Assessing long-term changes in early summer zooplankton communities around Iceland

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A summary of the Icelandic Spring Survey zooplankton data for May and June is
presented for the years 1960–1996, along with time-series information on sea surface
temperature. Changes in zooplankton abundance are assessed using displacement
volumes and simple index numbers modelled as various functions of temporal (year)
and location (latitude and longitude) covariates. Long-term displaced volumes of
zooplankton remained fairly stable although there were pronounced short-term
fluctuations. Further, the proportion of specimens in each sample belonging to species
with affinities of water of Atlantic type has fallen dramatically over the Icelandic Shelf
since the 1960s, whereas the proportion of species with Arctic affinities has increased
most markedly northeast of Iceland.

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Introduction

The purpose of this investigation is to summarize long-term variability in zooplankton communities around Iceland, in relation to hydrography, using data collected by the Icelandic Spring Survey, which was started in 1960. Iceland is situated on the Greenland–Scotland Ridge, where there is a pronounced boundary between the warm currents from the south and cold currents from the north (e.g. Stefánsson, 1962; Malmberg and Kristmannsson, 1992). The location of Iceland in this transitional area means that its environment and crucially important fisheries can be particularly susceptible to climate change. It is therefore of interest that the marine fauna of Icelandic waters is monitored and that past changes are explored, documented, and understood.

In order to put the interannual changes in zooplankton abundance and distribution in an environmental context, we first briefly outline the hydrography of the area. Relatively warm, saline Atlantic Water, borne by the Irminger Current, reaches the southern and southwestern coasts of Iceland [Figure 1(a)]. At the Iceland–Greenland Ridge, the northeast-flowing Atlantic Water separates into two parts. One branch travels west then southwest into the Irminger Sea, where it forms a cyclonic eddy, while the other (the North Icelandic Irminger Current) continues eastwards along the north coast. In the northwestern part of the Iceland Sea, the East Greenland Current carries cold, low-salinity Polar Water along the Greenland coast to the south and crosses the Greenland–Iceland Ridge (Stefánsson, 1962). North and northeast of Iceland, the cold, low-salinity East Icelandic Current flows southeast along the Northeast Icelandic continental slope carrying Arctic Water. Therefore, both Atlantic Water from the North Icelandic Irminger Current and Polar Water from the East Greenland Current contribute to the East Icelandic Current. The area north of Iceland is subject to a more variable hydrographic and biological regime than the more uniform Atlantic Water farther south (e.g. Malmberg, 1986; Astthorsson and Gislason, 1995).
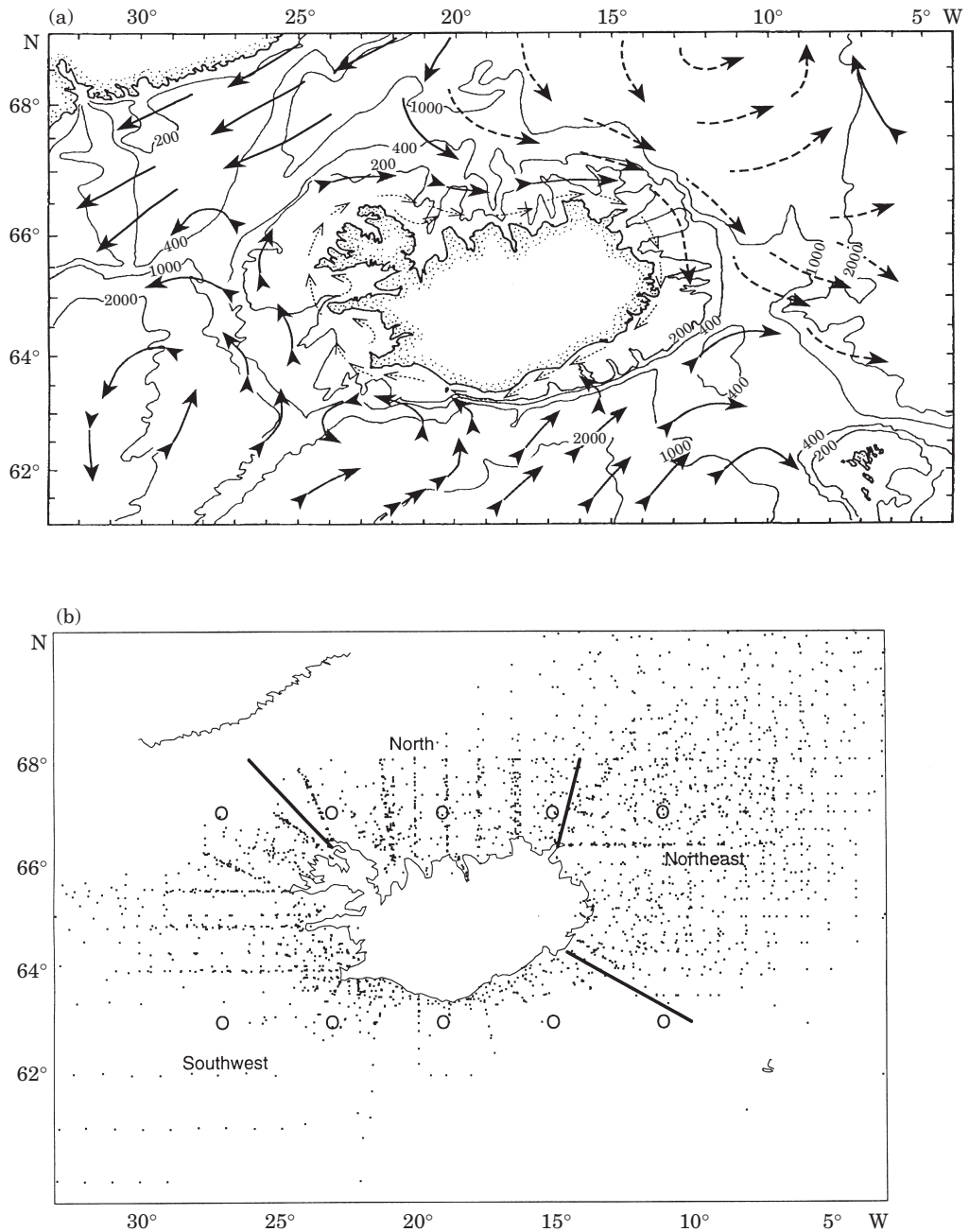
Figure 1. (a) Main currents around Iceland. Flighted arrows: Atlantic Water; normal arrows: Polar Water: thick broken arrows: Arctic Water; thin broken arrows: Coastal Water. (b) Map showing location of Icelandic Spring-Survey samples and the three subregions. Circles correspond to locations of sea surface temperature data.

Icelandic waters have been well studied and a good picture of long-term changes in the hydrography of the region has accumulated (e.g. Stefánsson and Jakobsson, 1989; Malmberg and Kristmannsson, 1992; Stefánsson and Ólafsson, 1991). Stefánsson and Ólafsson (1991) summarized the available information on long-term

changes in the hydrographic conditions of Icelandic waters as follows:

- before 1965 (starting in the 1920s), the temperature of the water around Iceland was high and Atlantic Water influx was large;

- between 1965 and 1971 there was a negligible inflow of Atlantic Water onto the shelf north of Iceland and a strong Polar Water influence over the entire North Icelandic area;
- since 1972, Atlantic Water and Polar Water have dominated alternately in periods of 2–4 years, but the degree of Atlantic Water inflow witnessed between 1952 and 1965 has never been attained since.

