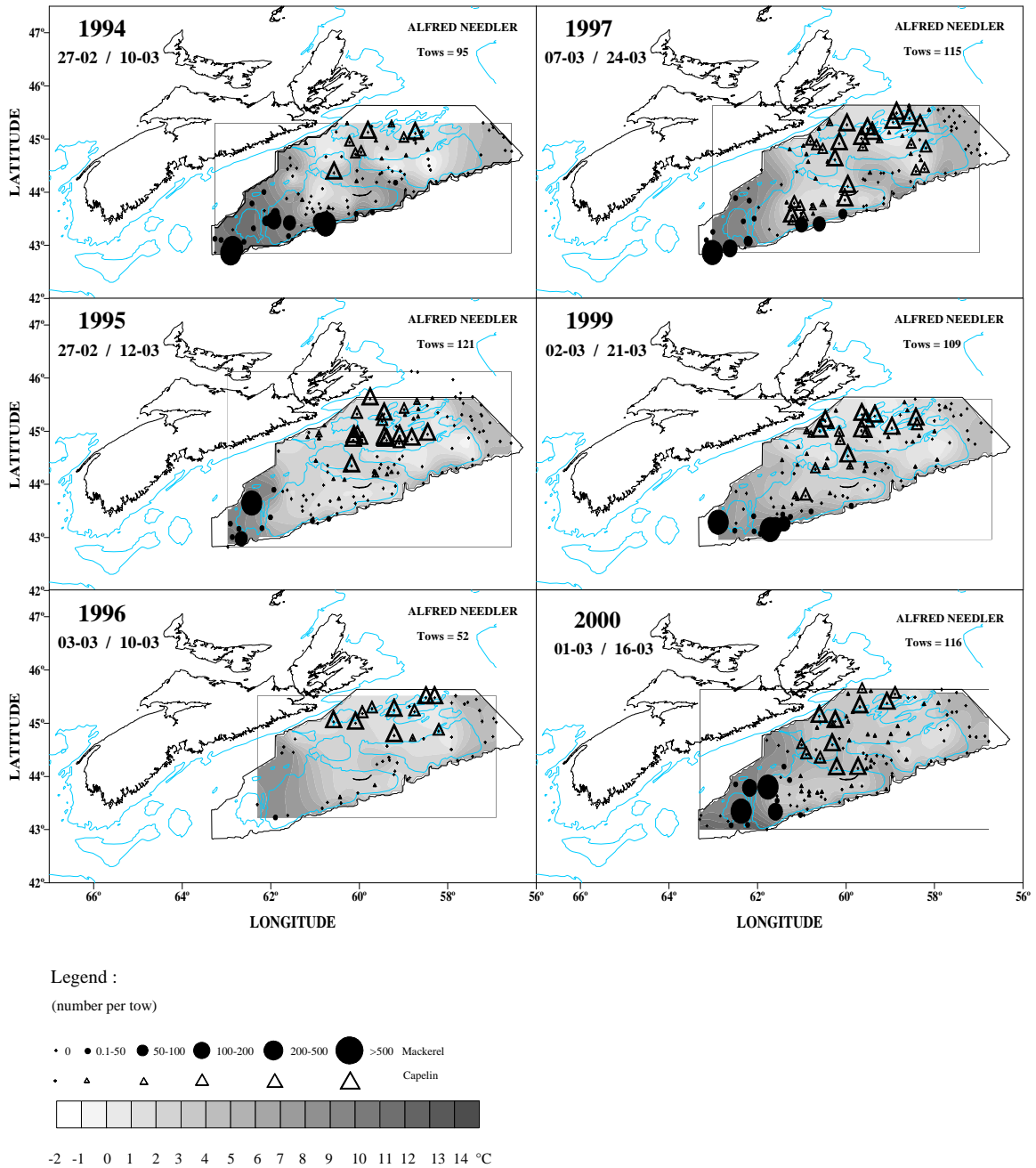


Figure 3. Atlantic mackerel and capelin abundances and bottom temperatures (°C) from winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.

