THIS PAPER NOT TO BE CITED WITHOUT PRIOR REFERENCE TO THE AUTHORS

International Council for
the Exploration of the Sea

ICES CM 1986/C:37
Hydrography Committee
Ref: Biological Oceanography Committee
Theme Session Q

NORTH WINDS AND PRODUCTION IN THE EASTERN NORTH ATLANTIC

R R Dickson
Ministry of Agriculture, Fisheries and Food,
Directorate of Fisheries Research, Fisheries Laboratory,
Lowestoft, Suffolk NR33 OHT, UK

P M Kelly
Climatic Research Unit, School of Environmental Sciences, University of
East Anglia, Norwich, Norfolk NR4 7TJ, UK

J M Colebrook
Natural Environment Research Council,
Institute for Marine Environmental Research,
Prospect Place, The Hoe, Plymouth, Devon PL1 3DH, UK

W S Wooster
Institute for Marine Studies HF-05, University of Washington, Seattle WA
98195, USA

D H Cushing
198 Yarmouth Road, Lowestoft, Suffolk NR32 4AB, UK

ABSTRACT

A long-term increase in northerly wind component over the eastern North Atlantic and European Seaboard between 1950 and 1980 is associated both with a decline of phytoplankton and zooplankton biomass in sea-areas around the British Isles, and with an increase in upwelling intensity along the Iberian west coast. The implications for certain pelagic fish stocks in the area are assessed.

RÉSUMÉ

L'augmentation à long terme de la composante vent du Nord sur l'Atlantique du nord-est ainsi que sur les eaux côtières de l'Europe de 1950 à 1980 est associée à une baisse des biomasses du phytoplancton et du zooplancton dans les zones marines qui entourent les îles britanniques, ainsi qu'à une augmentation de l'intensité de l'upwelling le long de la côte ouest de la péninsule ibérique. On a évalué les implications pour certains stocks de poisson pélagique de la région.

INTRODUCTION

Within the continuum of change, at all time scales, that exists in both the physical environment and the biota, our best chance of identifying causal relationships and mechanisms occurs during extreme events or during periods of long-sustained trend. Even then, these interrelationships are unlikely to be simple especially when, in the case of fish stocks, the observed fluctuations are likely to depend on changes in the environment, the primary and secondary production cycles and on fishing activity.

The present paper was motivated by an apparent co-linearity of trend in two production-related parameters in the eastern North Atlantic over the period 1948-83 (Figure 1); first, the long-term decline from 1950-1980, followed by a partial recovery, in the first principal component for zooplankton of the annual fluctuations of abundance in 12 sea areas around the British Isles, identified from Continuous Plankton Recorder data by Colebrook et al (1984); second, a similar but inverse trend in upwelling index off the Portuguese coast in the months of April through September identified in an unpublished study by W. S. Wooster. In Figure 1 the general long-term trend in upwelling at the Portuguese coast is represented by the index for Porto (41°N; units are offshore Ekman transport in tonnes per second per 100 m width; note that y-axis scale is inverted so that upwelling increases, 1950-80, followed by a decrease).

Maximum entropy cross-spectral analysis confirms that the correlation of the two curves in Figure 1 is limited to the longest wavelengths (i.e. the trend) and not the high frequency variations. Second, it shows that the upwelling index is correlated with zooplankton trend in all of the 12 CPR sub-regions (Figure 2) but is best correlated with zooplankton trend in the western and southern North Sea (Areas B2, C2, C1, D2, D1), rather than the open ocean (D5, C5).

To support the view that these widely-separated patterns of change in upwelling and zooplankton are both separate manifestations of a single atmospheric "cause", it is clear that we must first demonstrate the existence of an accompanying change in the atmospheric circulation over the Eastern Atlantic with the following characteristics: it must be of large areal extent, long-sustained trend, meridional in orientation (to connect the two areas under discussion), and should include the months of key importance to the development of production in the sea.

To establish the months of greatest meridional - wind variation between the 1950's and 1970's over the eastern Atlantic, a northerly wind index was calculated from the mean pressure difference, 20°W minus 10°E, over the latitude interval 35°N to 65°N, and the monthly values of this index for the 1950's and 1970's are shown in Figure 3. While northerlies were generally stronger in the 1970's than the 1950's in almost every month from March to November, it is clear that the north wind intensification of the 1970's reached its greatest development in March and April - months of crucial importance to the initiation and development of production in the sea.

Figure 4 illustrates the mean hemispheric change in surface pressure, 1970's minus 1950's for the months of March-April. The increased northerly airflow sweeping the western European littoral from the North Sea to NW Africa in the 1970's (c.f. 1950's) is shown to be due to the establishment of an intense ridge over the eastern North Atlantic amounting to +4.7 mb in inter-decade pressure change (the largest change in the entire northern hemisphere in March-April), coupled with a lesser tendency towards anomalous troughing (-1 to -2 mb) in a meridional band from Scandinavia to the central Sahara. As a result an additional east-west pressure gradient of up to 6.5 mb (inter-decade mean) lay across the western European seaboard in the 1970's. [Significantly, Van de Kamp (1983) has reported a quasi-linear decrease in the north<u>ward</u> current component at the Light Vessel Noord Hinder in the Southern Bight of the North Sea, 1951-77 during this increased northerly airflow].

Figure 5 illustrates the <u>normal</u> seasonal occurrence of northerlies in the eastern Atlantic. In Figure 5a average monthly values of northerly wind index are calculated for the whole east Atlantic sector, 35°-65°N, 20°W-10°E over the period 1873-1981, while Figure 5b shows mean monthly values of curl and upwelling indices (driven by northerlies) for Porto over the period 1946-84. It is plain that both the local and regional northerlies share a common seasonality, each building to a peak in April-July as the Azores-Bermuda High intensifies and spreads towards the north and east.

Coupling this result to our earlier discussion, it is equally clear that the <u>anomalous</u> increase in northerlies over the eastern Atlantic in March-April between the 1950's and 1970's was simply an exaggeration of the <u>normal</u> seasonal trend towards increasing northerlies at this time of year. In other words the seasonal strengthening of the Azores-Bermuda High was earlier and more intense during the 1970's.

Finally, Figure 5c describes the trend in northerly wind index for April-September 1946-80 in the sector 35°-65°N, 20°W-10°E, confirming that the trend towards increased northerlies in spring and summer was a progressive one.

We have thus established that an atmospheric circulation change did exist over the eastern Atlantic with the required characteristics of scale, trend, orientation and seasonality to explain the colinearity of trends shown in Figure 1. It remains, however, to demonstrate plausible linking-mechanisms to the biota in each case.

CASE 1. <u>The trend in CPR zooplankton abundance in waters around the British Isles</u>

In detail the characteristics of this change appear to be as follows. First, the trend is not confined to the zooplankton (Figure 6: based on 12 areas, 24 species, 247 series) but is shared by the time trend in phyto-plankton abundance (12 areas, 24 species, 263 series). Second, of the 12 CPR standard areas which exhibit the decline in zooplankton abundance from the 1950's to 1970's, (Figure 7) the areas which show the most coherent commonality of trend among all 24 zooplankton species considered for each area are C4 and C2, flanking Britain to west and east (Figure 2b). Third, as a measure of the overall decline, Table 1 shows the mean abundance of Total Copepods in 1978-82 (lowest) as a percentage of the mean abundance in 1948-52 (highest).

Table 1. Ratio of mean Total Copepod abundance in 1978-82 cf 1948-52, for each CPR standard area, expressed as a percentage

	5	4	2	1
B	32	58	50	39
C	35	32	17	22
D	62	38	29	29

The greatest decline - to 17% of former abundance - is centred on the west central North Sea (C2), but the isopleths of "equal decline" appear to show some common alignment with the isopleths of increased northerly airflow (cf Figure 4). The question, of course, is how could an earlier intensification of the normal northerly wind progression in March-April have caused such a decline in zooplankton abundance?

The characteristics of the change (just described) provide two clues as to mechanism; first, they suggest that we are really seeking a change in the various controls on phytoplankton production rather than any direct effect of the environment on the zooplankton; second, since the plankton trends are observed in all 12 CPR areas which range over deep, intermediate and shallow water, exposed and semi-enclosed habitats from Rockall to Denmark and from the Faroes to Biscay, it is plain that the change in phytoplankton controls must be basic and regional in scope rather than specialised and site-specific (e.g. depending on local turbidity, wind-fetch etc).

There are essentially three candidate environmental controls on the initiation and development of primary production which are sufficiently basic to have regional effects under a broad-scale change in the wind regime; i.e. the effects of wind mixing, irradiance (cloud/solar radiation) and temperature. Of these we have no evidence for a progressive change in insolation in spring or of a sufficient change in ocean temperature but there is evidence for a regional and progressive change in wind mixing over the period in question.

Sverdrup's (1953) classic representation of the initiation of primary production at OWS MIKE in the spring of 1949, (reproduced as Figure 8) illustrates how sensitively primary production responds to the steady deepening of critical depth (Dcr) and to the less regular shallowing of the wind-mixed layer (Dm) in spring. Production begins whenever Dm < Dcr but in the early stages, the development of production is frequently interrupted by a succession of strong-wind events until, towards the end of May, strengthened insolation drives Dcr to "inaccessible" depths, while the establishment of the seasonal thermocline reduces the effectiveness of wind mixing. From that point onwards, production develops more smoothly, according to the ratio of compensation depth to depth of mixing $(\frac{Dc}{Dm})$. Since Dm participates in both of these relationships, it is clear that an increased strong-wind frequency in the critical spring months can lead not only to a delay in the initiation of production (a shortening of the production season), but also to a reduced rate of production - development thereafter (leading to a shallowing of the spring production peak).

There is fairly reliable evidence for an increasing trend in strong-wind frequency over the period 1950-80 in sea areas off NW Europe. Figure 9a and b, from Lamb and Weiss (1979) shows the rising trend in the incidence of winds > F8 for selected sites in the North Sea together with isopleths representing the percentage change in winds > F8 per decade from the 1950's to the 1970's; based on Jenkinsons Gale Index, Figure 6b of Lamb and Weiss (not shown here) indicates that a rising trend in the annual number of days of gale force winds also characterised the eastern Atlantic from the 1950's to the 1970's (50°-60°N, 0-10°W). Though the data of Lamb and Weiss are not stratified by season the analysis of mean (pressure gradient) windspeeds in the E Atlantic area 35-65°N, 20W-10°E shows that the major increase in windspeed from the 1950's to the 1970's took place in spring and autumn (Figure 10).

Time-series estimates of windspeed and gale frequency (such as the Jenkinson Index) based on the analysis of daily pressure maps are known to be problematic since the smoothing and interpolation techniques applied are known to have varied over the years, and the corrections to account for these changes in technique were perhaps applied in a rather ad hoc manner throughout the series. Nevertheless the trends just described are confirmed in the time-series data from North Sea lightvessels (eg. Fig 9a, b) which are more firmly based on the annual percentage frequency of 3-hourly watches with windspeeds > F8. The trends towards increased northerlies and increased storminess from the 1950's to the 1970's in seas around the British Isles are therefore accepted as valid.

We know theoretically that increased storminess in spring should lead to delayed and reduced production, and Glover et al. (1972) do indicate a delay in production of phytoplankton in the North Sea and waters west of the British Isles amounting to ~ 1 month over the period 1948-72. While theoretically expected, the evidence for this shift in timing is itself hardly robust. The CPR "colour" index on which it is based depends mostly on the retention of the larger cells (eg. diatoms) on the silk; nevertheless the production of cells of all sizes has to start under the same set of physical conditions and there is no evidence of a succession in cell-sizes within the spring outburst. It is probably for this reason that the seasonal bloom is well described in CPR colour data (Robinson, 1970; Gieskes and Kraay, 1977).

