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Long-term changes of seagrass beds in the Glenan Archipelago (South Brittany)

Zostera beds
Climatic fluctuations
Ecological amplification

Herbiers de Zostères
Fluctuations climatiques
Amplification écologique

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ABSTRACT

Aerial photographs and in situ data of the Glenan archipelago permit the establishment of a cartography of its *Zostera marina* seagrass beds. Due to the exceptionally clear water, it was possible to distinguish submerged structures, such as rocks, sand dunes, maerl beds and seagrass meadows on the photographs. The distribution of *Zostera* meadows was incorporated into a geographical information database through scanning, and then compared with historical data. Ten aerial photographic surveys, made over a sixty-year period from 1932 to 1992, were available. The earliest of these surveys showed the seagrass beds to be in good condition. Low cover in 1952 suggests that the *Zostera* meadows within the studied area were subject to severe destructions, presumably due to the "wasting disease", which caused a general breakdown of the North-Atlantic populations during the 1930s. During the 1970s, the distribution of *Zostera* beds increased; this was followed by a gradual decline during the 1980s and early 1990s.

For the investigation of the environmental circumstances under which *Zostera* beds are fluctuating, the Glenan site is unique. This site being relatively remote from direct anthropogenic disturbances (light irradiance decline, sewage inputs), the causes of such fluctuations during this 60-year period can be more easily identified. *Z. marina* is a boreal species naturally affected by climate changes and in particular by global warming, which was at a maximum during the 1940s and 1950s. Various human activities, such as scallop dredging, maerl exploitation, yachting and anchoring, should also be considered. However, these anthropogenic disturbances were of limited importance in comparison with the dramatic decline and recovery of the seagrass beds as a result of climate fluctuations.

RÉSUMÉ

Évolution à long terme des herbiers de Zostères dans l'archipel des Glénan (Bretagne).

Des photographies aériennes et des observations de terrain permettent de cartographier les herbiers de *Zostera marina* dans l'archipel des Glénan. Etant donné l'exceptionnelle clarté des eaux, il est possible, grâce à ces photographies de délimiter sans difficultés les structures géomorphologiques sous-marines, tels les fonds rocheux, les sables dunaires, les bancs de maërl et les herbiers. Par scannage, cette zonation est incorporée dans une base de données pour être comparée avec des données historiques.

Sur la période de 60 années, de 1932 à 1992, dix missions de photographies aériennes ont été analysées. Au début de cette série, en 1932, les herbiers apparaissent en bonne santé et leur déclin est évident jusqu'aux années 1960, comme pour l'ensemble de l'Atlantique Nord. Au milieu des années 1970, les herbiers sont de nouveau prospères, mais des signes d'affaiblissement sont perceptibles dans les années 1980 et au début des années 1990.

Pour déterminer les circonstances environnementales exactes responsables de ces fluctuations à long terme, le site des Glénan apparaît unique. Par rapport à d'autres secteurs en Bretagne, il est relativement éloigné des perturbations anthropogéniques directes (turbidité des apports fluviaux, stations d'épuration); il est plus aisé d'identifier les causes des fluctuations de l'herbier sur cette longue période.

Zostera marina est une espèce boréale naturellement affectée par le réchauffement général qui a atteint son maximum dans les années 1940 et 1950. Différentes sources anthropogéniques peuvent être avancées: pêche par dragages, exploitation du maërl, activités de plaisance, mais ces facteurs sont estimés de peu d'importance face au déclin impressionnant ou/et à la restauration surprenante des herbiers en réponse aux fluctuations climatiques.