Materials and methods

Data for the present analysis were collected during annual cruises under the auspices of the Marine Research Institute in Iceland between 1960 and 1996, mostly during May and June. Spatial coverage varied between years (Figure 2). In the early 1960s, only the northwestern area was covered. From 1964, data were collected farther west and north, with particularly dense coverage in 1966 and 1967, when efforts focused on the movements of the Norwegian spring spawning herring. Since 1971, data have been collected along transects all around Iceland and coverage has been more regular and representative of the whole area. Between 1961 and 1991 a standard Hensen net was used for the zooplankton sampling, but from 1992 to 1996 samples were taken with a WP-2 net.

The Hensen and WP-2 nets had opening diameters of 73 and 57 cm, respectively, and both had a mesh aperture of 200 µm. The samples were taken in vertical hauls from 50 m to the surface or from near the bottom to the surface in places where it was shallower than 50 m. Prior to the measurement of displacement volume, large animals such as coelenterates and ctenophores were removed from the samples. The samples were then analysed according to the "short-cut method" (Einarsson, 1956; Hallgrimsson, 1958). With this method, the displacement volume of the zooplankton within each netted sample is measured and a random subsample of approximately 100 animals removed and identified to the lowest taxonomic level possible. Displacement volumes were standardized to zooplankton displaced volume per cubic metre of seawater filtered. In all, 43 constituent species and groups were identified and counted. Some of the groups are wide-ranging aggregations such as "cirripede larvae"; others are recorded to species level. The two most common copepods in the samples, *Calanus finmarchicus* and *C. hyperboreus*, were resolved into eight population categories: nauplii, copepodite stages 1–5 and adult males and females.

Most of the data were collected during May or June (although in certain years other months were also sampled), and there is little information on seasonality. Therefore, throughout the current analysis, only data from May and June are analysed and presented.

Environmental time-series data are difficult to summarize because of changing interannual, seasonal, and spatial patterns (Broekhuizen and McKenzie, 1995; Beare and McKenzie, 1999a,b). For the current purpose, the Icelandic data were examined in two different ways, allowing a picture of change in the zooplankton populations to be constructed. First, the data were divided into three fairly homogeneous subregions with respect to hydrographic conditions [Figure 1(b)]: southwest (SW), north (N), and northeast (NE). Then time-dependence (dependence on year) of the data within each subregion was modelled. Subsequently, the effect of location on the data was considered in more detail. To do this, all data were summarized by modelling the relevant response variable as a simultaneous three-dimensional smooth function of location (longitude, latitude) and time (year).

It is worth stressing here that the only information available to the authors for each station sample are displacement volume and proportion of individual zooplankton taxa from each of the random samples. It is not known exactly how many animals of each taxa there were in each sample. Unfortunately, statistical science cannot compensate for this shortfall, but this does not prevent us from trying to extract and summarize the available information.

Displacement volumes

The dependence of displacement volume on year (1960–1996) within each of the three locations was modelled using standard linear models with natural spline functions (de Boor, 1978) for the non-linear component (Model 1).

$$\text{Log}_e(\text{DV}) = \beta_0 + S(\text{year}) + \varepsilon \tag{1}$$

A straightforward log-transformation of the displaced volumes produced acceptably symmetrical data; zeros are infrequent. The spatio-temporal dependence of the displaced volumes was summarized using local regression techniques (Venables and Ripley, 1994; Kaluzny *et al.*, 1998), displaced volumes being modelled simultaneously as a three-dimensional smooth function of year, longitude, and latitude (Model 2).

$$\text{Log}_e(\text{DV}) = \beta_0 + L(\text{latitude, longitude, year}) + \varepsilon \tag{2}$$

Model selection was done by manually fitting the data to successively more complex models until a sensible balance was achieved between the two extremes of over- and underfitting. For example, to obtain a model for dependence on year for the displaced volume data in the northeastern subregion, seven models with increasing degrees of freedom in the natural spline function were fitted until the successive reductions in variance were no longer significant. At all times the standard statistical

Figure 2. Sample coverage (May and June) around Iceland between 1960 and 1996. Circles denote samples with a displaced volume measurement, dots samples that were further analysed using the short-cut method and for which more detailed information on proportions of each taxa or life-history stage is available.

Table 1. Comparison of regression models A–D for the displaced volume data in the northeastern subregion (S is the natural spline function).

Terms	Residual degrees of freedom	Residual sum of squares	Test degrees of freedom	Sum of squares	F-value	p(F)
A. 1	33	367.8				
B. Year	31	278.1	1	89.77	13.89	0.0009
C. S (Year, 2)	32	244.3	1	33.77	5.23	0.0307
D. S (Year, 3)	30	236.9	1	7.36	1.14	0.2956

Table 2. Comparison of regression models C and E for the displaced volume data in the northeastern subregion (S is the natural spline function).

Terms	Residual degrees of freedom	Residual sum of squares	Test degrees of freedom	Sum of squares	F-value	p(F)
C. S (Year, 2)	32	244.3	1	33.77	5.23	
E. S (Year, 6)	27	149.6	1	94.66	3.66	0.0170

rule of parsimony, i.e. the simplest model possible is selected, was adopted.

According to Table 1, inclusion of the year term causes a significant (p=0.0009) reduction in residual sum of squares (RSS) over the fitting of the Null Model, i.e. a slope or gradient term for year is better than the mean or average displaced volume. Similarly, a natural spline function with two degrees of freedom (d.f.) causes a further significant reduction in RSS from 278.1 to 244.3 (p=0.0307). A natural spline function with 3 d.f., however, is not significantly better than the natural spline with 2 d.f. (p=0.2956). After experimentation, a spline function with 6 d.f. was eventually chosen by the authors because a comparison with 2 and 6 d.f. causes a significant reduction in RSS from 244.3 to 149.6 at a cost of only 4 d.f. (see Table 2). Model E (Table 2), with 6 d.f. in the spline function, has an R^2 value of 51%. Examination of the residuals also indicated that the model was acceptable. The output from this model is displayed in Figure 3.

Whether the model was a simple linear model (LM), as above, a Generalized Linear Model (GLM) for binomial data, a Local Regression Model (LRM) or a Generalized Additive Model (GAM), the most appropriate model was selected using basically analogous procedures to those described above for the simple case of a linear model. It should be noted that the above is a linear model despite the fact that the natural spline terms are clearly non-linear. This is because the terms enter the model equation linearly.

In statistics, the term "fit" is used to describe literally how close a modelled value is to the original data. A well-fitting model, however, is not necessarily the best.

In biological applications where data are often sparse, skew, or missing, a model that misses most of the data but that captures the salient patterns or trends is often the most useful. In this paper we assessed the "fit" of each model carefully using visual (residuals), statistical, and scientific criteria. Given the characteristics of these data (short-cut method, sparseness, etc.) it is difficult to see how we could sensibly do more. As an example, consider the displaced volume data in Figure 3. The points are mean displaced volumes per year. We could easily get a model to pass through each data point by fitting an n-1 polynomial function; the R^2 would then be 100%. Such a model would, however, be poor despite "fitting" well. Our goal here is to summarize complex data and not to recreate them, so we should opt for a simpler function (the spline smoother), which has only 6 d.f. but nevertheless captures the important aspects of the long-term trend adequately.

Indices

The Icelandic data are difficult to summarize, and there are many different ways to do it. Here, one scientifically useful possibility is described. There are 43 different taxa for which percentage (proportion) of taxa within a subsample are available for May and June, 1960–1996. A common technique for reducing the dimensionality of such multivariate, time-dependent data is to build index numbers. These can be extremely useful summaries, especially for assessing change.