In Figure 11, recent changes in the timing and abundance of the spring bloom are examined in two areas of the North Sea using a group of

12 individual phytoplankton species rather than the "colour" index itself. These 12 spring species are:

Skeletonema costatum
Thalassiosira spp.
Rhizosolenia imbricata shrubsolei
Rhizosolenia styliformis
Rhizosolenia hebetata semispina
Chaetoceros (*Hyalochaete*) spp.
Chaetoceros (*Phaeoceros*) spp.
Asterionella glacialis
Thalassiothrix longissima
Thalassionema nitzschioides
Nitzschia seriata
Nitzschia delicatissima

The two sea-areas selected are C2 (west central North Sea) and C1 (east central North Sea) which exhibited contrasting changes in strong wind frequency between the 1950's and 1970's (Figure 9b). In both areas, the month/year contour diagrams of Figure 11 show a clear and progressive diminution in the amplitude of the spring abundance-peak with time, followed by a partial recovery during the 1980's; this tendency is much more strongly developed in area C2 however, where the maximum increase in storm frequency took place ($> + 50\%$; Figure 9b), and only in C2 were these changes in abundance accompanied by a clear shift in the timing of the spring bloom, from an April peak in the 1950's to a May peak in the mid-to late 1970's.

Thus it remains our hypothesis that the observed declining trend in zooplankton abundance in waters around the British Isles was the consequence of a reduced and delayed production of phytoplankton in spring, so that the carrying capacity for zooplankton was reduced and the growing season of the zooplankton was shortened. In turn the changes in phytoplankton abundance and timing were the result of a northerly-wind-induced increase in strong-wind frequency, principally during spring. Where the increase in storminess was relatively modest, these changes appear to have acted through a change in the "production ratio", $\frac{Dc}{Dm}$, to reduce the development-rate of the spring bloom. However, where the increase in storminess was greatest, this effect was also exaggerated through a delay in the initiation of production resulting from a less-rapid shallowing of the wind-mixed layer to the point where $Dm < Dcr$.

CASE 2 Upwelling and sardines off Portugal and NW Africa

Thus far, we have demonstrated a long-term increase in upwelling intensity in spring from the 1950's to 1970's in the relatively weak upwelling zone along the Portuguese coast. Figure 4 also shows however that the build-up of the eastern Atlantic ridge during the 1970's was also responsible for an increased coastwise northeasterly wind component at the NW African coast, a zone of moderate to strong upwelling.

Figure 4 applies to March-April, before the summer upwelling at this coast has reached its seasonal maximum, but the mean April-September pressure field (not shown) confirms a similar (if lesser) increase in northeasterly wind along the Morocco coast between the 1950's and 1970's. Bakun has calculated the only available monthly upwelling index for this coastline for a point 28°N 13°W near Cape Juby, in the sector of the shelf where the principal Moroccan sardine stock (Sardina pilchardus, Walbaum) overwinters, spawns (winter-spring) and spreads north from in summer (Belveze and Erzini, 1983). Annual values of this index for 1946-81 from Belveze and Erzini (op cit) are shown in Figure 12 and confirm an increasing trend in upwelling intensity over the period in question.

The question of whether these changes might have had an effect on sardine recruitment at these coasts is clearly of relevance to the present Sardine and Anchovy Recruitment Project (SARP) of the International Recruitment Program (IREP) and it is instructive to include evidence of such effects also from the intense upwelling zone along the Californian coast.

(a) Intense upwelling off California. Ahlstrom (1966) has published a summary of the distribution and abundance of sardine (Sardinops caerulea) and northern anchovy (Engraulis mordax) larvae in the California Current during the 1950's during a period when a major change in upwelling intensity took place, according to Bakun (1973). [Larval distributions indicate spawning distributions quite well because the eggs hatch in 2-3 days]. Figure 13 shows Bakun's index of upwelling intensity at 33°N, 1948-59 in both April-May and July-September and it is plain that from 1951-54 to 1955-59, the mean upwelling intensity rose from values around 160 tonnes per second per 100 m coastline (for convenience described below as upwelling units or simply "units") to values exceeding 250 units. Over the same period, the lesser upwelling of July-September rose from ~ 100 units to a mean of 220 units.

From Ahlstrom's data, Figure 14 describes the differential response to this change by the spawning populations of anchovy and sardine. The anchovy, whose spawning peaks in February when upwelling intensity is weak (< 50 units), but which continues to spawn until June, showed no change in the time of peak spawning throughout this period. By contrast the sardine showed a dramatic shift in their time of peak spawning from an April-May peak in 1951-54 to a bimodal February and July-September distribution in 1955-59. Evidently the anchovy can tolerate almost any upwelling intensity from 50 to 300 units, but the spawning sardine have a preferred range of upwelling intensity, requiring 150 units, tolerating 200-250, but avoiding extreme upwellings of > 250 units.

Cushing (1971) showed that maximal production in the rising water is obtained at moderate to low upwelling velocities < 0.5 m d^{-1}; then the grazing capacity by zooplankton is fully developed within an upwelling plume. At greater vertical velocities the production is carried offshore at the surface and, in the turbulent waters may be subject to larger and more efficient grazers. The turbulence itself may disrupt the formation of high-density layers of food particles. Thus the total production may be less under such conditions. This greater sensitivity of sardine to upwelling rate is perhaps compounded by the more exacting requirements of their larvae for food (c.f. anchovy larvae) shortly after hatching. In the first 11 days after hatching, sardines show a much faster growth rate at 1.0 mm d^{-1} (Kimura, 1970; Butler and de Mendiola, 1985) than the 0.2-0.5 mm d^{-1} of anchovy larvae (Kramer and Zweifel, 1970; Methot and Kramer, 1979), and require a sufficient density of nauplii to grow at the optimal rate. The anchovy learns to feed slowly taking up to 3 weeks to achieve 90% feeding success (Hunter, 1972), grows slowly in the initial stages so that its requirements for food are met by almost any strength or intermittency of upwelling, and it reaches metamorphosis later than the sardine (Theilaker and Dorsey, 1980). From Soutar and Isaacs (1969) it is clear that anchovy have been the dominant species off California over 2000 years suggesting that a relative indifference to upwelling and its changes is perhaps the better strategy!

(b) Moderate to strong upwelling off North West Africa

While the increasing northeasterly wind component along the NW African coast has apparently supported a gradual intensification of upwelling there over recent decades, Figure 12 shows that mean upwelling has generally lain within the limits of 100-230 units, with a mean of ~ 160 over the period 1946-81. Since the sardine catch in the principal Moroccan fishing zone is composed mainly of 1-3 year old fish, Belveze and Erzini (op. cit.) have compared the annual catch with the average upwelling index over the preceding three years and in fact show a rather simple dependence of catch on mean upwelling intensity (Figure 15). They continue to be sceptical of the relationship however, in view of the shortness (12 years) of the available catch series, and because there seems to be no consistent and corresponding agreement between values of upwelling index and recruitment.

(c) Weak upwelling off Portugal

Finally, we return to the events off Portugal with which this paper began - and are faced with a final enigma. Whether we compute the upwelling index for the height of the upwelling season (April-September), for the months when the upwelling develops to that peak (March-May) or the month with the greatest increase in northerlies (April) there is little doubt that the intensification of the Eastern Atlantic Ridge brought a long-term relative increase in upwelling intensity at this coast from the 1950's to the 1970's. In absolute terms however the upwelling intensity is weak throughout, ranging from values of 20-30 units in the 1950's to 40-60 during the maximum of the 1970's.

One might expect that such low upwelling intensities and such a slight interannual change might have little discernable effect on sardine survival, recruitment and catch. Yet when we compare the Iberian sardine catch (as in the Moroccan case) with the average upwelling index over the preceding three years (Figure 16) we find that over a data set of more than 30 years duration, there is a close correlation, that it is closest for the April upwelling index, and that the correlation is inverse, in total contrast to Belveze and Erzini's findings off Morocco. [Note however that Marr's (1960) positive correlation between sardine year-class-strength and cumulative temperature at Scripps Pier, 1934-55, implies a negative correlation between sardine success and upwelling intensity off California, similar to the Portuguese case.]

There are two spawnings of sardines off Portugal, in March and October (T. Wyatt, pers. comm.) so the high correlation with April upwelling is not unexpected. Neither is it difficult to establish a working hypothesis for the inverse relationship: successful sardine recruitment depends on late inception of upwelling and weak upwelling in spring; late upwelling allows larvae to be retained in coastal waters and weak spring upwelling favours the development of a suitable initial food supply for the larvae (small flagellates, not large diatoms). The enigma lies in the fact that if catch is an index of abundance, if upwelling is related to fish productivity, and if interannual variability in upwelling is responsible for interannual variations in abundance, as we suppose, then one might also suppose a common control mechanism in the coastal areas we have examined. Such a unifying mechanism, from our present partial data sets, is by no means evident. This does not necessarily mean that the observed relationships are wrong, but it does suggest that our present conceptions of such relationships are over-simplistic.

CONCLUSIONS

1. The establishment and subsequent intensification of a pressure-anomaly ridge over the eastern Atlantic between the 1950's and the 1970's supported an increased northerly airflow along the European littoral from the North Sea to NW Africa in almost every month from March to November but with the greatest increase during March-April. In effect the seasonal build-up of the Azores-Bermuda High was earlier and more intense during the 1970's.

2. In the northern part of the area, this circulation change was accompanied by a progressive increase in storminess over the north eastern Atlantic and European shelf but with the greatest increase in the west central North Sea. This trend is suggested to be responsible for a progressive delay in the initiation of the spring phytoplankton bloom in certain areas and, more generally, for a reduced rate of bloom development hence a shortening of the growing season and a reduced carrying capacity for zooplankton resulting in a long-term declining trend in zooplankton abundance. This trend was general throughout the area, but was also most clearly-marked in the west central North Sea.

3. Further south the increasing northerlies were reflected in a rising intensity of upwelling in the 1970's along the Portuguese coast and possibly (though the evidence is less certain) along the Moroccan Atlantic coast also. Reviewing relationships between sardine abundance and upwelling intensity for areas of weak, moderate and strong upwelling, it is clear that relationships do exist but these show little sign of operating via a simple common control mechanism.

REFERENCES

AHLSTROM, E. H., 1966. "Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja

California 1951-64: a summary". Spec. Scient. Rep. U.S. Fish. Wildl. Serv., (534): 71 pp.

BAKUN, A., 1973. Coastal upwelling indices, west coast of North America 1946-71. Spec. Scient. Rep. U.S. Nat. Mar. Fish. Serv., (671): 103 pp.

BELVEZE, H. and ERZINI, K.,1983. "The influence of hydroclimatic factors on the availability of the sardine (Sardina pilchardus Walbaum) in the Moroccan Atlantic fishery". Proc. expert conf. to examine changes in abundance and species composition of neritic fish resources San Jose Costa Rica 18-29 April 1983. FAO Fish Rep., (291) 2: 285-327.

BUTLER, J. L. and DE MENDIOLA, B. R. 1985. "Growth of larval sardines off Peru". CalCOFI, Rep., 26: 113-118.