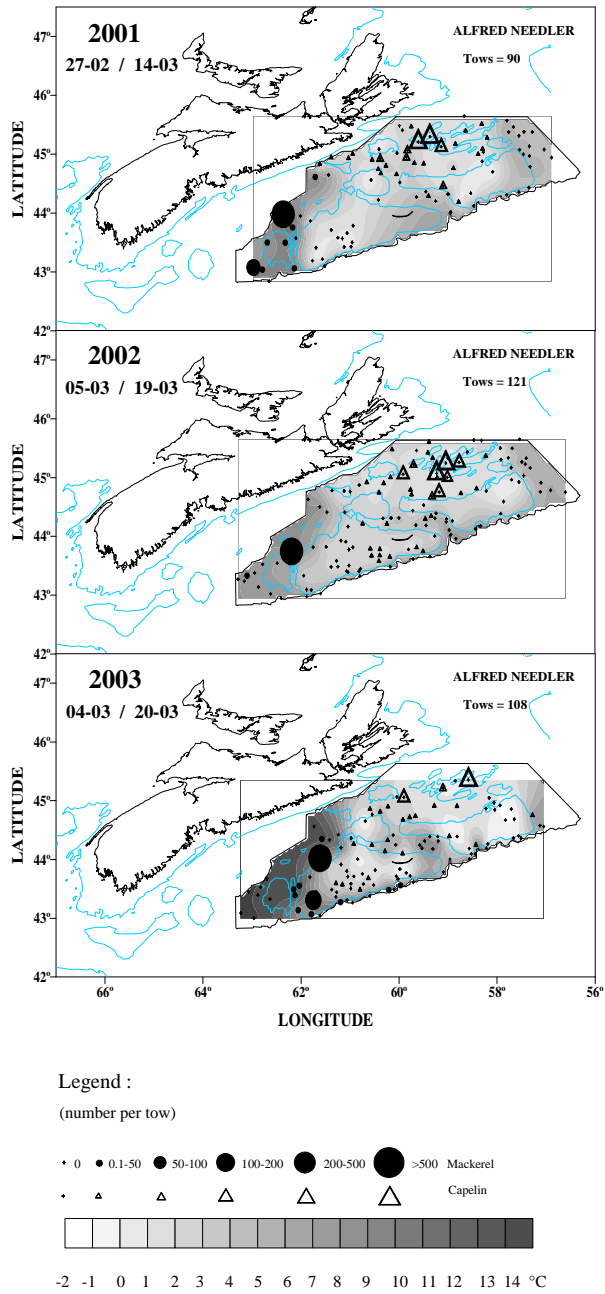


Figure 3. (Continued).