Three simple indices were constructed by summation of the proportions from specific groups of the Icelandic taxa. Each index was intended to define the zooplankton
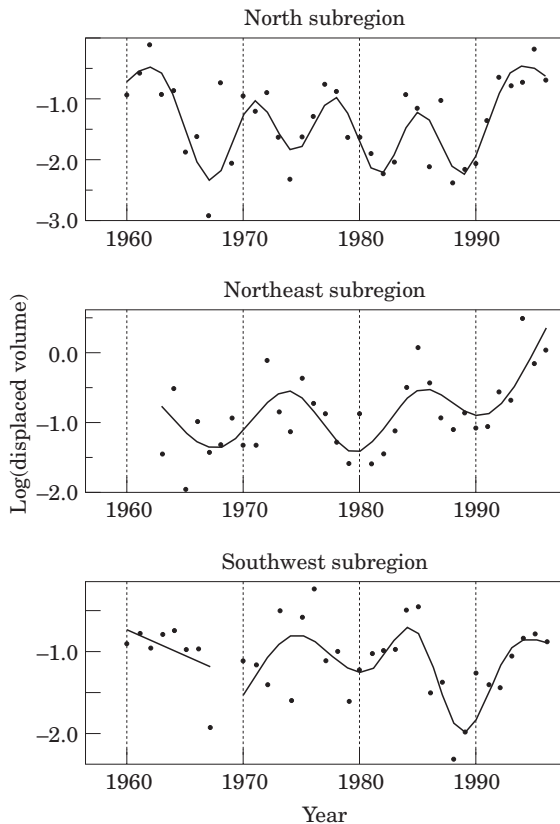
Figure 3. Temporal change in average zooplankton logged displaced volumes (ml m^{-3}) in May and June in each subregion. Points are logged average displaced volumes in each subregion per year. Solid lines are the output from three linear models fitted to the data with natural spline functions (see Model 1). Multiple R^2 values are 76.2% (northern subregion), 59.3% (northeast subregion) and, for the two separate models used for the southwest subregion, 26% (1960–1967) and 51.9% (1970–1996).

fauna of a particular water type. The notion that planktonic "indicator species" can adequately characterize different water masses is accepted, and the concept has a long history (Russell, 1935, 1939, 1952; Fraser, 1962, 1965).

The Atlantic index involves only those species most common in water of an Atlantic type; it comprised C1–5 and adult *Calanus finmarchicus* and all population categories of *Metridia lucens*. The Arctic index is the proportion of species with Arctic biogeographic affinities in each subsample and incorporates C1–5 and adult *C. hyperboreus* and all population categories of *Metridia longa*. Finally, the Coastal index represents those taxa tending to be commonest in shallow, inshore waters and was composed of decapod and cirrepede larvae and the inshore copepod *Temora longicornis*. The sum of the proportions of Atlantic, Arctic, and Coastal species does not necessarily sum to unity, because some of the taxa

recorded during the surveys (e.g. "chaetognaths") could not readily be assigned to any specific water type.

The temporal dependencies of these indices (basically proportions) were modelled using GLMS (McCullagh and Nelder, 1983; Beare and McKenzie, 1999a,b) and the spatiotemporal dependence was modelled using GAMs (Hastie and Tibshirani, 1990; Borchers *et al.*, 1997a,b; Maravelias and Reid, 1997). GLMs and GAMs were used because standard linear models are inappropriate for modelling proportion data (Lindsey, 1995).

Consider an Atlantic species that constitutes 40% of the individuals within a subsample. This quantity can be translated into 40 "successes" and 60 "failures" and the data are then binomial, a standard parametric distribution that can be modelled stochastically on the logit scale (McCullagh and Nelder, 1983).

Variables of year, longitude, and latitude only were considered as predictor variables, although others may well be important. In Model 3 (a GLM), the function used to describe the shape of the data was a natural spline function, whereas in Model 4 (a GAM), the three-dimensional smooth function fitted simultaneously to longitude, latitude, and year was fitted using a locally weighted regression function.

$$\mathrm{Log}_e(p/1-p)=\beta_0+S(\mathrm{year})+\varepsilon \qquad (3)$$

$$\mathrm{Log}_e(p/1-p)=\beta_0+S(\mathrm{latitude, longitude, year})+\varepsilon \qquad (4)$$

The flexibility (or degrees of freedom) used in the smoothing functions were selected by analysis of variance tests (linear models, e.g. Tables 1, 2) or analysis of deviance tests (GLMs and GAMs) on groups of nested models (Venables and Ripley, 1994). The complexity (bendiness) of the averaging (or smoothing) functions used was increased incrementally until the reduction in residual variance (LMs) or residual deviance (GLMs and GAMs) was no longer statistically significant. In Models 1–4 above, β_0 denotes an intercept term, S is a natural spline function, and L a three-dimensional LOWESS smooth term.

Sea surface temperature

Data for sea surface temperature (SST) from January 1958 to December 1992 for ten point locations around Iceland were obtained from the Comprehensive Ocean Atmosphere Dataset at http://ingrid.ldgo.columbia.edu/sources/.coads/ with the aim of making a visual qualitative comparison between them and the Icelandic zooplankton data. The SST data were analysed using standard time-series decomposition techniques (see Broekhuizen and McKenzie, 1995; Beare *et al.*, 1998; Beare and McKenzie, 1999a,b) that aim to summarize salient long-term and seasonal signals.

Results

Displacement volumes

Time-dependence was modelled by fitting log-transformed average displaced volumes (DV) per sub-region to natural spline functions of the variable "Year" (Model 1). May and June zooplankton DVs fluctuated considerably and were well correlated among the three subregions (Figure 3). The DVs collapsed between 1960 and the late 1960s in all three subregions. They then peaked in the mid-1970s, fell to a low around 1980, rose again to a new peak in the mid-1980s, fell to a further trough in the late 1980s, and then rose again in all three areas to maxima in 1996.

Spatiotemporal change was assessed by fitting the DVs to a three-dimensional locally weighted regression function of "Longitude", "Latitude", and "Year" (Model 2). The results for eight arbitrarily selected years (1961, 1966, 1971, 1976, 1981, 1986, 1991, and 1996) from the model output are displayed in Figure 4. DVs tended to be highest in the northeast and lowest in the north. In the early 1960s there were unusually high DVs of zooplankton over the North Icelandic Shelf (Figure 4).

Indices

The temporal dependencies of each index within the three subregions are displayed in Figure 5. The solid lines are the output from GLMs for binomial data fitted to the probability of recording a member of each group within each subsample (Model 3). The predictor variable in each case is a function of year and the non-linearity is modelled using natural spline functions. Model selection is analogous to that outlined in the Methods section (see Tables 1 and 2), except that reductions in deviance and the appropriate chi-squared tests were used instead of reductions in variance and F-tests. Residual deviance is analogous to the residual sum of squares quantity estimated during ordinary least-squares modelling. The dotted line is a summary spline smoother fitted directly through all of the raw data and was done for comparative purposes only. The points in Figure 5 are the raw data, i.e. the proportions of animals constituting each index within each subsample. For some years, particularly the period 1969–1973, there are few data available (Figure 5) as a result of the composition of samples not being analysed, and only DV measurements are available. The GLMs were fitted to the two separate periods that had reasonable temporal sampling coverage.

It is also worth reiterating again here that the proportions of taxa within subsamples that constitute the three indices do not necessarily reflect total abundance. The authors are fully aware of this limitation. Unfortunately, that information is unavailable within the Icelandic

Spring Survey data because of the manner in which they are collected. Nevertheless, we believe that the indices are realistic proxies for abundance. For example, if the proportion of *C. finmarchicus* within a subsample falls, then it is highly likely that its overall abundance did too, but we cannot actually know this for certain.

Atlantic index (Calanus finmarchicus, Metridia lucens)
The Atlantic index ranged between 25% and 80%, and was broadly similar in all three of the subregions, indicating that Atlantic species generally dominated all of the samples. It is difficult to compare trend patterns across the subregions during the period 1960–1969 because the time–series are short and non-contemporaneous (Figure 5).