COLEBROOK, J. M., ROBINSON, G. A., HUNT, H. G., ROSKELL, J., JOHN, A. W. G., BOTTRELL, H. H., LINDLEY, J. A., COLLINS, N. R. and HALLIDAY, N. C., 1984. "Continuous Plankton Records: a possible reversal in the downward trend in the abundance of the plankton of the North Sea and the northeast Atlantic". J. Cons. int. Explor. Mer, 41: 304-306.

CUSHING, D. H., 1971. "Upwelling and the production of fish". Adv. mar. Biol., 9: 255-334.

GIESKES, W. W. C. and KRAAY, G. W., 1977. "Continuous Plankton Records: changes in the plankton of the North Sea and its eutrophic Southern Bight from 1948 to 1975" Neth. J. Sea Res., 11 (3/4): 334-364.

GLOVER, R. S., ROBINSON, G. A. and COLEBROOK, J. M., 1972. "Plankton in the North Atlantic - an example of analysing variability in the environment. In: Marine Pollution and Sea Life (Ed. M Ruivo), pp 439-445. Fishing News (Books) West Byfleet, Surrey and London.

HUNTER, J. R., 1972. "Swimming and feeding behaviour of larval anchovy, Engraulis mordax". Fishery Bull. U.S., 70: 821-838.

KIMURA, M., 1970. Formation of a false annulus on scales of Pacific sardines of known age" CalCOFI Rep., 14: 73-75.

KRAMER, D. and ZWEIFEL, J. R.,1970. Growth of anchovy larvae (Engraulis mordax Girard) in the laboratory as influenced by temperature" CalCOFI Rep., 14: 84-87.

LAMB, H. H. and WEISS, I., 1979. "On recent changes of the wind and wave regime of the North Sea, and the outlook". Fachl. Mitt. Amtl. Wehrgeophys., 194: 108 pp.

MARR, J. C., 1960. "The causes of major variations in the catch of Pacific sardine, Sardinops caerulea, Girard." Proc. Wld. Scient. Meet. Biol. Sardine and Related Spec., 3: 667-791.

METHOT, R. D. and KRAMER, D., 1979. "Growth of northern anchovy Engraulis mordax larvae in the sea". Fishery Bull. U.S., 77(2): 413-423.

ROBINSON, G. A., 1970. "Continuous Plankton Records: variations in the seasonal cycle of phytoplankton in the North Atlantic. Bull. Mar. Ecol., VI 9: 333-345.

SOUTAR, A. and ISAACS, J. D., 1969. History of fish populations inferred from scales in anaerobic sediments off California" CalCOFI Rep., 13: 63-70.

SVERDRUP, H. U., 1953. "On conditions for the vernal blooming of phytoplankton. "J. Cons. int. Explor. Mer, 18: 287-295.

THEILAKER, G. and DORSEY, K., 1980. "Larval fish diversity, a summary of laboratory and field research". IOC Wkshop Rep., 28: 105-142.

VAN DE KAMP, G., 1983. "Long term variations in residual currents in the southern North Sea". ICES CM 1983/C:4, 5 pp + 5 figs (mimeo).

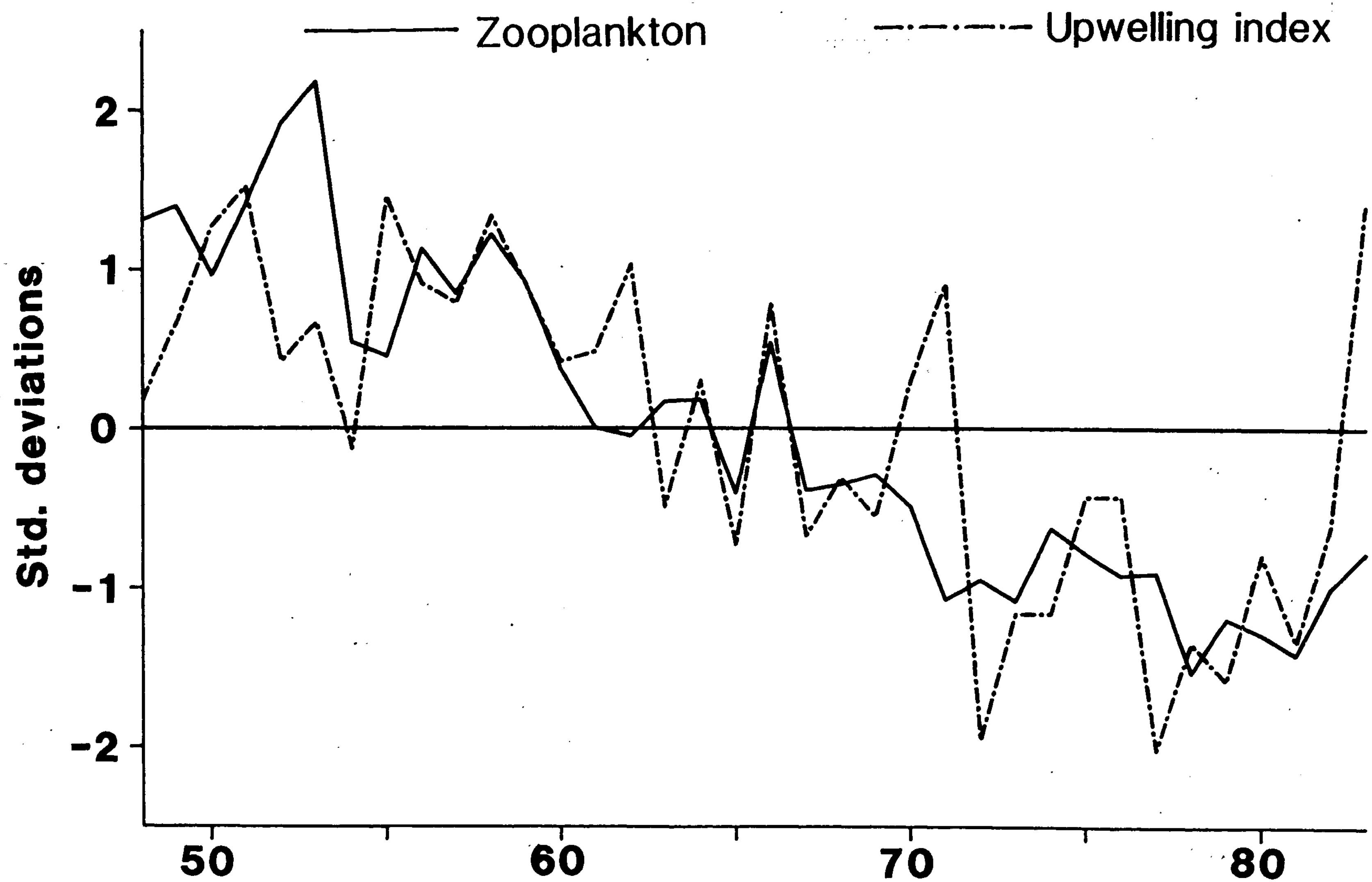
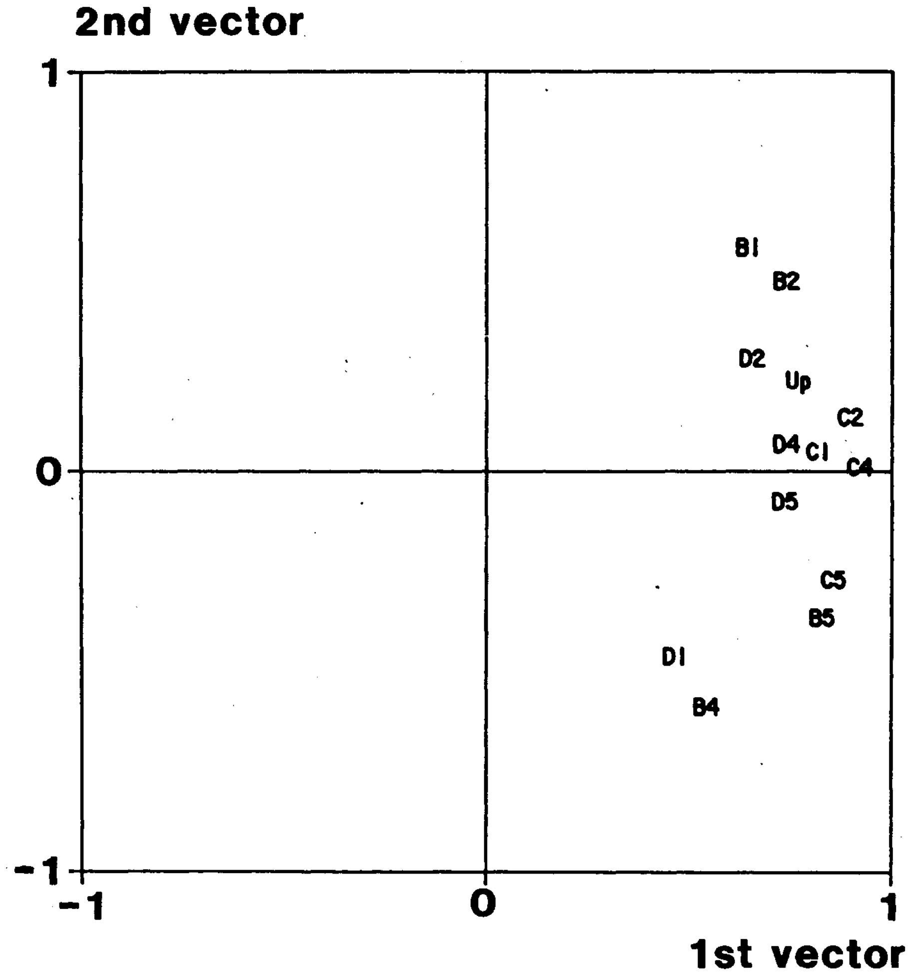


Figure 1. Normalized long-term trends, 1948-83, in April-September upwelling index at Porto, Portugal (graph inverted), and in the first principal component for zooplankton of the annual fluctuations in abundance for 12 sea areas around the British Isles (from Colebrook _et al_., 1984).

(a)



(b)

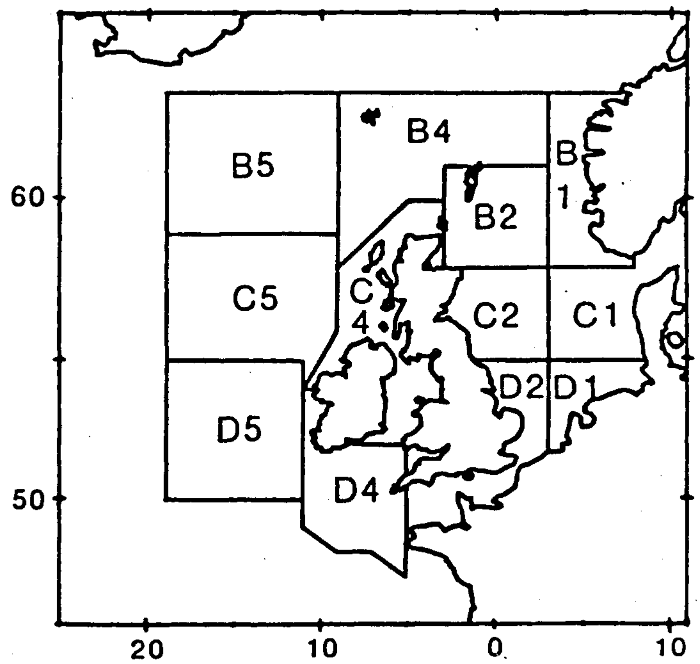


Figure 2. (a) Scatter plot of the first two eigenvectors from a principal component analysis of the first components of the zooplankton for each of the 12 CPR Standard Areas, April-September, upwelling data for Porto included (UP). Upwelling is clearly correlated with zooplankton in each of the CPR areas.