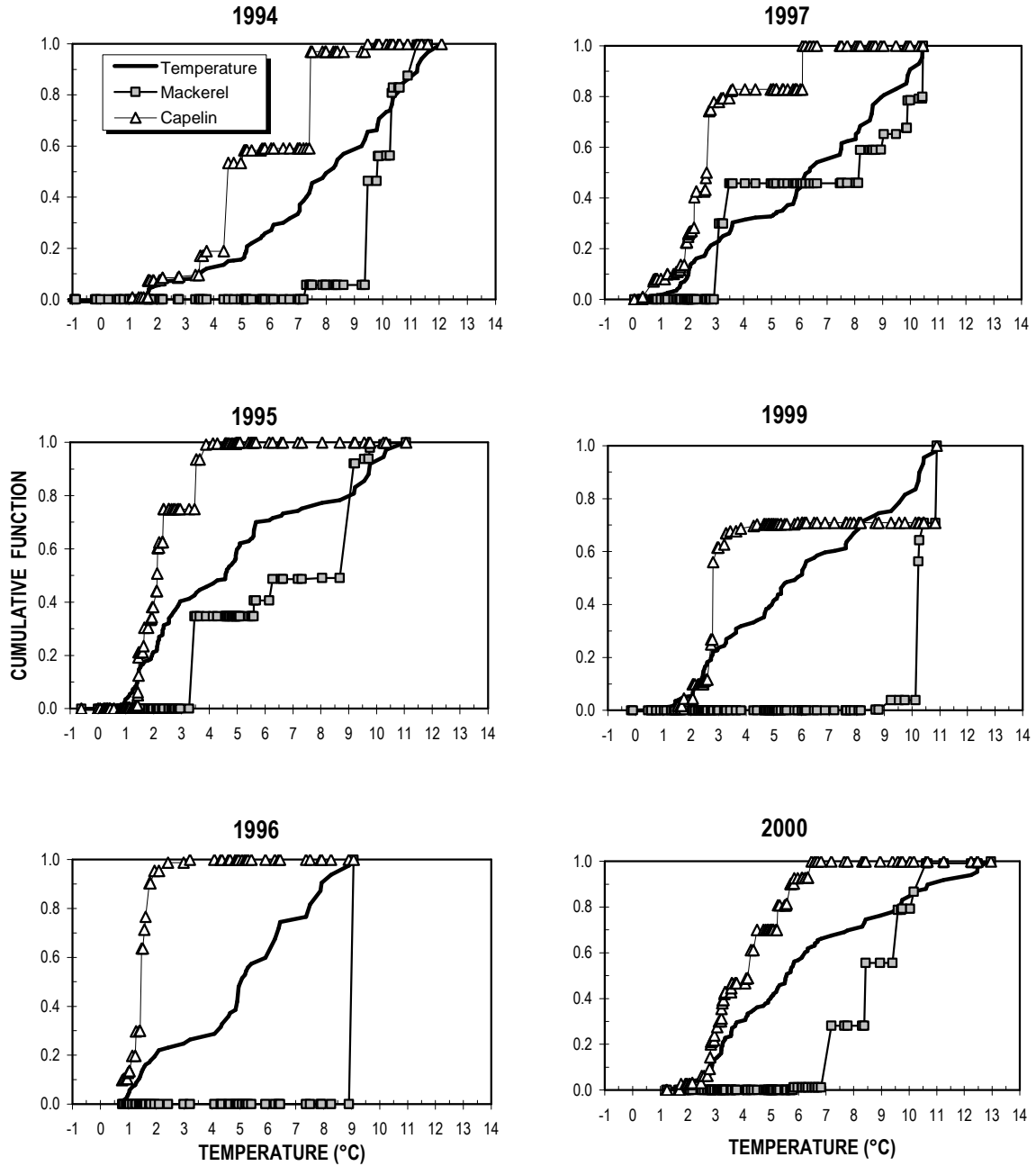


Figure 4. Atlantic mackerel and capelin cumulative abundance curves according to water temperature for winter groundfish surveys in NAFO Divisions 4VW conducted between 1994 and 2003.

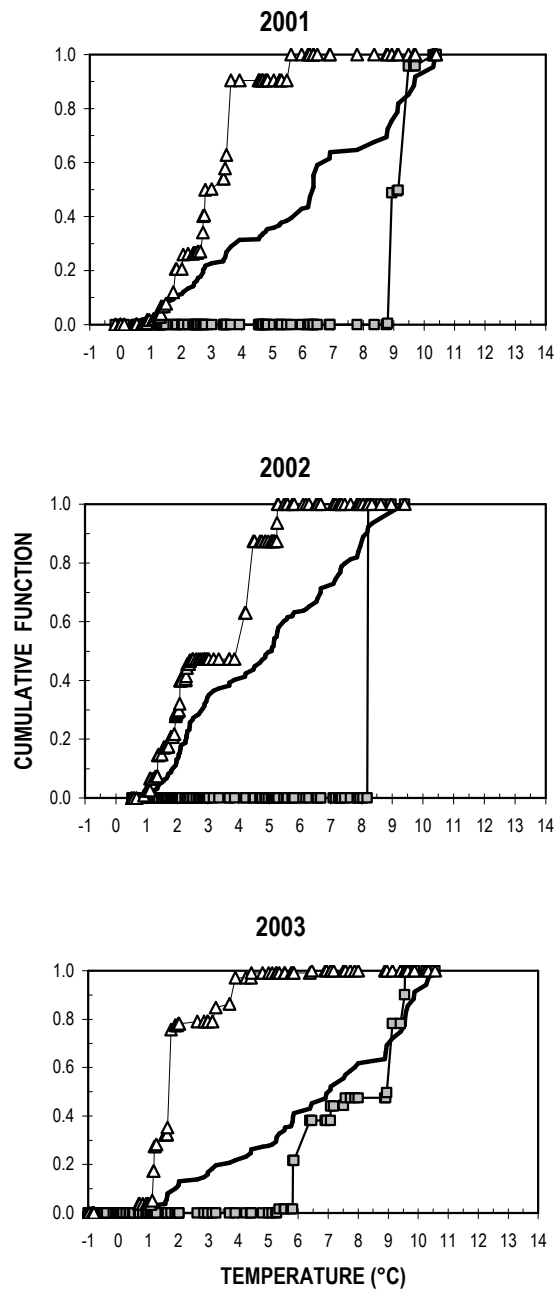


Figure 4. (Continued).