During the 1960s there was a fall in the northern subregion from ca. 80% Atlantic taxa per subsample in 1960 to <40% in 1969, whereas in the northeast there was a reduction between 1963 and 1965 and a rise thereafter (Figure 5). During the 1960s, only five years of data (1960–1964) were available for the southwest subregion and they indicate a slight increase in the proportion of Atlantic species per subsample (Figure 5). Data coverage in all three subregions improved after 1973, but there was a period in the north in the early 1980s (Figure 5) with no data. In all three subregions (N, NE, and SW) the Atlantic indices exhibited similar patterns after 1973, i.e. a long-term overall fall. A small recovery was seen in the northeast in the mid-1980s, after which the decline continued.

Arctic index (Calanus hyperboreus, Metridia longa)
There were also sharp interannual changes in the proportion of Arctic species in each subsample; these ranged from 2% to 18%. The value of the Arctic index was generally highest in the northeast and very low in the southwest (Figure 5). In the first decade (1960–1970) its value rose in the north and northeast but fell slightly (1960–1964) in the southwest. Between 1974 and 1996 it generally increased in the northeast and north, but the time-series are not correlated at all times throughout this period (Figure 5). In the north, the Arctic index fell gradually between 1974 and ca. 1988, from which time very sharp upward trends have continued into 1996, whereas in the northeast there was no clear fall in the late 1980s and the index rose steadily throughout the same period.

Coastal index (decapod larvae, cirripede larvae, and Temora longicornis)
Long-term trends in proportions of coastal taxa fluctuated irregularly at between 1% and 20% each year and were generally greatest in the southwest subregion, where proportions increased overall between 1960 and 1996 (Figure 5). In the north and northeast, pronounced maxima were recorded in 1980, whereas in the southwest
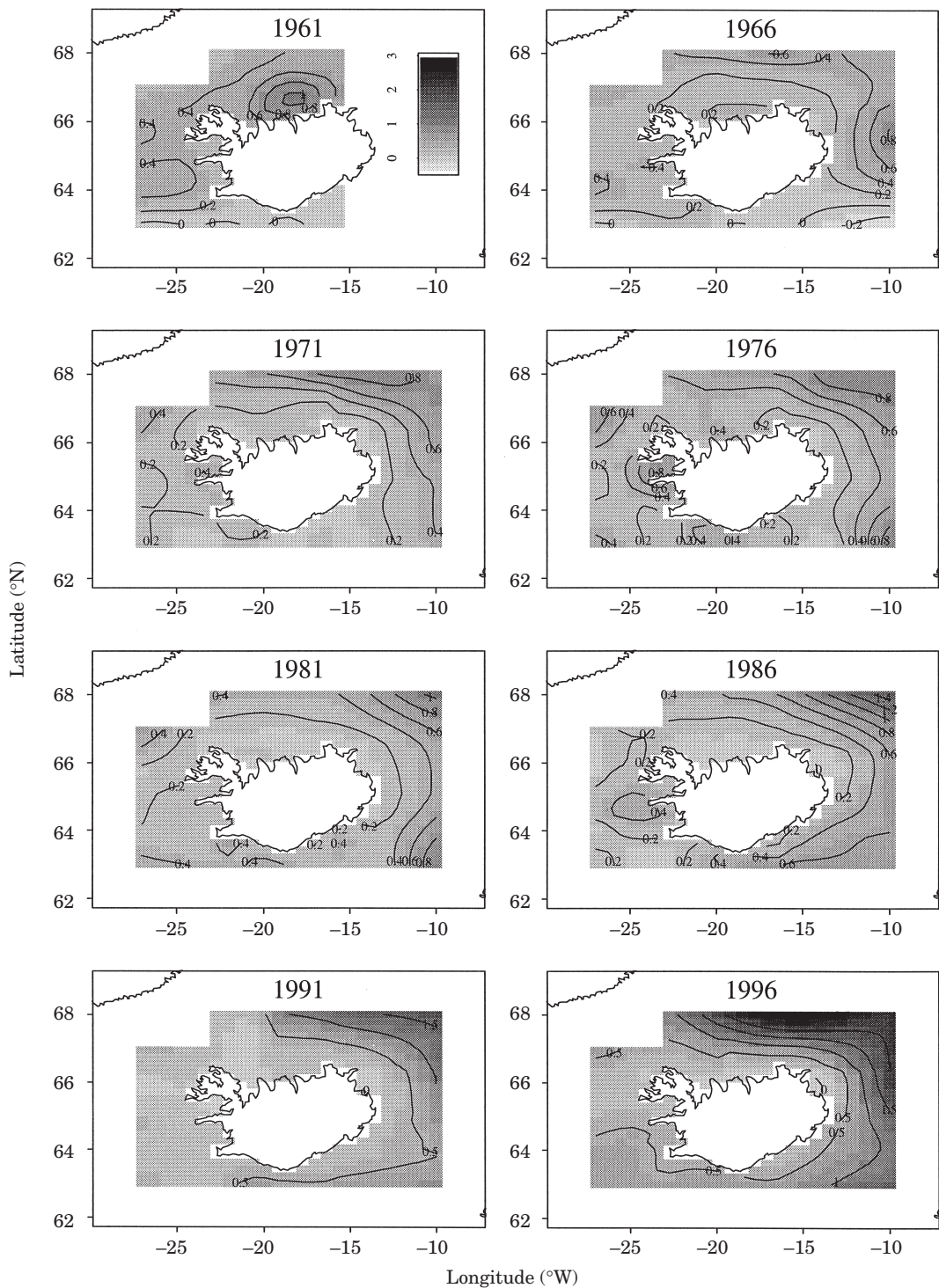
Figure 4. Spatiotemporal change in average displaced volume around the coast of Iceland in May and June. Numbers are millilitres of zooplankton per sample. The displaced volumes were fitted without transformation to longitude, latitude, and year with a three-dimensional locally weighted regression smoother (see Model 2).
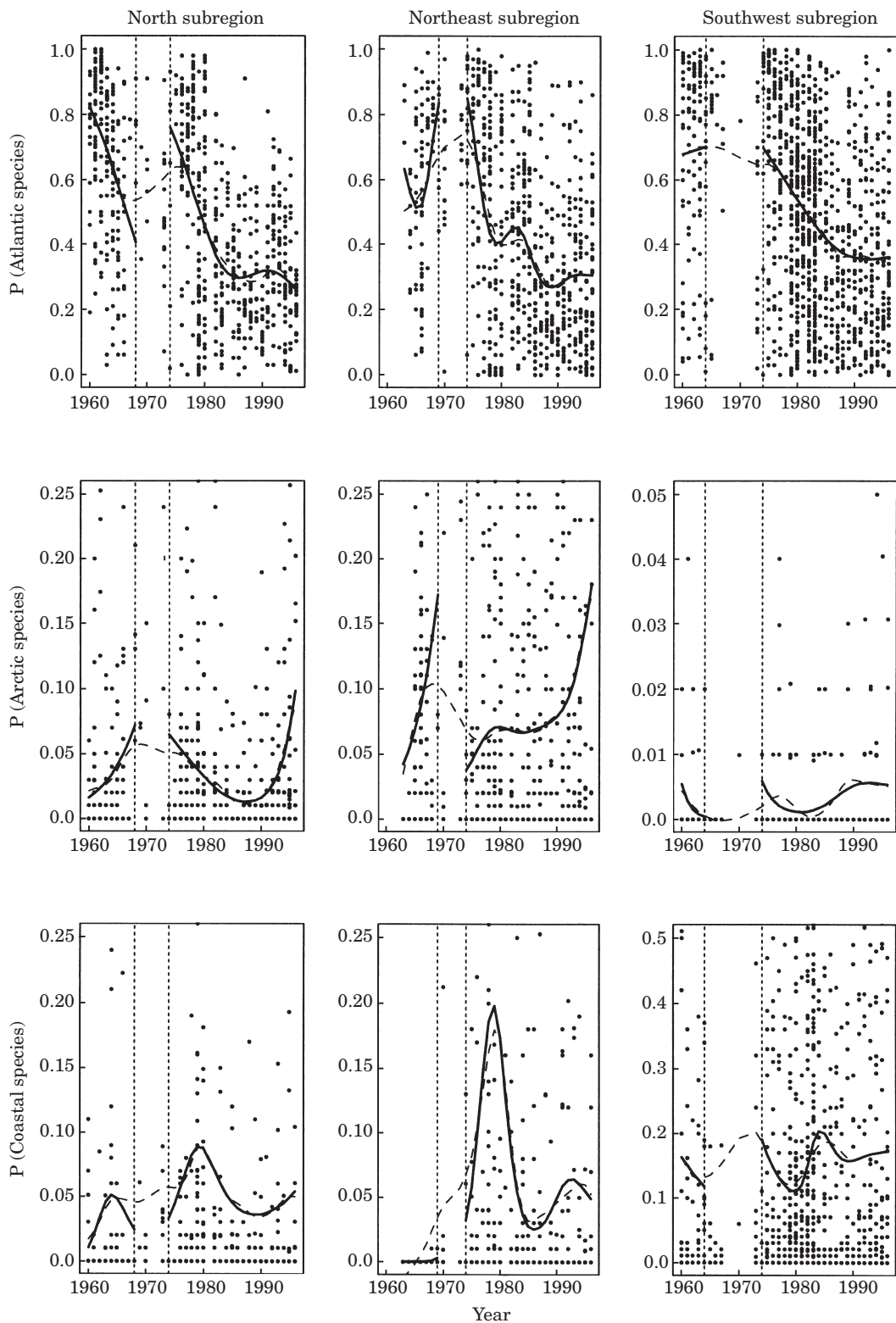
Figure 5. Temporal change in the average (top row) Atlantic index, (middle row) Arctic index, and (bottom row) Coastal index. Solid lines are output from GLMs for binomial data fitted to available subsets of each time-series (see Model 3); broken lines are output from a spline smoother fitted to the data. The points are the raw data. The vertical lines define periods when few data were available and for which formal models were not fitted.