(b) Location of the 12 CPR Standard Areas.

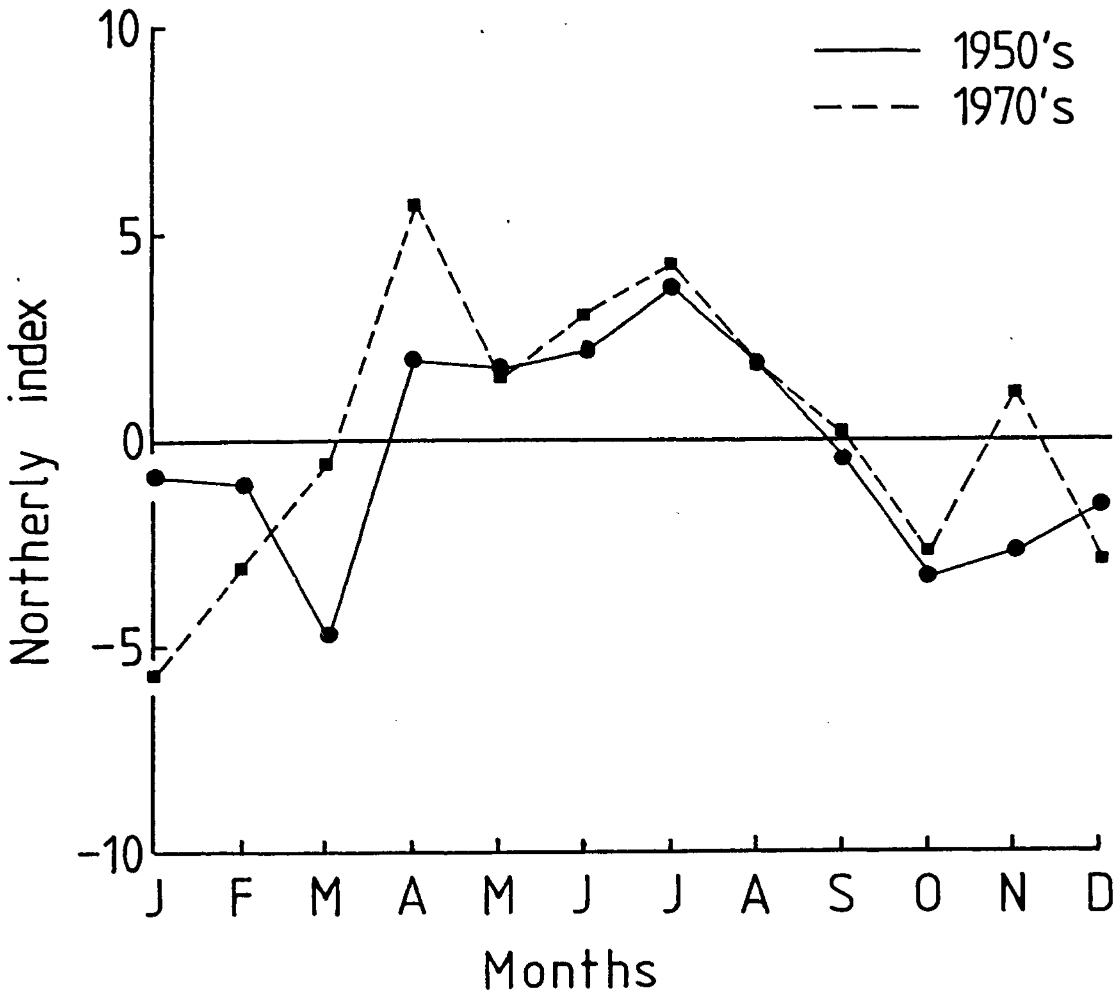


Figure 3. The seasonal march of northerly winds over the eastern Atlantic in the 1950s and 1970s. The northerly index (expressed in mb) is calculated from the mean zonal pressure difference between 20°W and 10°E, over the latitude interval 35°N to 65°N.

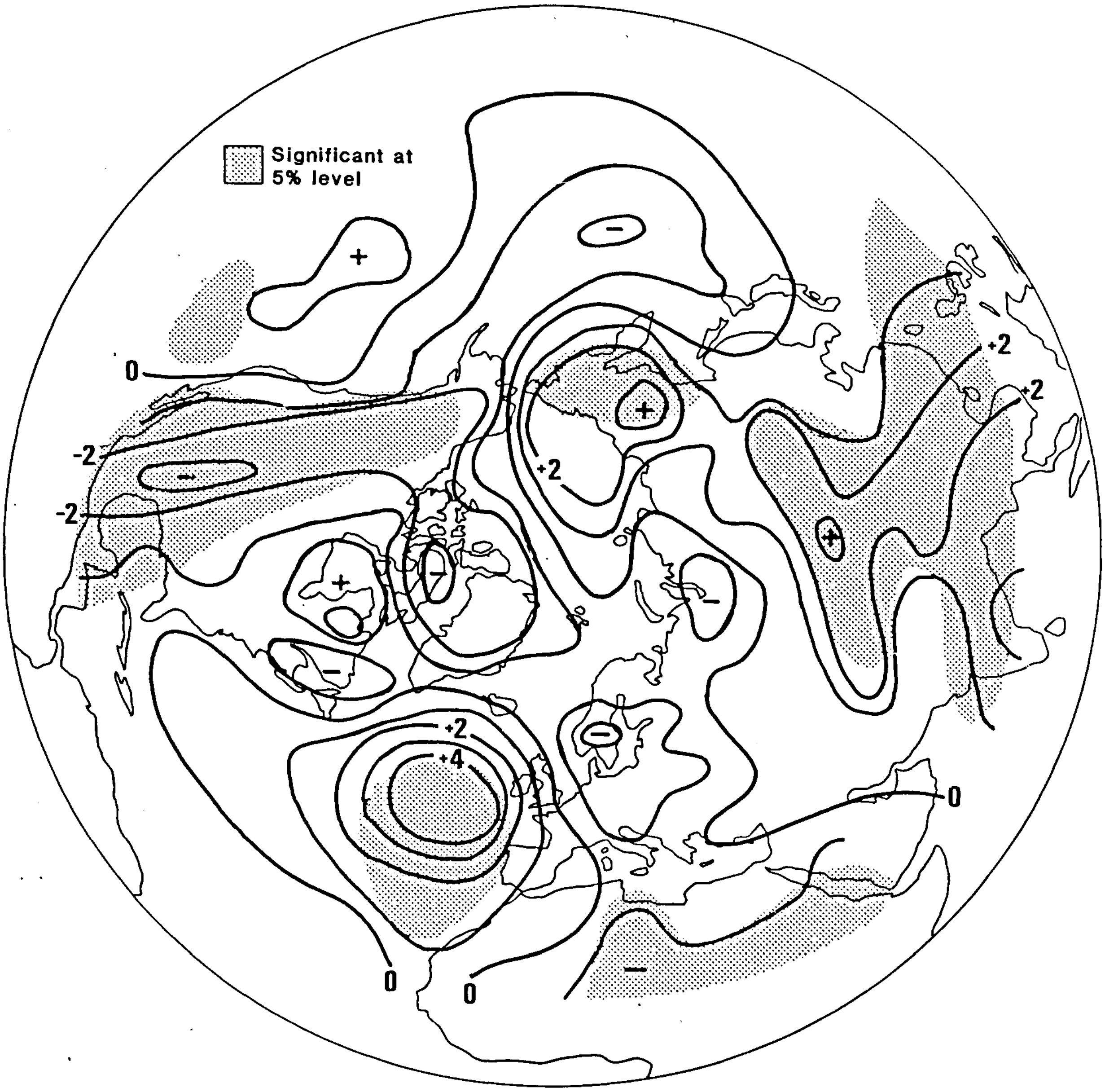


Figure 4. Hemispheric change in surface pressure (mb), 1970s minus 1950s, for the months March-April.

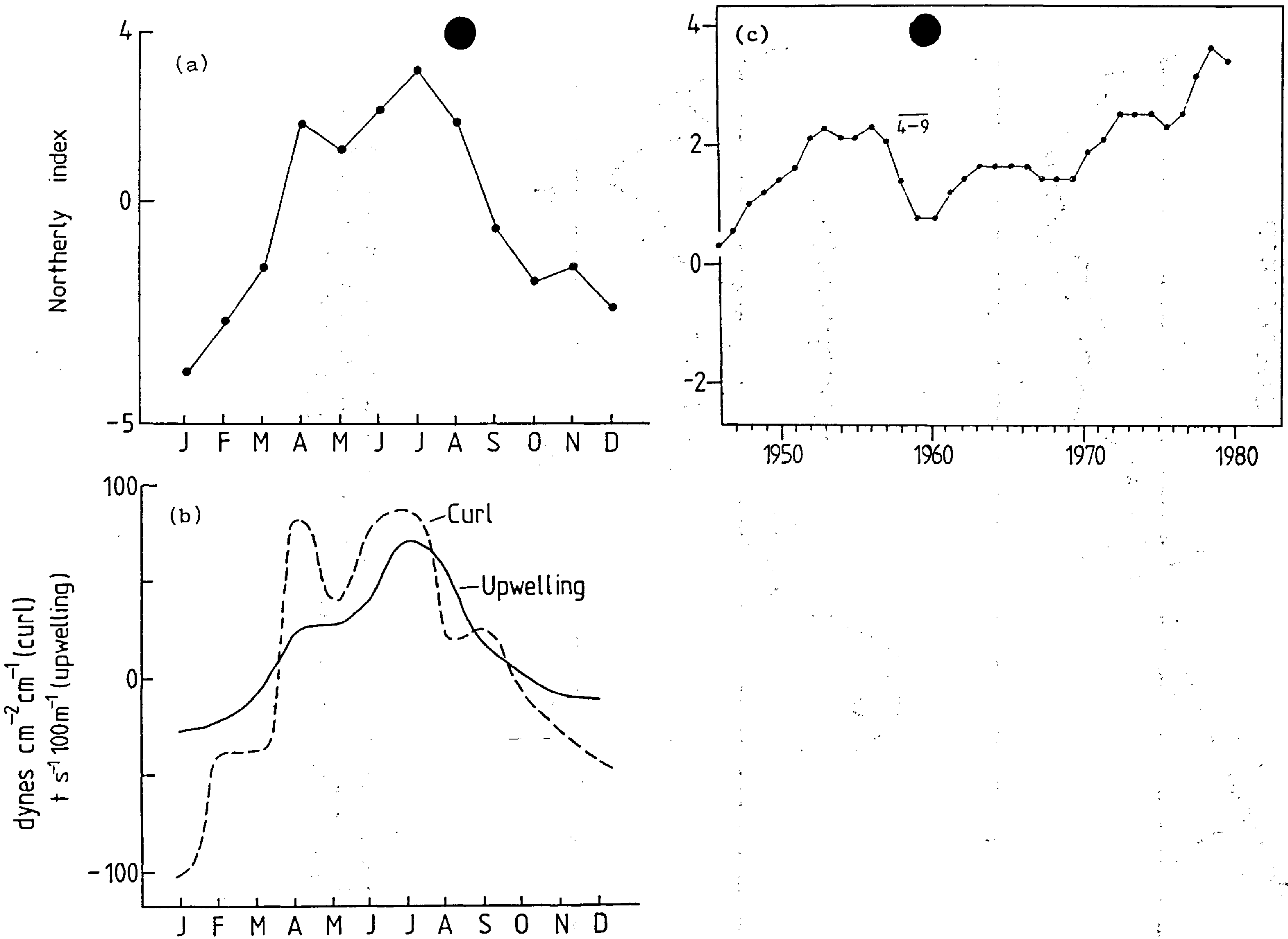


Figure 5. (a) Average monthly values of north-wind index for the east Atlantic sector 35°N-65°N, 20°W-10°E, 1873-1981.
(b) Mean monthly values of curl and upwelling indices for Porto over the period 1946-84. (Units are dynes cm^{-2} cm^{-1} and tonnes s^{-1} 100 m^{-1} respectively.) Bakun, pers. comm.
(c) Trend in northerly wind index for April-September 1946-80 in the east Atlantic sector, 35-65°N 20°W-10°E.