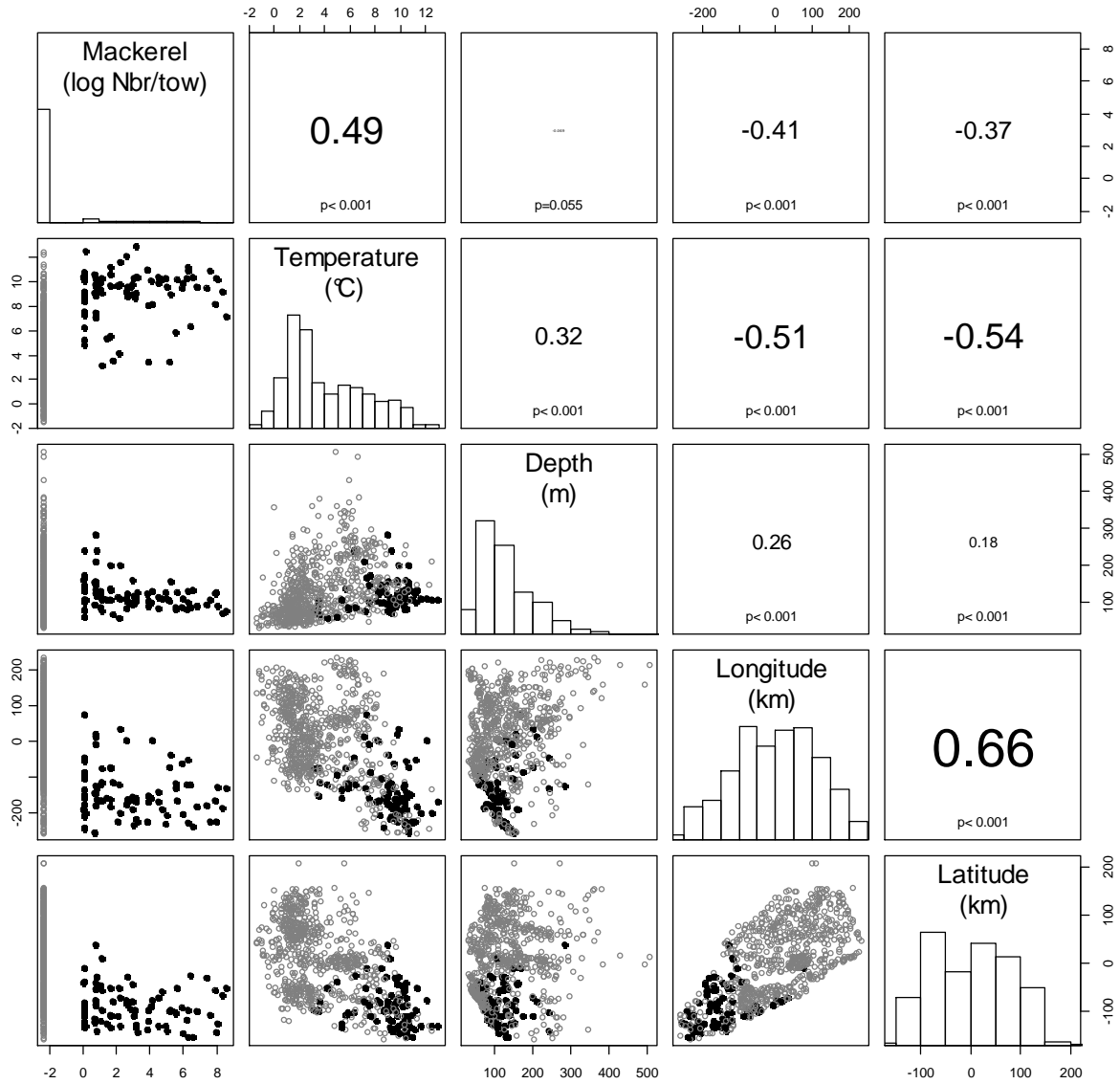


Figure 5. Relationships among longitude, latitude, depth, temperature and abundance variables for Atlantic mackerel. The upper right panels show the Spearman correlations and corresponding p values (estimated by permutation). The size of the indicated values is proportionate to the absolute value of the correlations. The diagonal panels contain the frequency histograms and the lower left panels the scatter plots. The grey dots represent the zero abundance values and the black dots the non-zero abundance values.