a minimum was seen in that year. The peak Coastal index in the southwest subregion was recorded later on in the decade during the mid-1980s (Figure 5).

Spatiotemporal patterns

Spatiotemporal patterns were obtained by fitting GAMs to smooth functions of the probability of recording any member of each index within each subsample (Model 4). Selection of the amount of smoothing was done in an analogous manner to that described above. Indices of the type used in the present analysis appear to map the relevant water types well (Ali, 1996), and the overall approach appears to be a useful way to summarize multivariate zooplankton data. Figure 6 displays the spatial distribution of the Atlantic index. Dominated by *C. finmarchicus*, the index increases generally offshore (Figure 6) and its magnitude strongly reflects the trend of Atlantic Water surrounding Iceland being more prevalent south and west (Astthorsson and Gislason, 1995). In the early 1960s the Atlantic index was notably high over the North Icelandic Shelf and the tongue of the northern branch of the Irminger Current can clearly be discerned (Figure 6). The importance of Atlantic species over Icelandic Shelf waters in general has fallen (Figure 6). The greater relative abundance of Atlantic species southwest of Iceland compared to the other areas may indicate that they are advected onto the shelf from the southwest (Gislason and Astthorsson, 2000).

The Arctic index exhibited a very different spatial distribution (Figure 7). Its value was very low (<2%) in the shallow coastal areas and also south and west of Iceland. In the northeast, however, it was relatively high, ranging from 10% to 50% of each sample. The most notable features of these data is the steep increase in the northeast since the 1960s (see also Figure 5).

The Coastal index is highest where the water is shallowest and was generally greater northwest of Iceland over the Greenland–Iceland Ridge and south-east of Iceland over the Iceland–Faroes Ridge. In the 1990s, unusually high values were recorded to the southwest (Figure 8) over the Reykjanes Ridge. We do not know any reasons for these spectacular fluctu-ations, but they could be linked simply to fluctuating seasonal timing of reproductive activity in the coastal populations.

Sea surface temperature

Long-term trends from the COADS SST data are dis-played in Figure 9 and there is considerable variability among them. It is colder in the north (67°N) than in the south (63°N), although missing values at 67°N prevent detailed interpretation, especially at 11°W. The most dramatic long-term changes were in the northwest at 67°N 27°W, where average SSTs fell from between

ca. 4°C and 8°C in the early 1960s to between ca. 0°C and 3°C in 1992 (Figure 9). There were particularly sudden declines in the mid-1960s, mid-1970s, and mid-1980s. It is regrettable that the data are so sparse for the early 1960s at 67°N 11°W, because there is an indication of rather anomalous strongly rising temperatures there (Figure 9). Farther south, at 63°N, the SSTs were more stable than at 67°N. Temperature declined gradually between 1958 and the mid to late 1970s, rose thereafter and a trough was observed at all five locations between ca. 1974 and 1980 (Figure 9). Interestingly, as of 1992, the last year for which data were available, the high SSTs of the 1960s have not been reattained in any location except at 67°N 11°W, where temperatures have risen steadily since the late 1950s.

Discussion

The Atlantic index has fallen in most areas. This obser-vation might possibly be due to a change in the timing of the sampling cruises or possibly to changes in the timing of the annual seasonal cycle (Beare *et al.*, 1998). In Figure 10, the time of year (Julian Day) of each cruise is plotted against year for the three subregions. The smoothing filter fitted to the data summarizes the salient features of the long-term trend. In the north and north-east subregions, the cruises have become progressively earlier in the year with particularly early cruises carried out in 1966, 1967, 1979, and 1980. In the north, samples tended to be taken around late May or early June, whereas in the northeast most were taken between early and mid-June. In the southwest, on the other hand, most of the samples was taken earlier in the year from the beginning of May to mid-June (Figure 10), although there is no evidence of a persistent negative or positive long-term trend in the area. These observations are clearly cause for concern because they may reflect bias in the sampled data.