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INTRODUCTION

Molinier and Picard (1951) were the first authors to recognize a successional development in the seagrass beds of *Posidonia oceanica.* On the other hand, large-scale and long-term patterns in the breakdown of *Zostera marina* L. populations during the 1930s were frequently described in connection with the mysterious "wasting disease", which almost exterminated the species over its entire North-Atlantic area of distribution (Den Hartog, 1987). Martin (1954) was the first to correlate this decline with climatic factors (extreme precipitations), followed by McRoy (1966) for *Zostera* beds along the United States coasts. In Denmark, Rasmussen (1973, 1977) related the *Zostera marina* decline to high summer water temperatures following exceptionally mild winters. The fact that eelgrass died almost simultaneously over such a large area suggested that a large-scale climatic factor was involved. A clear correlation, however, is always difficult to establish, and Den Hartog (1987) considered it highly unlikely that a plant species should be brought almost to extinction, over its entire range, due to a temporary rise in temperature of only two degrees. He concluded that the "wasting disease" remains an unexplained phenomenon, but nevertheless acknowledged the elevated summer temperatures in the North Atlantic as an important factor. Rejecting the notion of a single climatic factor as being responsible for such a large-scale event, Den Hartog argued in favour of several other factors, which can act locally in the Netherlands or in Germany (*e.g.* frost, increasing turbidity, storm, erosion, hydrographical changes, dam building). In earlier studies, a similar phenomenon of seagrass bed decline and recovery was described in the Bay of Morbihan, France (Glémarec, 1979; Glémarec *et al.*, 1986); the consequence was a general cycle of erosion and sedimentation. Other authors have been tempted to emphasize some similarity between these benthic events and the changes in the plankton populations in the Western Channel known as the Russell Cycle (Southward *et al.*, 1975). Local observations in the Bay of Morbihan were used to describe erosion/sedimentation of *Zostera marina* cycles within this site (Glémarec *et al.*, 1986). The almost complete disappearance of eelgrass, however, seems to have been a general phenomenon in Brittany (Lami, 1933, around St-Malo; Prenant, 1934, in the Bay of Quiberon; Blois *et al.*, 1961, around Roscoff).

The primary aim of the present study was to describe the disappearance and recovery of *Zostera marina* beds in the oceanic Glenan archipelago site, in South Brittany. This site was chosen in order to eliminate the secondary impacts, generally of anthropogenic origin, which can mask the natural causes of fluctuation in the distribution of *Zostera* beds.

The species

Zostera marina L. is a holarctic seagrass species widely distributed throughout the temperate province (Glémarec, 1978). It is the most widespread seagrass species along the northern coasts of the Atlantic and Pacific oceans (Den Hartog, 1970) and is described as eurybiontic (Jacob, 1982). *Zostera marina* is able to colonize different sedimentary substrates, which in Brittany include sands, muds and mixed bottoms with gravels (unpublished data).

The site

The Glenan archipelago is located nine miles off Concarneau, South Brittany, in the northern part of the Bay of Biscay (Fig. 1). In the Celtic language, Glenan signifies "circle", and the area is characterized by small islands, ten in number, and numerous rocky islets, surrounding an enclosed area protected from the dominant westerlies (Fig. 2). The enclosed lagoon is shallow, being less than five metres deep. The distance from the coast is sufficient to minimize continental influence, and seasonal fluctuations in water temperatures are low (annual range: 7-8 °C). The

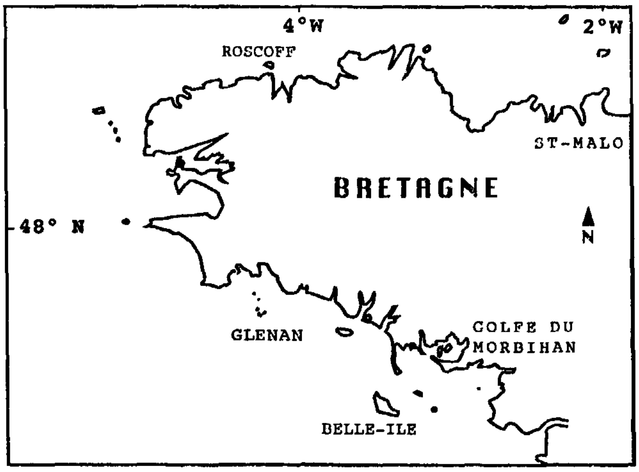


Figure 1

Location of the Glenan archipelago off the south Brittany coast.

extreme temperatures measured over several years are 7.5 and 17.5 °C and no variations in salinity appeared (Castric, 1988).

The archipelago is bordered by muddy areas to the south and to the northeast, so that winter gales are responsible for particle resuspension. However, only the outer parts of the archipelago may be subjected to reduced sunlight intensity, and the lagoon itself is characterized by very clear waters (Castric, 1988). Thus the combination of high transparency, shallow depths, relatively cool waters and protection from the south-western swells offers ideal conditions for the development of *Zostera marina* beds. Anthropogenic pressures at this site appear to be of little importance. The role of meadows in stabilizing the sediment is well described (Blois *et al.*, 1961). Meadows can be eroded by storms, and in the Glenan lagoon they compete in time for space and convenient substrates with moving sand dunes and with gravels which penetrate the lagoon from the north or from the south in the eastern part of the archipelago. Meadows are essentially located in the subtidal zone and their development can be described in equilibrium with their surroundings after periods of relative hydrodynamic stability. Figure 2 was established in September 1972 on the basis of direct observations and sedimentological analyses.