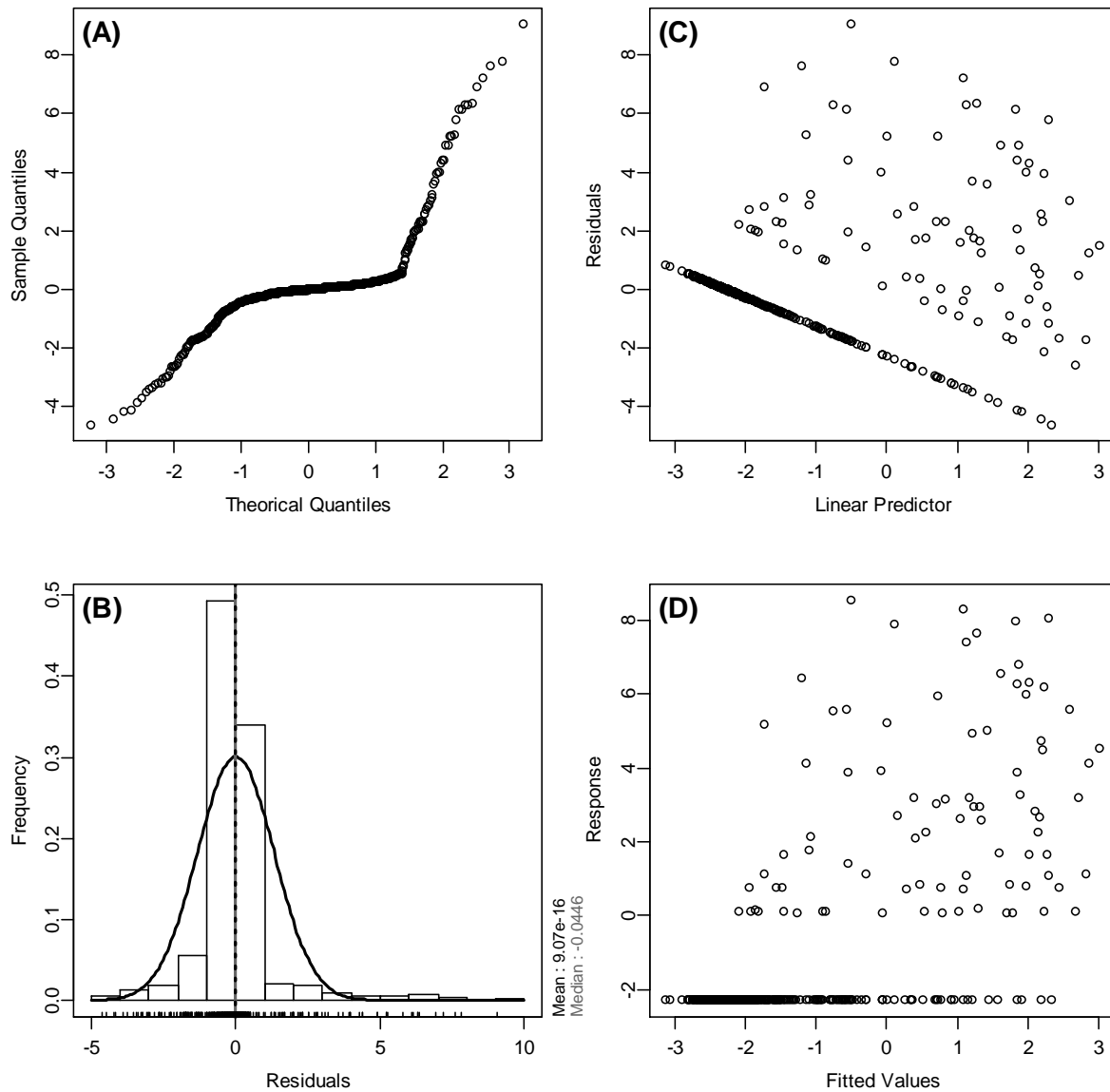


Figure 6. Diagnosis of the generalized additive model for log-transformed Atlantic mackerel abundance data: (A) quantile–quantile diagram, (B) frequency histogram of residuals with the mean and median indicated on the right side of the graph and represented by vertical lines (dotted black: mean; grey: median), (C) residuals and linear predictor, and (D) observed and adjusted values.