Seasonal cycles of activity (feeding, growth, reproduc-tion) in marine fauna can be subject to large interannual fluctuations in timing, amplitude, and shape (Beare and McKenzie, 1999a,b), so even if all Icelandic data were taken on the same day each year, there might still be problems of interpretation. It is not known how severely this problem has affected our results and, in the absence of year-round data, it will never be known. There are certainly no statistical solutions to such problems. We can easily fit a "significant" regression model to the time-series data in Figure 5, for example, but the value of such "significance" in the absence of any data for the period 1969–1974, and in the presence of serial correlation, would be open to debate. Any pattern might conceivably have been witnessed between 1969 and 1974 had data been collected and made available. Never-theless, the Icelandic Spring Survey Data are an
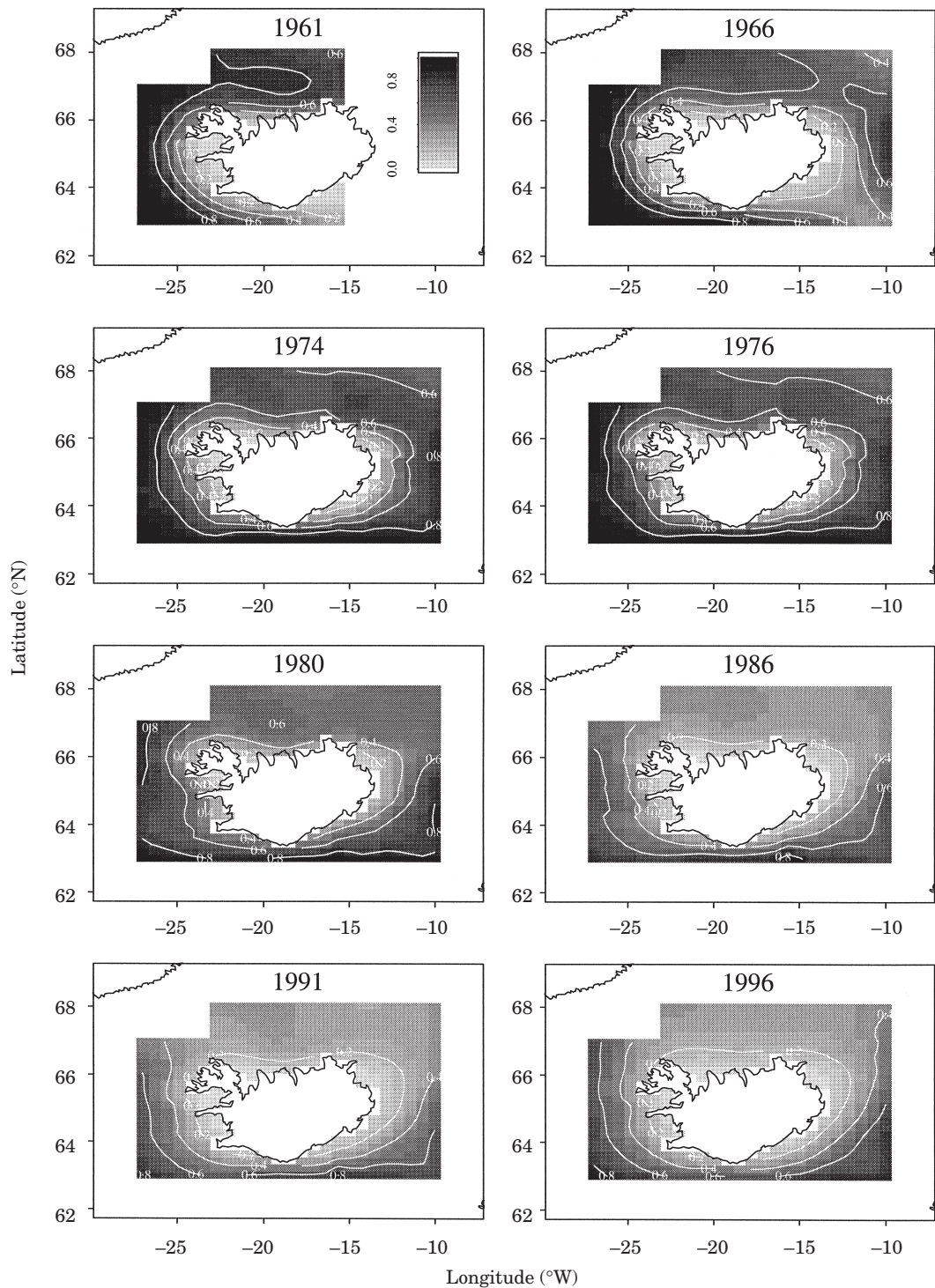
Figure 6. Spatiotemporal change in the average Atlantic index around Iceland in May and June between 1960 and 1996. Proportions of Atlantic species per subsample were fitted to longitude, latitude, and year with a three-dimensional smoothing function within the framework of a GAM for binomial data (see Model 4).