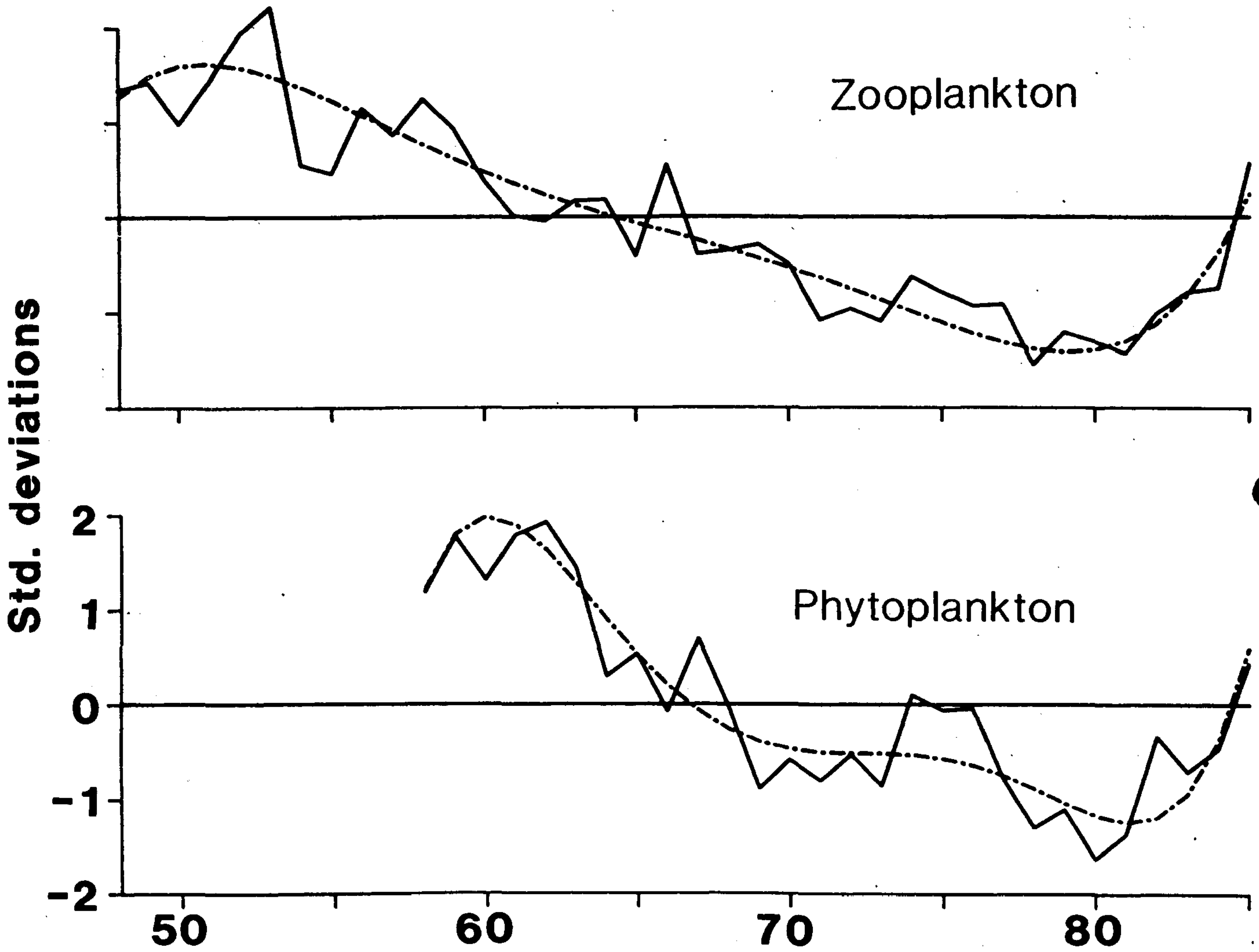


Figure 6. Mean trends in the abundance of zooplankton (based on 12 areas, 24 species, 247 series) and phytoplankton (12 areas, 24 species, 263 series), 1948-83. From Colebrook et al., 1984

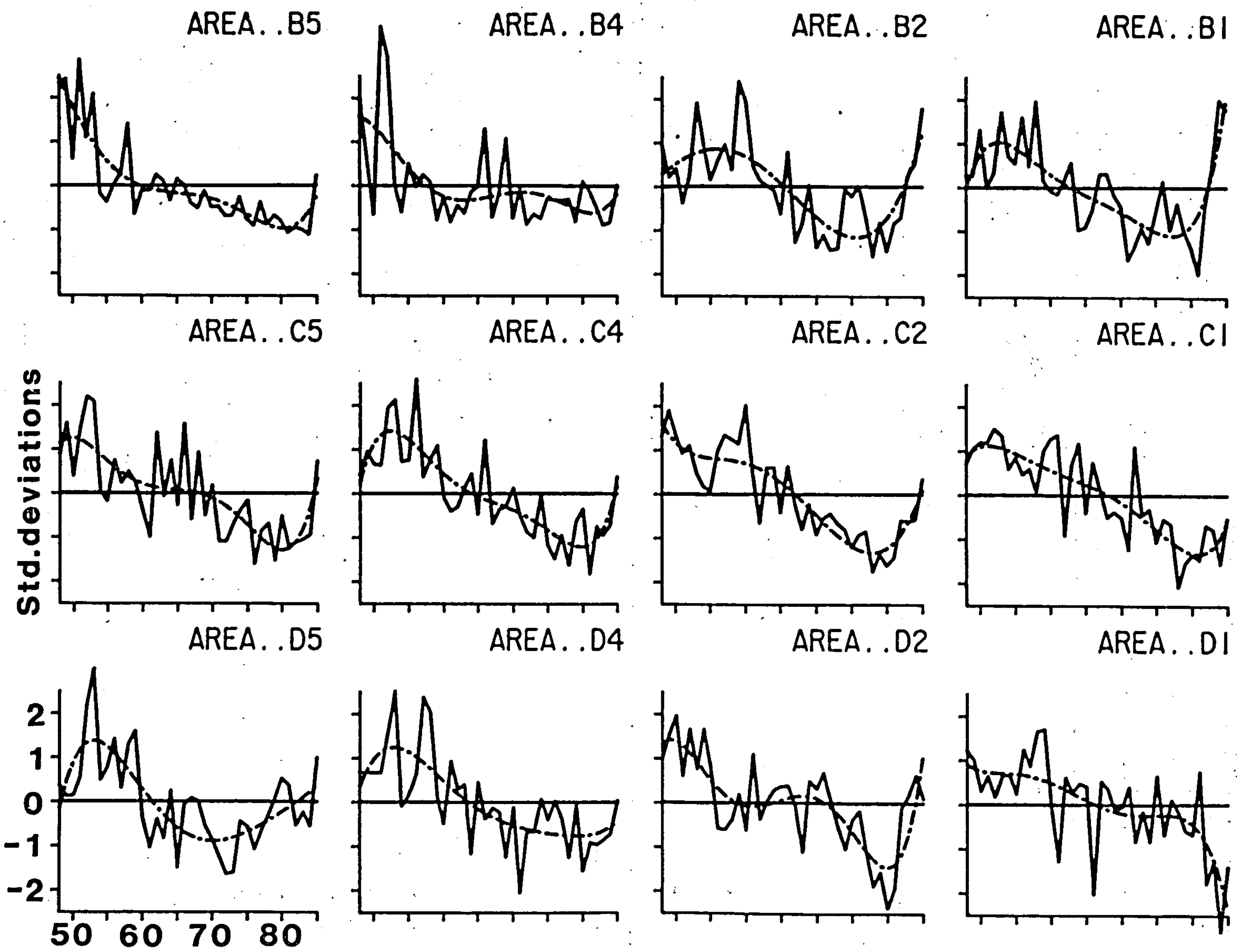


Figure 7. Trends of zooplankton abundance in 12 CPR Standard Areas around the British Isles. (Locations are shown in Figure 2b).

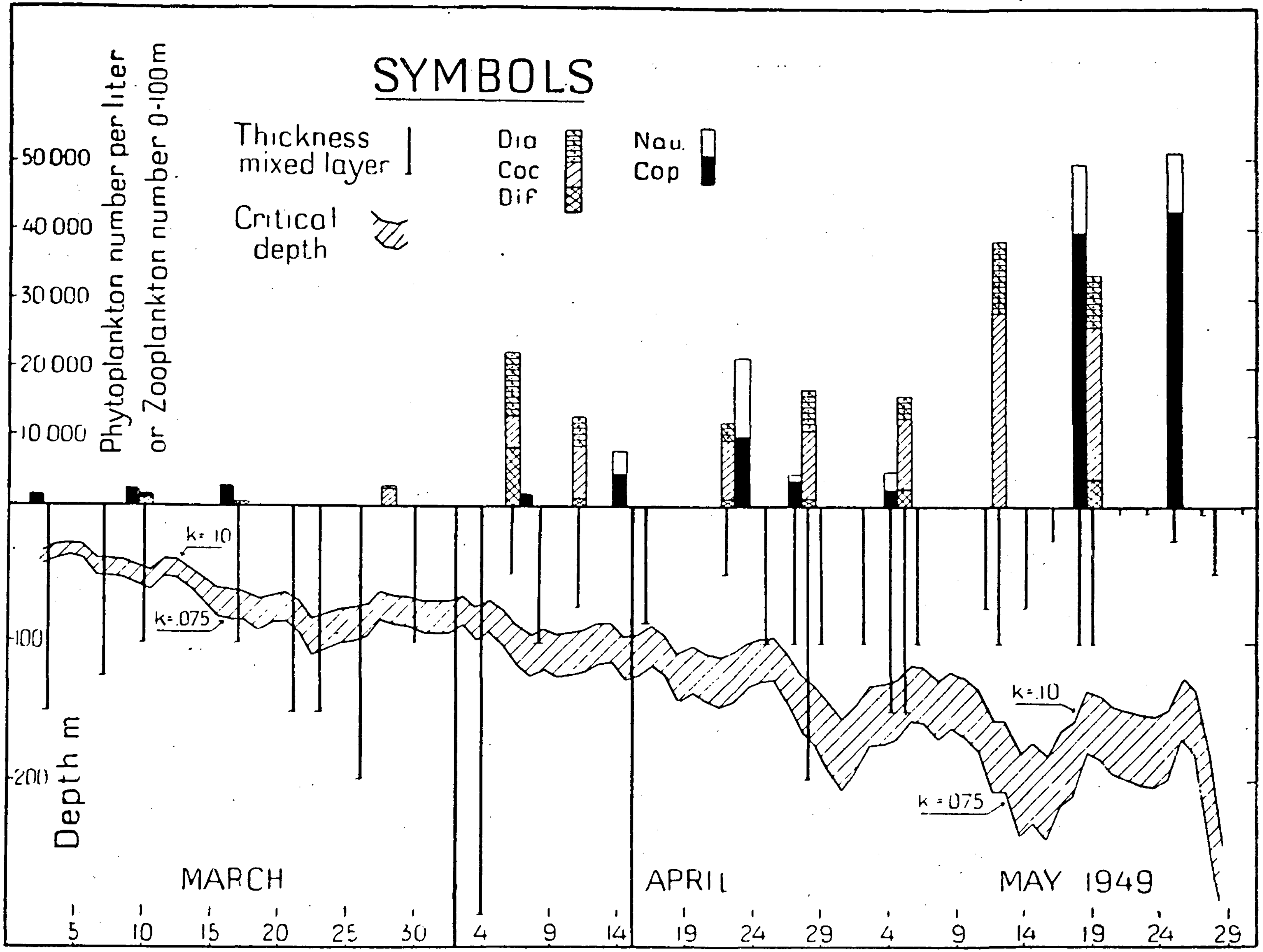


Figure 8. Sverdrup's observations of the initiation and development of primary production at OWS Mike (66°N 2°E) in spring 1949. From Sverdrup, 1953.