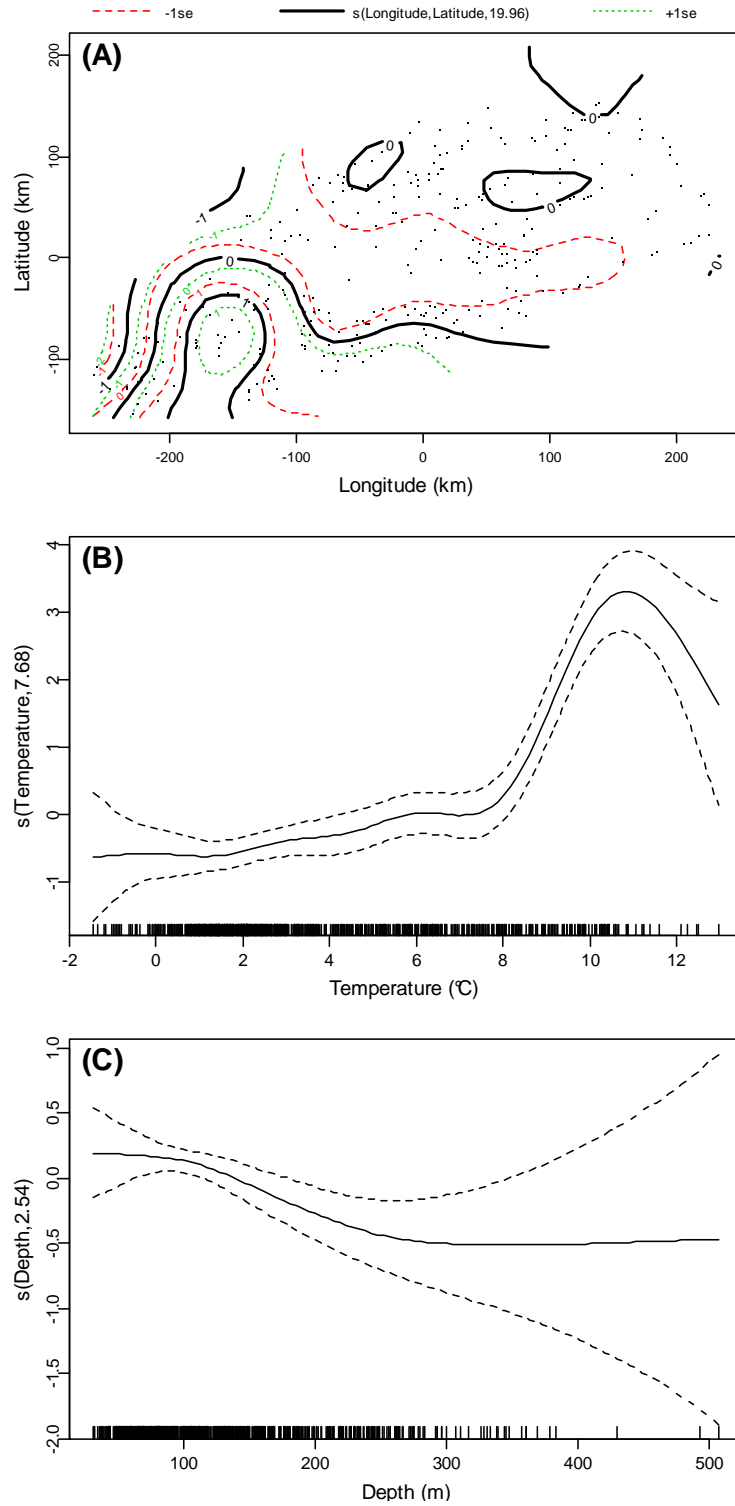


Figure 7. Smoothing functions (with standard errors) for geographic positioning (A), temperature (B), and depth (C) for Atlantic mackerel abundance data (log). The vertical lines on the horizontal axis represent the observed values for temperature (B) and depth (C).