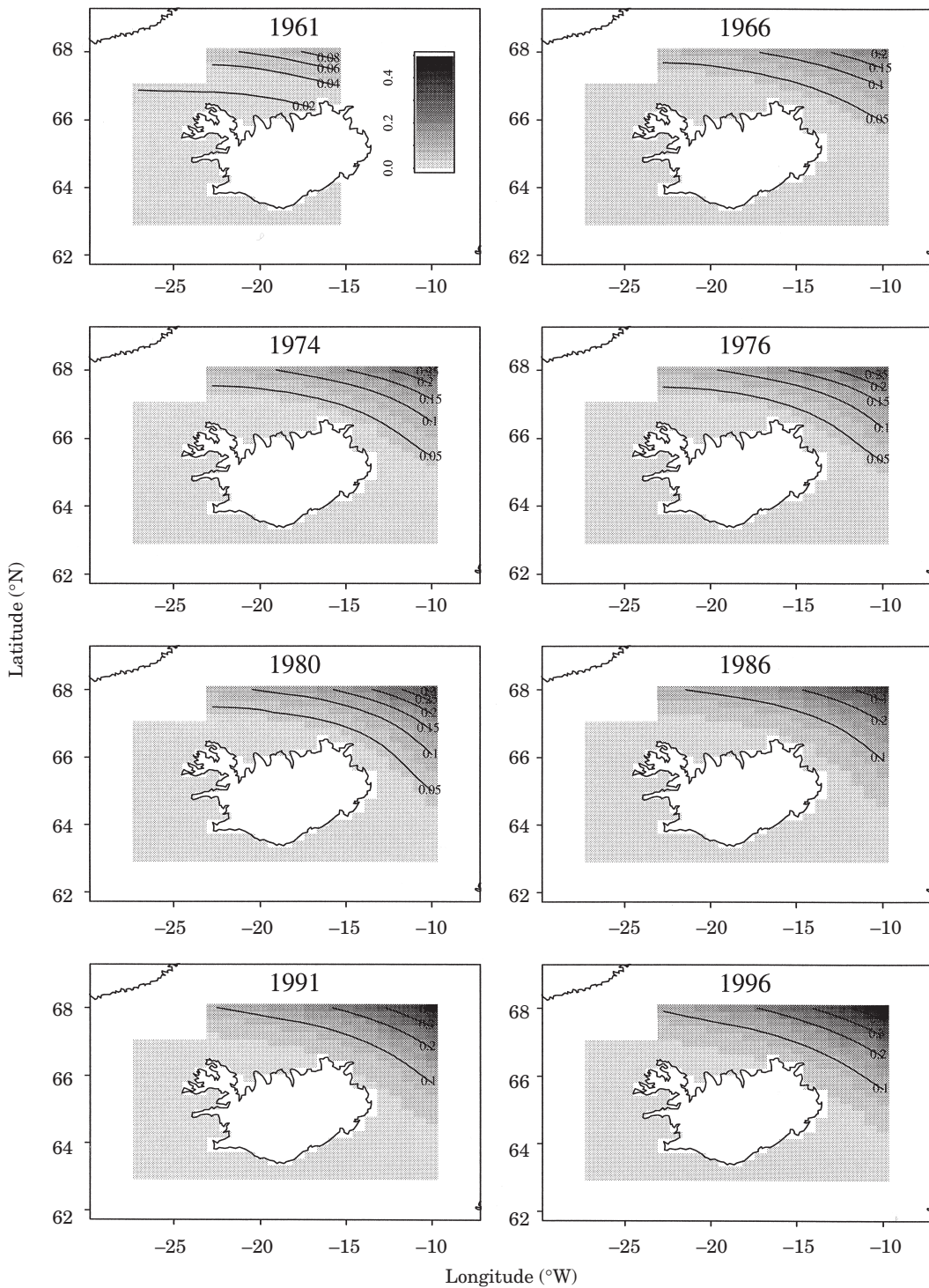
Figure 7. Spatiotemporal change in the average Arctic index around Iceland in May and June between 1960 and 1996. Proportions of Arctic species per subsample were fitted to longitude, latitude, and year with a three-dimensional smoothing function within the framework of a GAM for binomial data (see Model 4).
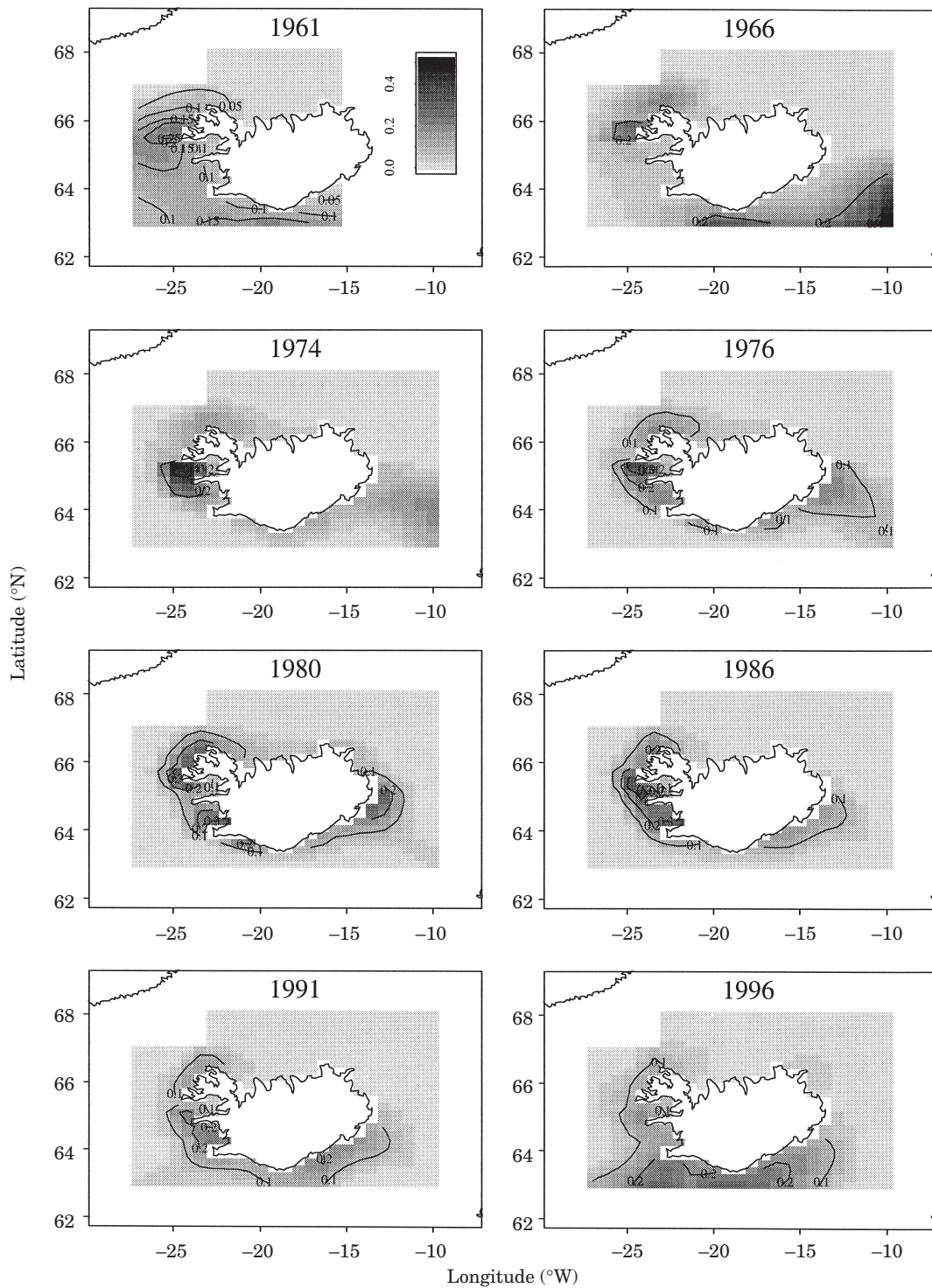
Figure 8. Spatiotemporal change in the average Coastal index around Iceland in May and June between 1960 and 1996. Proportions of Coastal species per subsample were fitted to longitude, latitude, and year with a three-dimensional smoothing function within the framework of a GAM for binomial data (see Model 4).
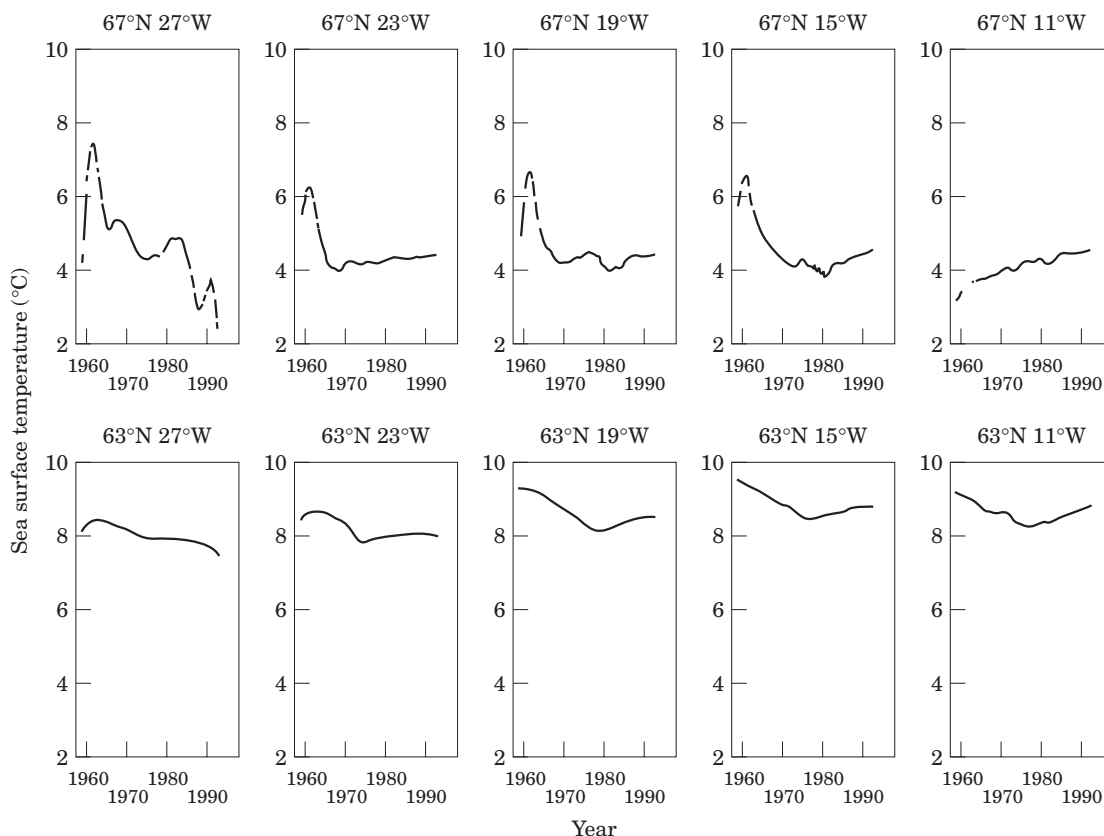
Figure 9. Long-term change in sea surface temperature between 1958 and 1992 at 10 locations around the coast of Iceland (see Figure 1b). The trends were estimated using a variable-span smooth function of temperature against absolute monthly time. The smoother (supsmu) is available with the S-plus software package.