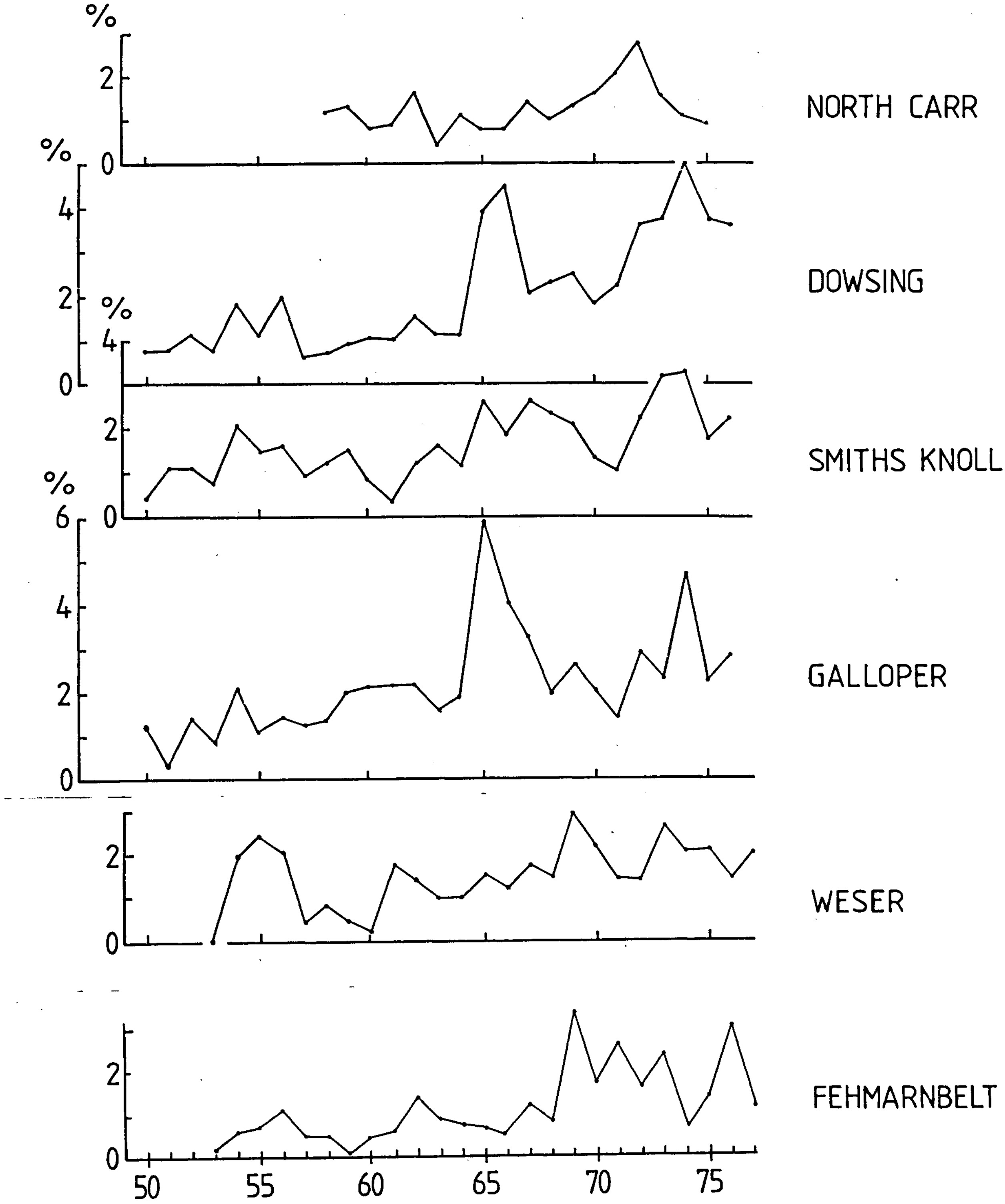


Figure 9. (a) Annual percentage frequency of 3-hourly watches with windspeeds ≧ Force 8 at selected North Sea lightvessels, 1950-77. From Lamb and Weiss, 1979.

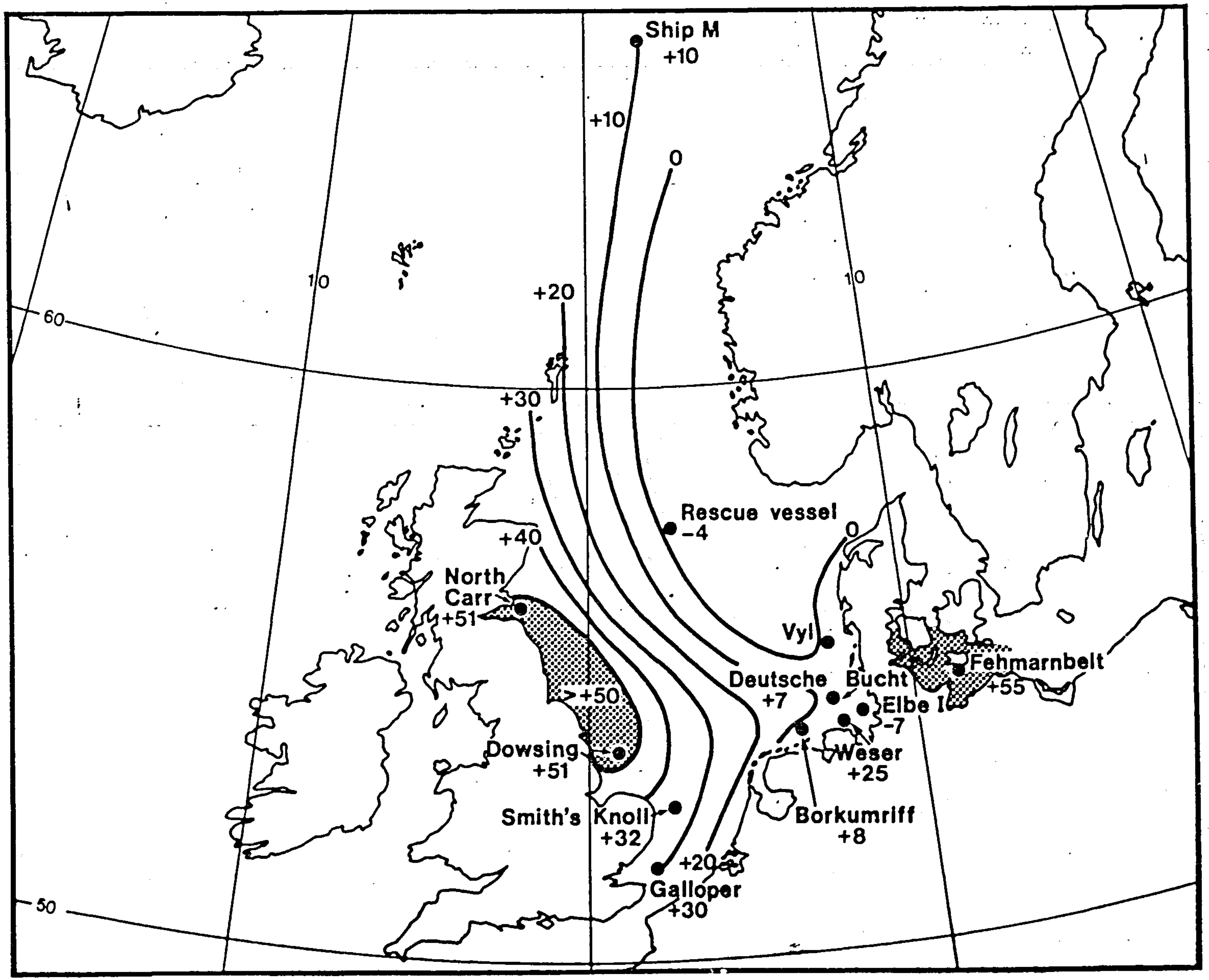


Figure 9. (b) Isopleths of the percentage change in the incidence of windspeeds ≧ Force 8 between the 1950s and 1970s. From Lamb and Weiss, 1979.

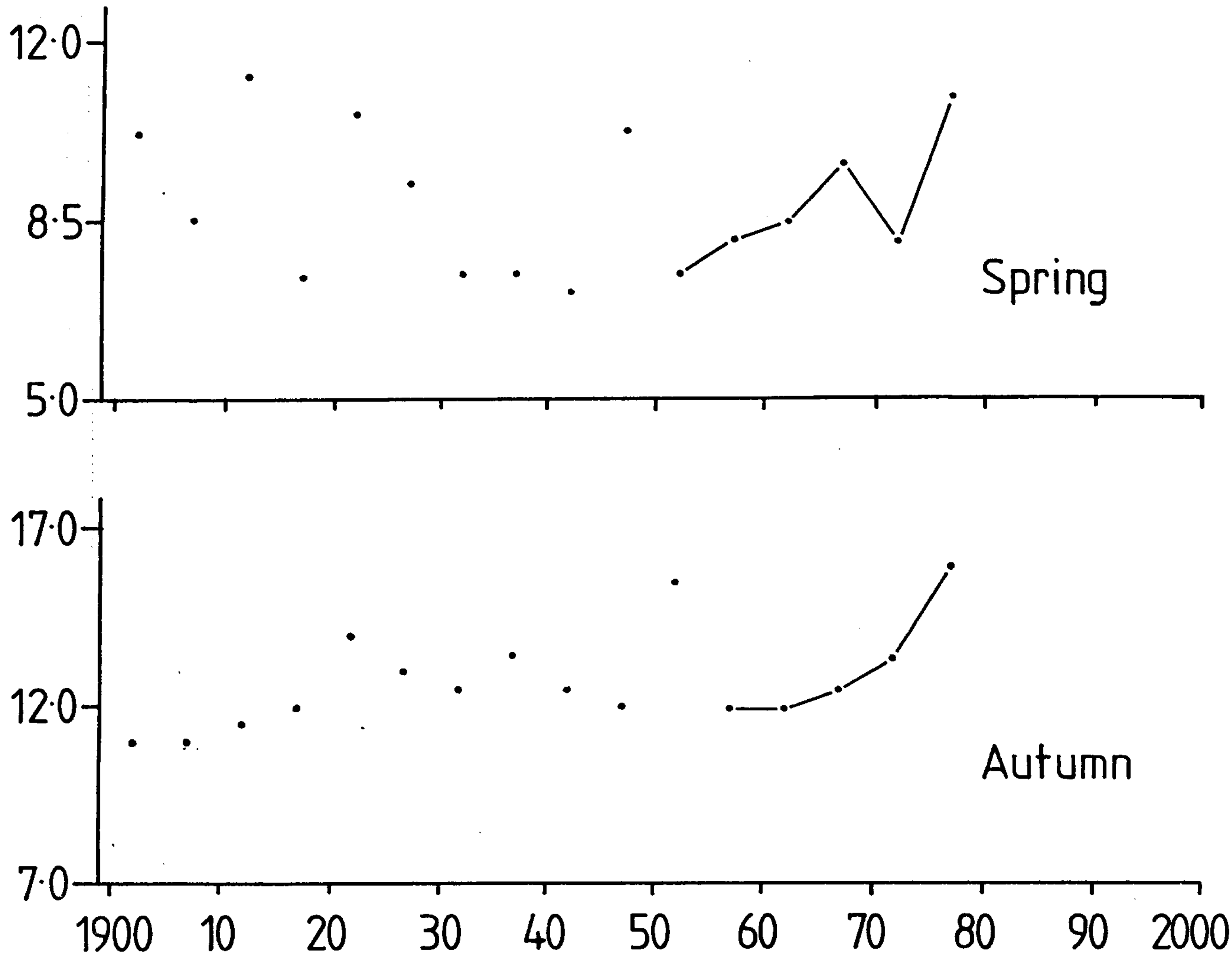


Figure 10 Windspeed indices for the East Atlantic in spring and autumn, 1900-1980, based on the analysis of pressure gradients in the sector 35-65°N 20°W-10°E.