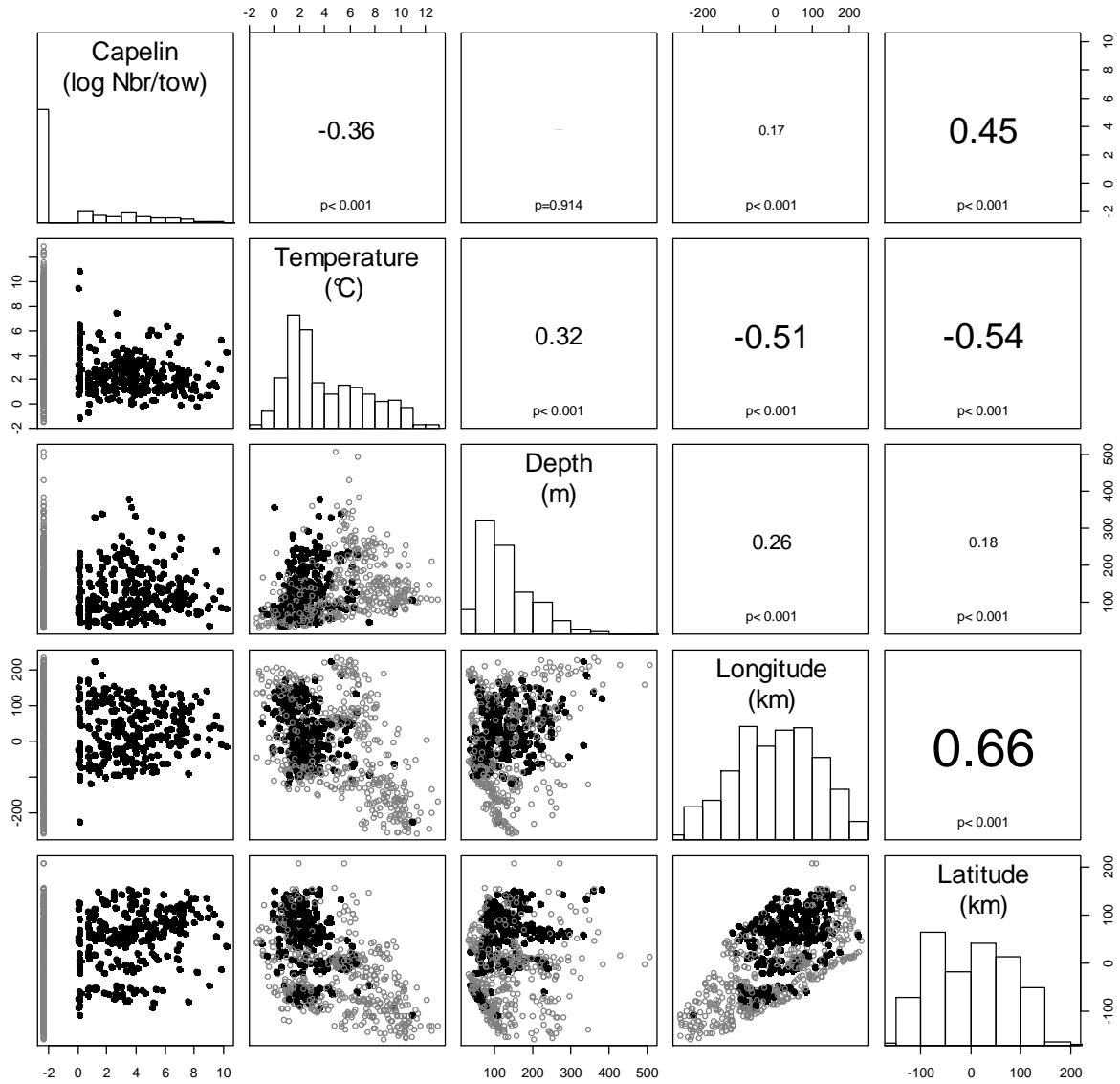


Figure 8. Relationships among longitude, latitude, depth, temperature, and abundance variables for capelin. The upper right panels show the Spearman correlations and corresponding p values (estimated by permutation). The size of the indicated values is proportionate to the absolute value of the correlations. The diagonal panels contain the frequency histograms and the lower left panels the scatter plots. The grey dots represent the zero abundance values and the black dots the non-zero abundance values.