internationally important scientific resource and such considerations should not prevent us from exploring them and reporting the results carefully.

After a thorough examination of the data (e.g. we tried many different spatial aggregations, splitting May and June data and investigating them independently), however, we remain convinced that the relative abundance of species with Atlantic affinity has decreased in May and June over the Icelandic Shelf areas, whereas that of Arctic species has increased in deep water northeast of Iceland (Figure 5). One reason for this belief is because the respective long-term trend signals from the data are so strong that they are seen regardless of how the data are aggregated or transformed prior to analysis. Another is that the long-term trends are consistent with the pattern that could be anticipated from examination of the long-term trends in hydrographic data (e.g. Malmberg and Kristmannsson, 1992).

One particular observation that has probably been caused by the progressively earlier timings of the Icelandic cruises is the increasing prevalence of the copepod nauplii and *C. finmarchicus* C1–2 noted since the early 1980s. Work carried out by Gislason and

Astthorsson (1996, 1998a,b) shows that, during April and May, after hatching of the eggs produced by the overwintering generation, C1–3 dominate the *C. finmarchicus* population. Copepod nauplii and *C. finmarchicus* C1–2 increased markedly in all areas around 1980, a year of exceptionally early cruises in all three subregions (Figure 10).

If the results described above reflect real changes in relative abundance during May and June and are not a product of changing seasonality and/or non-random sampling, the question is what caused them and what else do we know about the zooplankton ecology of the area? During the TASC (Trans-Atlantic Study of *Calanus finmarchicus*) project, Continuous Plankton Recorder (CPR) data were also made available to the authors for *C. finmarchicus* C5 and C6 in areas south of Iceland every month between 1958 and 1996 (e.g. Colebrook, 1982, 1984a,b). These data allow estimates of long-term trends to be made, while recently developed modelling techniques (Beare and McKenzie, 1999a,b) permit the impact of unstable seasonality to be assessed. The results of an analysis of CPR data collected immediately south of Iceland have also been described
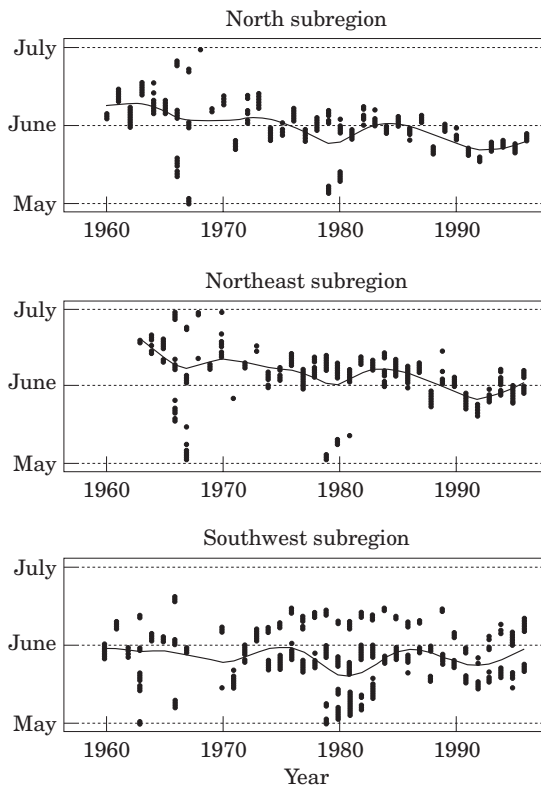
Figure 10. Timing of Icelandic Spring Surveys between 1960 and 1996 in the three subregions. Long-term change is highlighted using a variable-span smooth function available with S-plus (supsmu).

by Planque and Ibanez (1997). The main conclusion from their analysis and from our own more recent analysis of the CPR data is that the long-term abundance of *C. finmarchicus* has risen overall in that area during recent years. When individual months are examined it is clear that abundance during April has fallen between 1958 and 1996 and that the increase has been focused on the months of May and June. This corresponds to the general increase in DV of total zooplankton recorded here (Figures 3 and 4). However, at the same time our study shows that the relative abundance of *C. finmarchicus* from the Icelandic Spring Survey data has generally been decreasing.

The differences between Icelandic Spring Survey and CPR data are difficult to explain. The differences may be related to the different sampling depths of the two programmes. The Icelandic data are integrated samples from the upper 50 m, whereas the CPR data are restricted to a narrow depth layer near the surface (ca. 7 m; Warner and Hays, 1994). The difference may therefore reflect a long-term change in the vertical ontogenetic migration pattern of *C. finmarchicus*. Furthermore, it should be noted that the CPR and Icelandic

Spring Surveys tend not to be close together in space. Most of the CPR data cover the area south of 63.5°N, whereas the majority of the Icelandic data were collected north of this. Further, it is possible that different localities might exhibit different long-term trends in the abundance of a single species of zooplankton, and this is what we believe may be happening. If more extensive CPR data were available farther north and closer to the coasts of Iceland for May and June, we would expect also to have seen declining abundances of *C. finmarchicus* and other Atlantic taxa between 1958 and 1996 in those data.

The key to providing a mechanistic explanation for the fall in the relative abundance of Atlantic taxa and the rise in abundance of Arctic taxa probably lies in the fluctuating influence of the North Atlantic Current system on the entire ecology of the North Atlantic Ocean. It is well established that Atlantic inflow to the North Icelandic Shelf was greater in the 1960s, and that its influence there has not been re-established (Stefánsson and Ólafsson, 1991) in more recent years. Whether the reduction in Atlantic inflow caused the fall in the Atlantic index by reducing the advective supply of animals from overwintering offshelf locations, or whether a declining Atlantic influence results in a reduction in food availability to zooplankton by changing nutrient (Stefánsson and Ólafsson, 1991), temperature, and primary production (Thordardottir, 1984) relationships is not known. What is certain is that Atlantic inflow and "influence" genuinely declined north of Iceland during the mid-1960s (Astthorsson *et al.*, 1983; Astthorsson and Gislason, 1995) and that it has severely affected the zooplanktonic community and the feeding migrations of the herring (Astthorsson *et al.*, 1983; Jakobsson, 1985; Stefánsson and Jakobsson, 1989).

North and northeast of Iceland, the Arctic index increased between 1960 and 1996 (Figures 5 and 7). The SST data (Figure 9) indicate an overall fall that might favour *C. hyperboreus*. Northeast of Iceland, where the increase of the Arctic index is most pronounced (Figures 5 and 7) SSTs, perversely, have risen slightly since the mid-1960s. In this context, however, it is worth bearing in mind that the SSTs presented here may not necessarily reflect what is taking place in the entire water column. *C. hyperboreus* is a cold and deepwater species, and spends only a very limited part of its life cycle near the surface (OSA, unpublished).

Icelandic hydrographic observations in waters northeast of Iceland (East Icelandic Current) demonstrated a marked cooling during the period 1964–1971, when the East Icelandic Current changed from an ice-free Arctic Current to a Polar Current transporting and maintaining drift ice (Malmberg and Kristmannsson, 1992). Since 1971, the Icelandic data suggest that hydrographic conditions have fluctuated between warm and cold periods with a 2–3 year periodicity (Malmberg and

Kristmannsson, 1992; Anon., 1999) rather than the steady long-term temperature changes suggested by the time-series decompositions presented in Figure 9.

The spatial distributions of the three biological indices around Iceland generally reflect the distribution of water masses of different origin [cf. Figure 1(a) and Figures 5–8]. Therefore the Atlantic index (mainly *C. finmarchicus*) was generally highest offshore south and west of Iceland, which may be taken as an indication that the offshore areas act as sources of *C. finmarchicus* for the shelf areas southwest of Iceland (Gislason and Astthorsson, 2000). On the other hand, the Arctic index (mainly *C. hyperboreus*) is generally highest northeast of Iceland, suggesting that *C. hyperboreus* was transported into the area by the cold East Greenland and East Icelandic Currents. Modelling the spatio-temporal movements of such biological indices may then ultimately provide useful insight into how long-term hydrometeorological change might actually be affecting oceanic ecosystems and, given the key location of Iceland at the junction between warm Atlantic and cold Arctic water, be useful for assessing the progress of climate change.

Acknowledgements

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