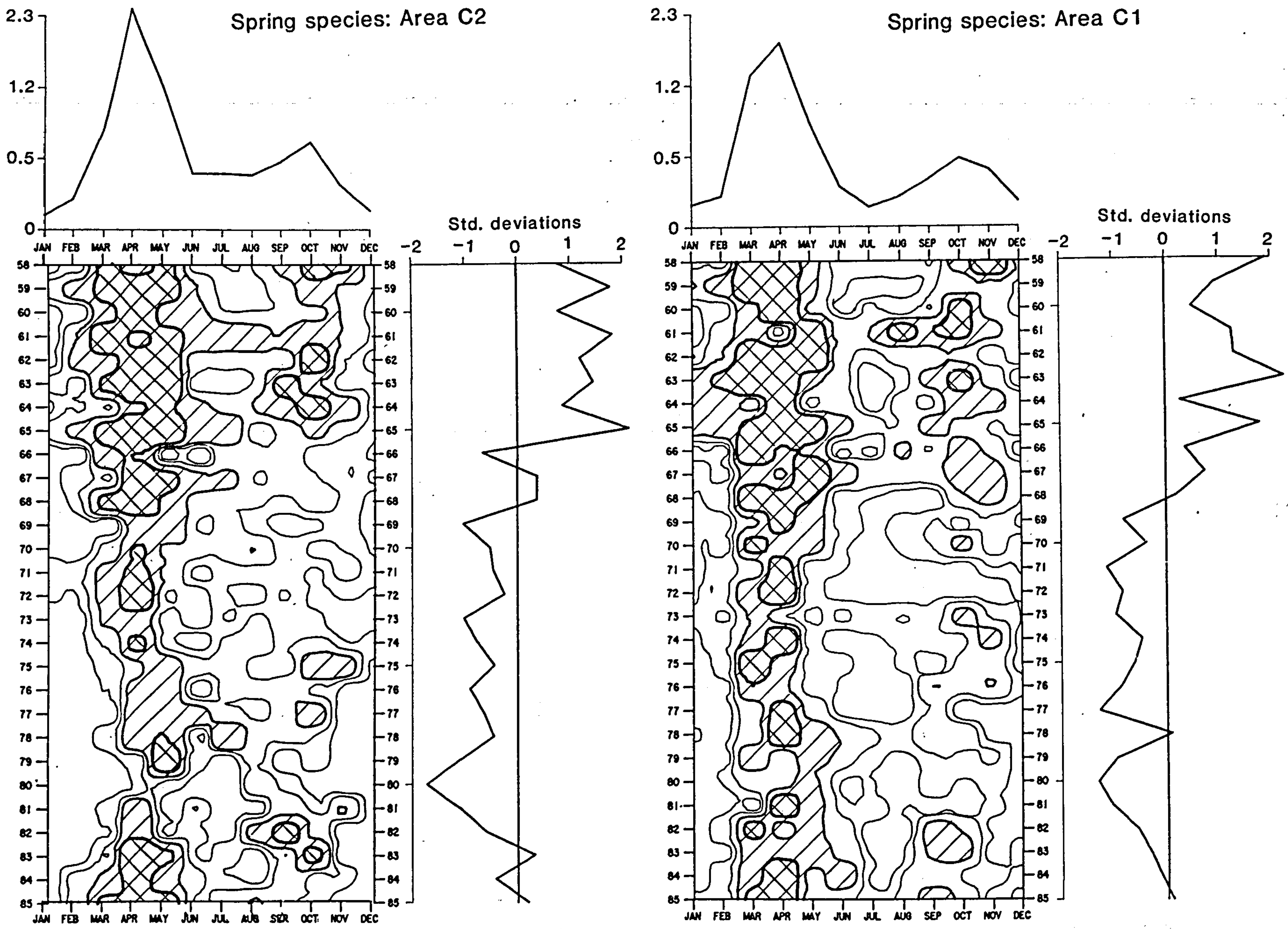


Figure 11. Month/year contour plots, annual means and long-term monthly means describing the abundance of 12 spring phytoplankton species in CPR Standard Areas C2 (west-central North Sea) and C1 (east-central North Sea), 1958-85. For species-list, see text.

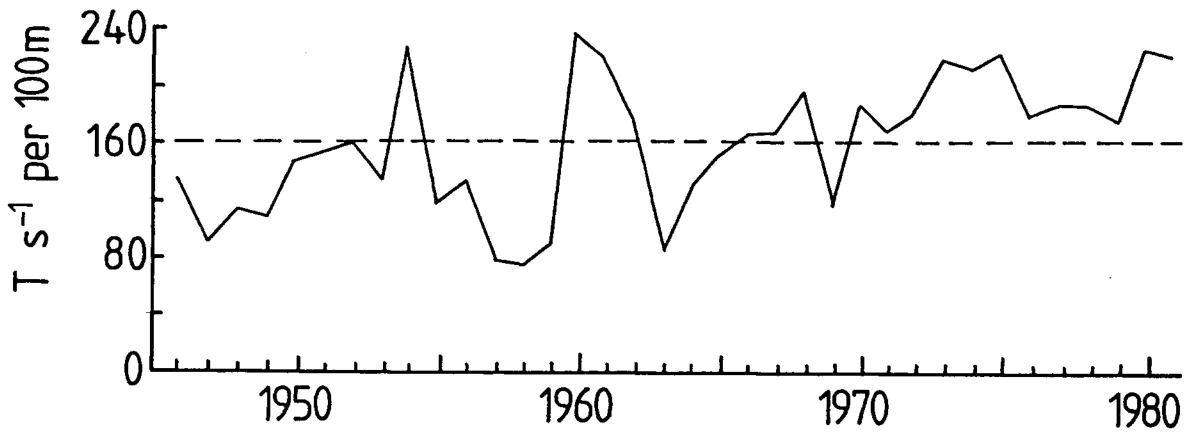


Figure 12. Mean annual upwelling index for 28°N, 13°W, 1946-81, based on unpublished monthly estimates by Bakun. From Belveze and Erzini, 1983.

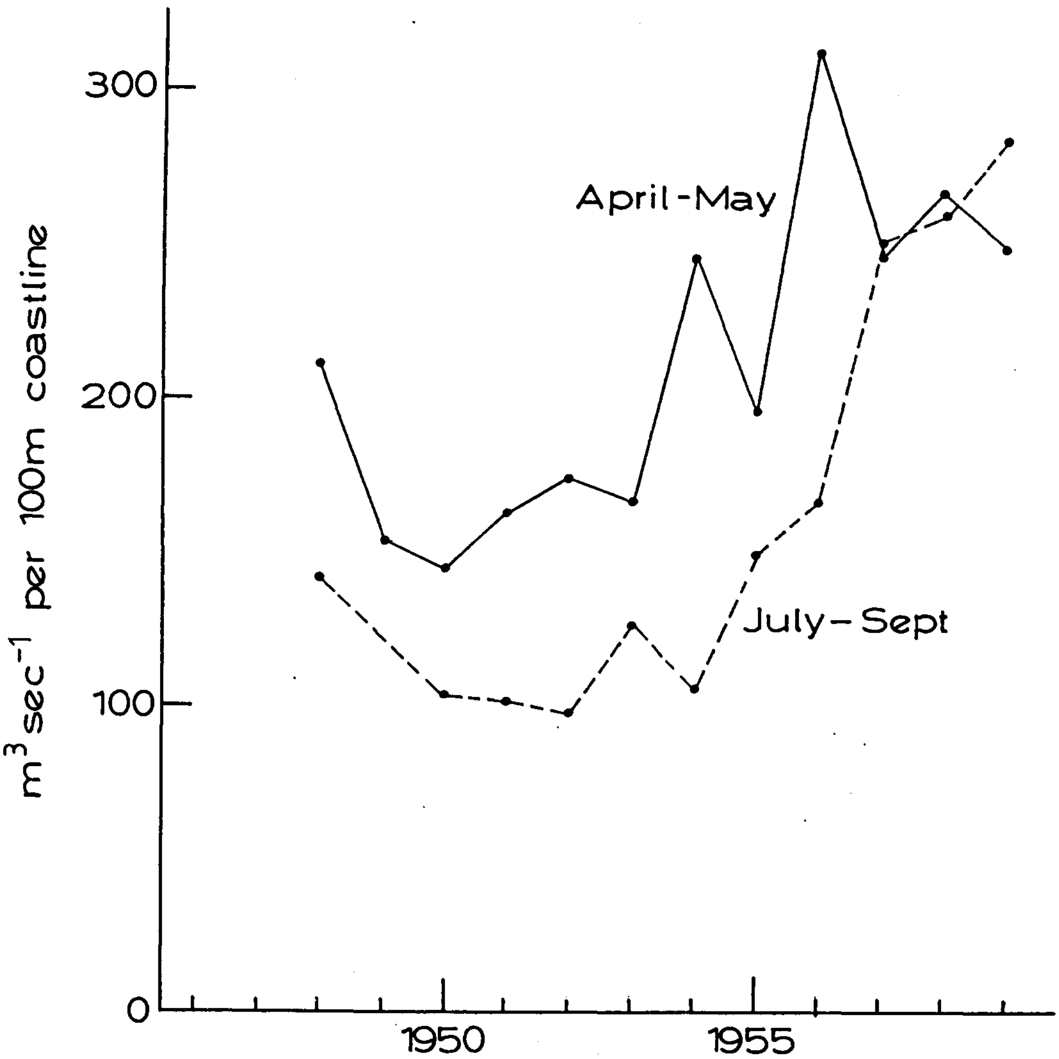


Figure 13. Bakun's indices of upwelling intensity for the Californian coast at 33°N in April-May and July-September, 1948-59.