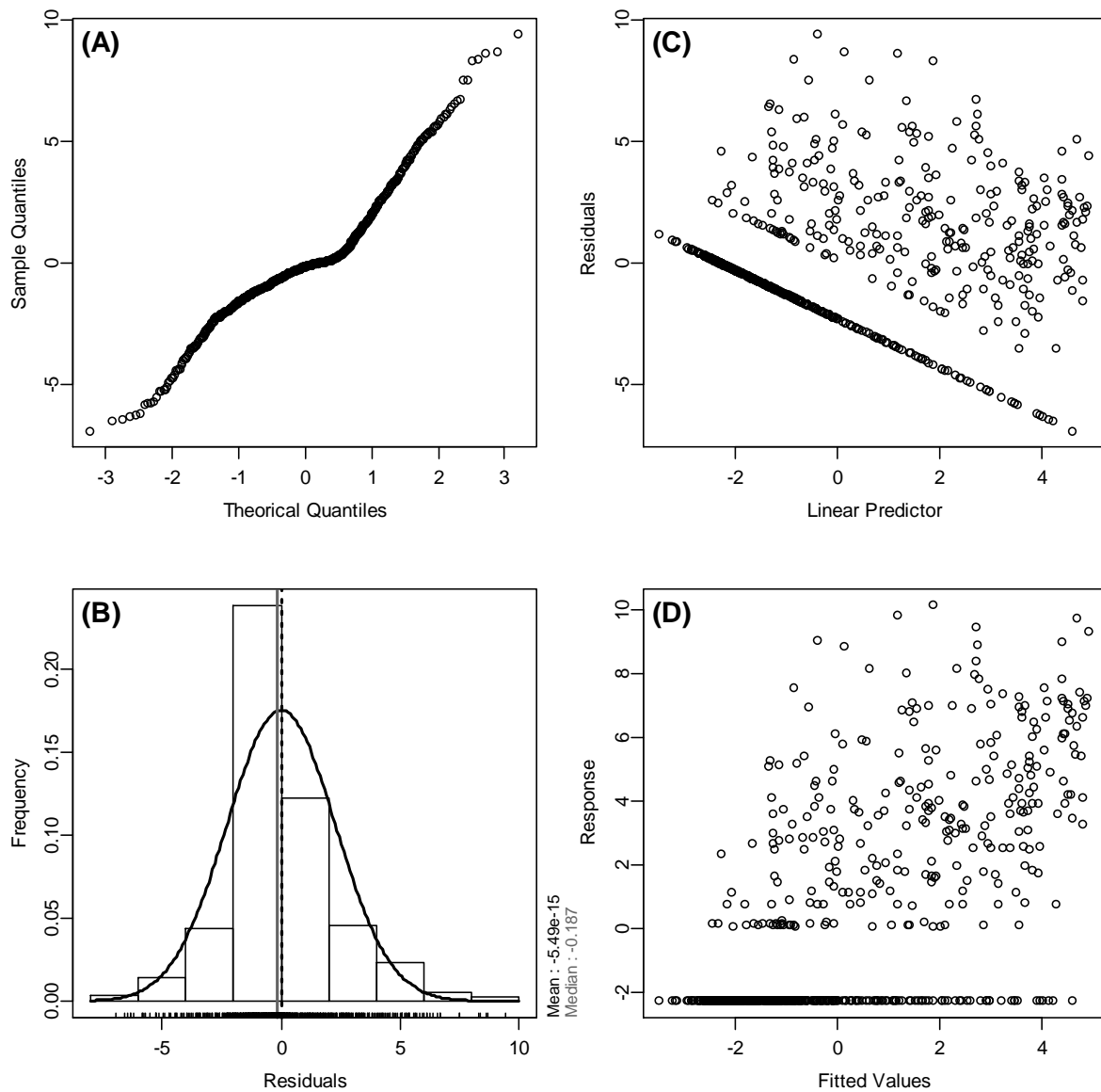


Figure 9. Diagnosis of the generalized additive model for capelin abundance data (log): (A) quantile–quantile diagram, (B) frequency histogram of residuals with the mean and median indicated on the right side of the graph and represented by vertical lines (dotted black: mean; grey: median), (C) residuals and linear predictor, and (D) observed and adjusted values.

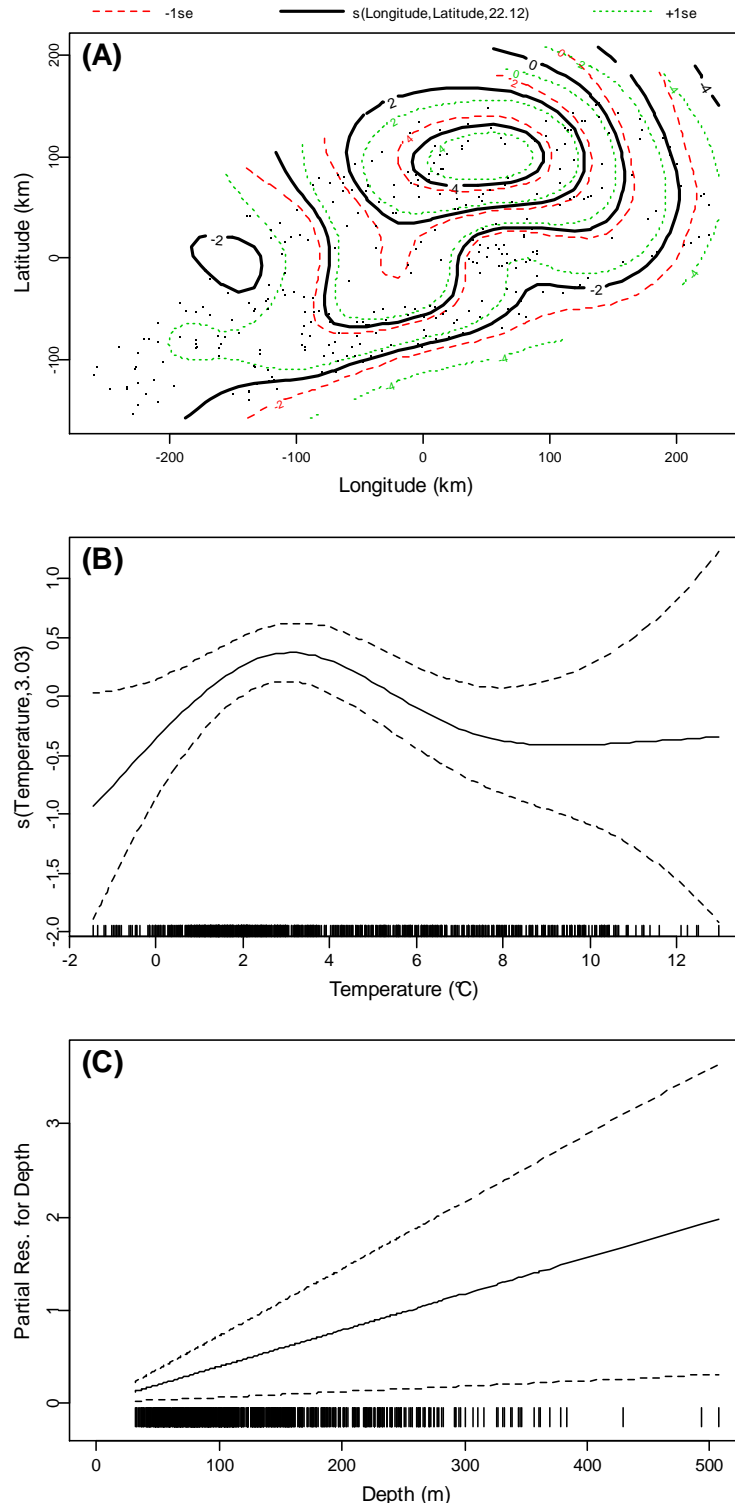


Figure 10. Smoothing functions (with standard errors) for geographic positioning (A), temperature (B), and the linear function of depth (C) for capelin abundance data (log). The vertical lines on the horizontal axis represent the observed values for temperature (B) and depth (C).