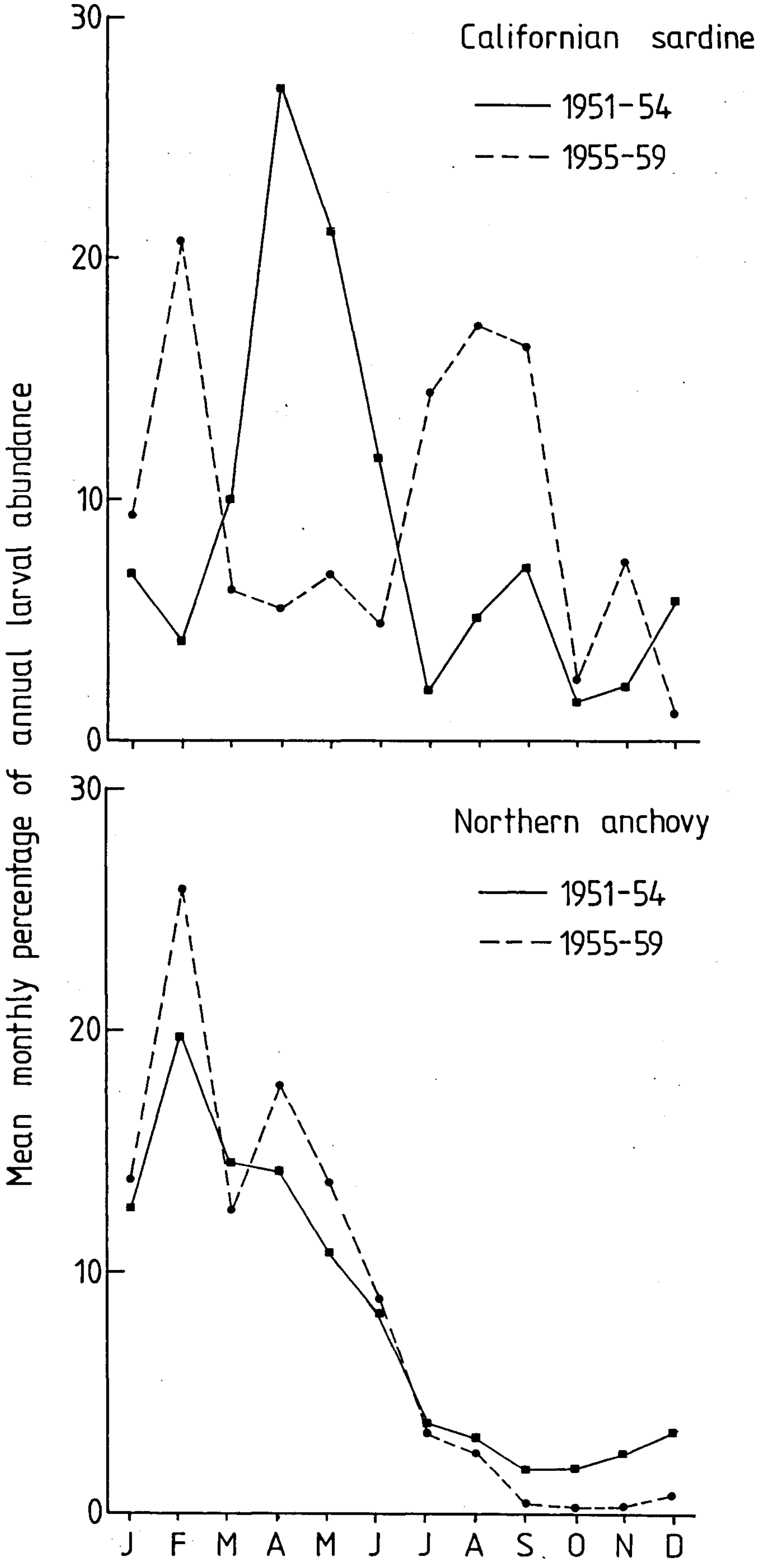


Figure 14. Monthly mean abundance of sardine (*Sardinops caerulea*) and anchovy (*Engraulis mordax*) larvae in the California Current in 1951-54 and 1955-59. Data from Ahlstrom, 1966. A major intensification of upwelling took place between the former and the latter period.

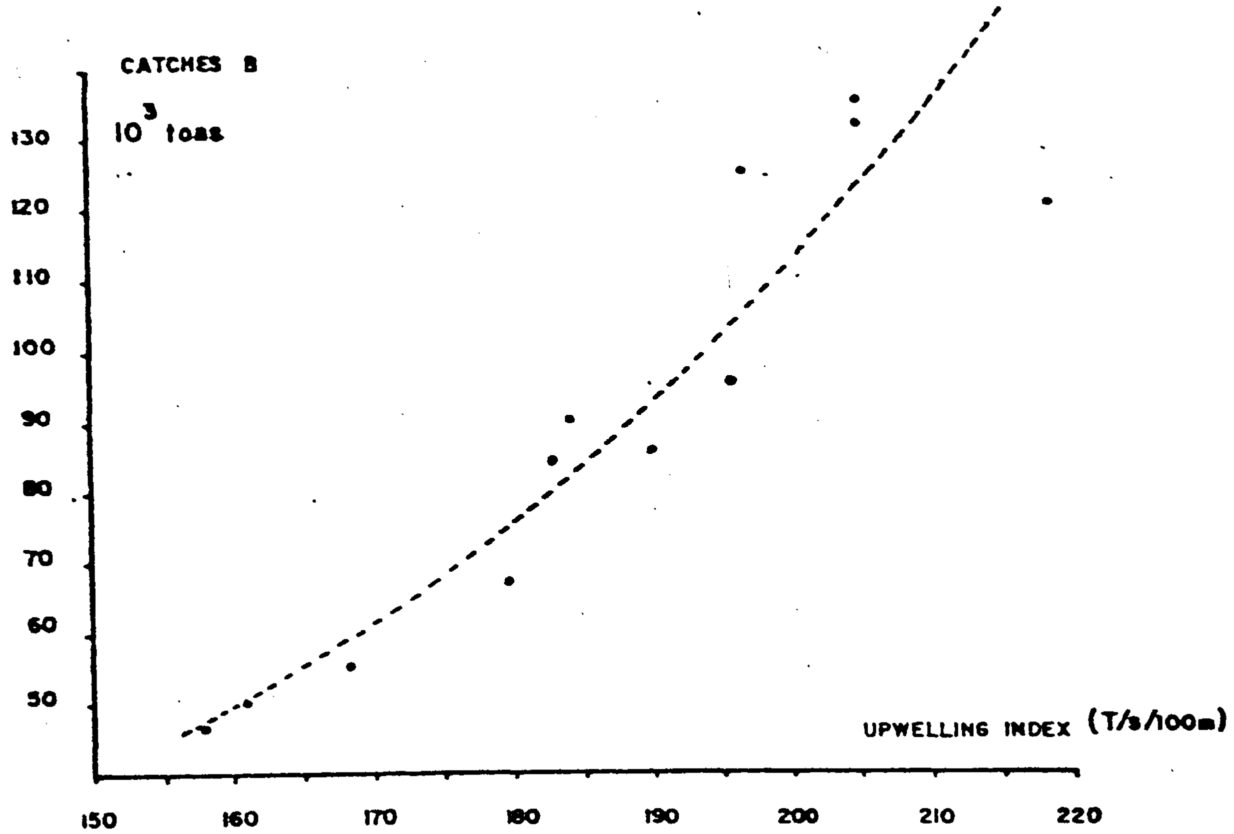


Figure 15. Dependence of the Moroccan sardine catch (1-3 year old fish) on the average upwelling index over the preceding three years. From Belveze and Erzini, 1983.

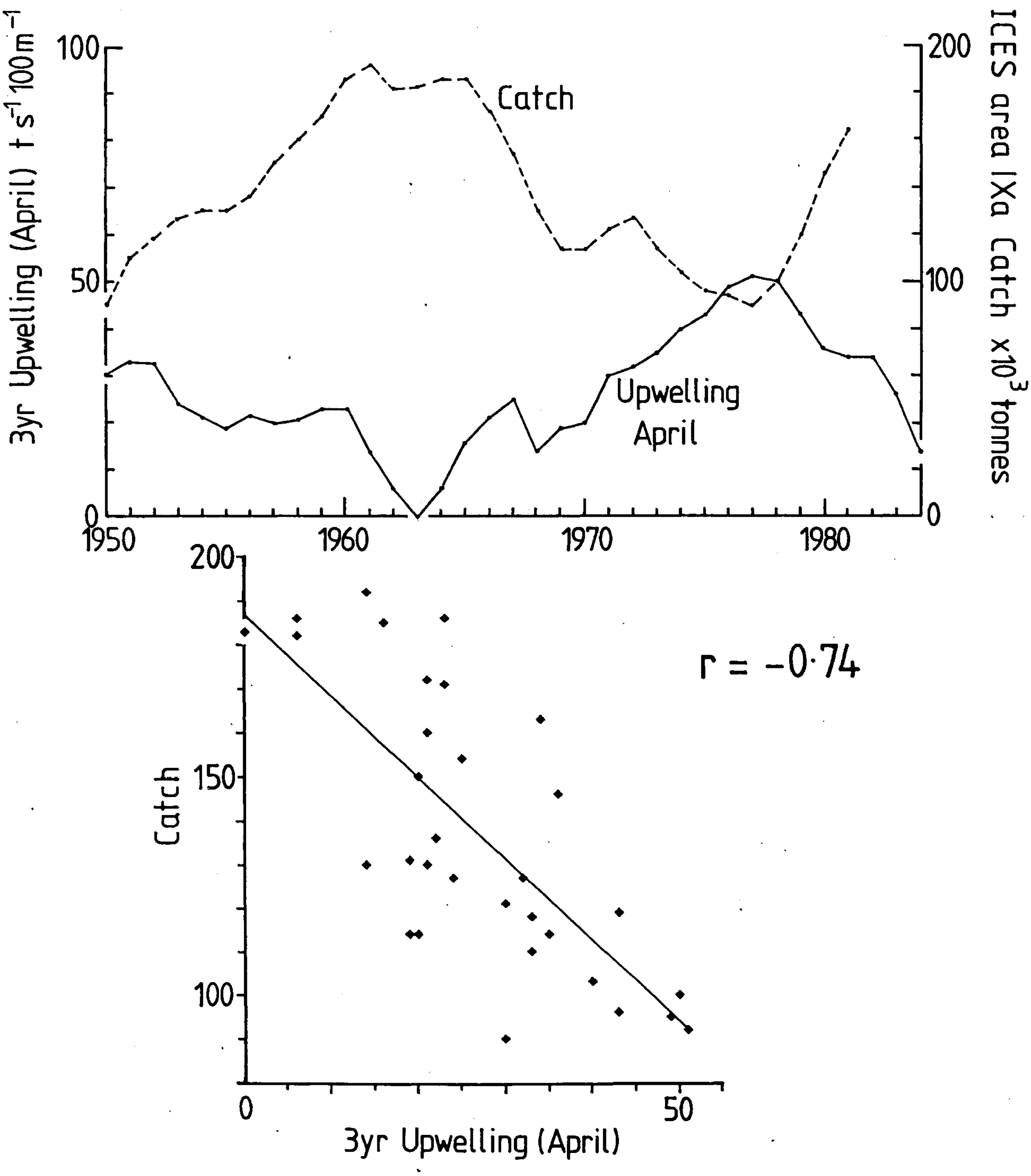


Figure 16. Comparison of Iberian sardine catch, 1950-84, with the average April upwelling index at Porto over the preceding 3 years. (The corresponding correlation coefficients for catch versus March-May and April-September mean upwelling indices are -0.69 and -0.41 respectively).