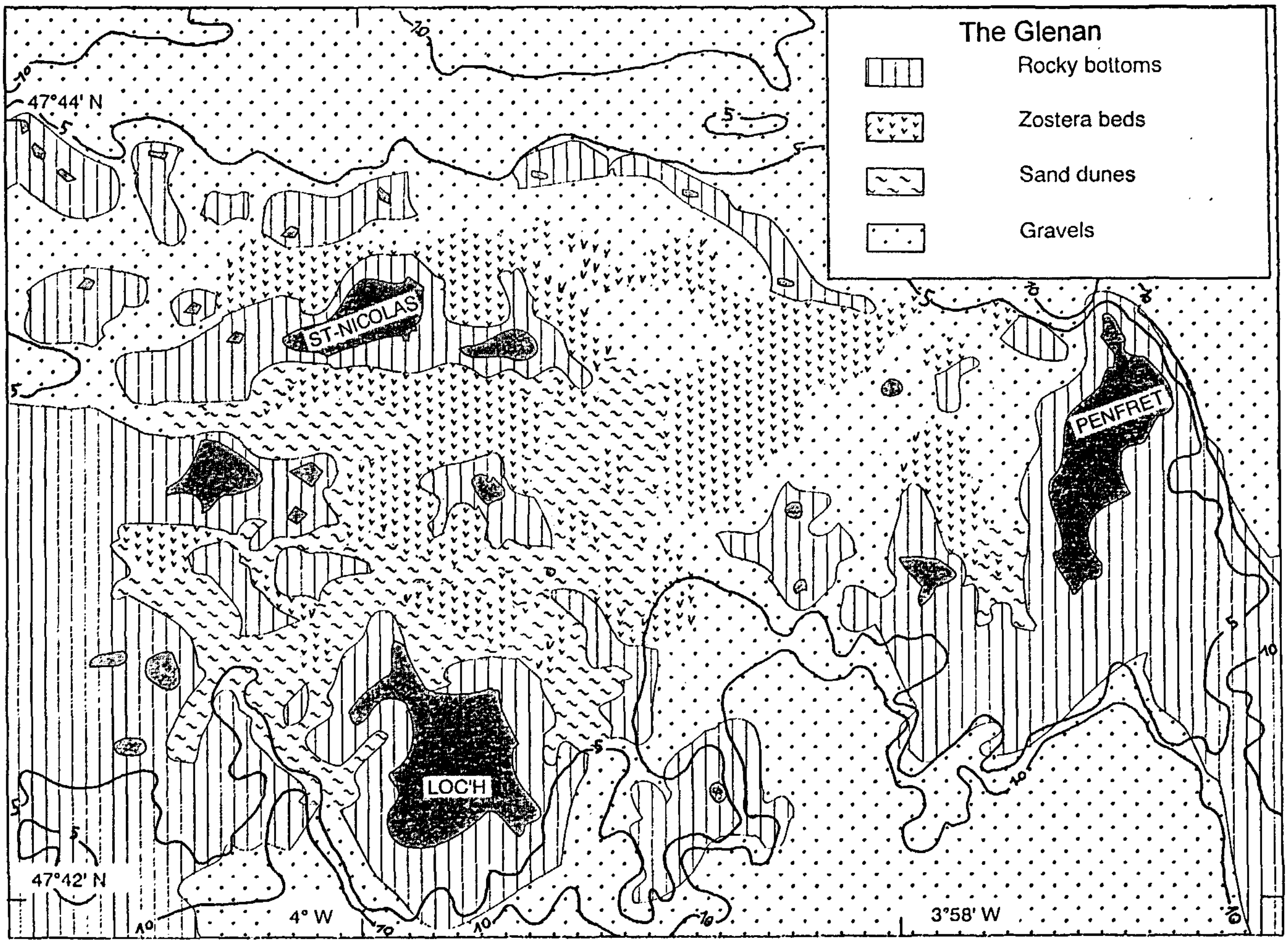
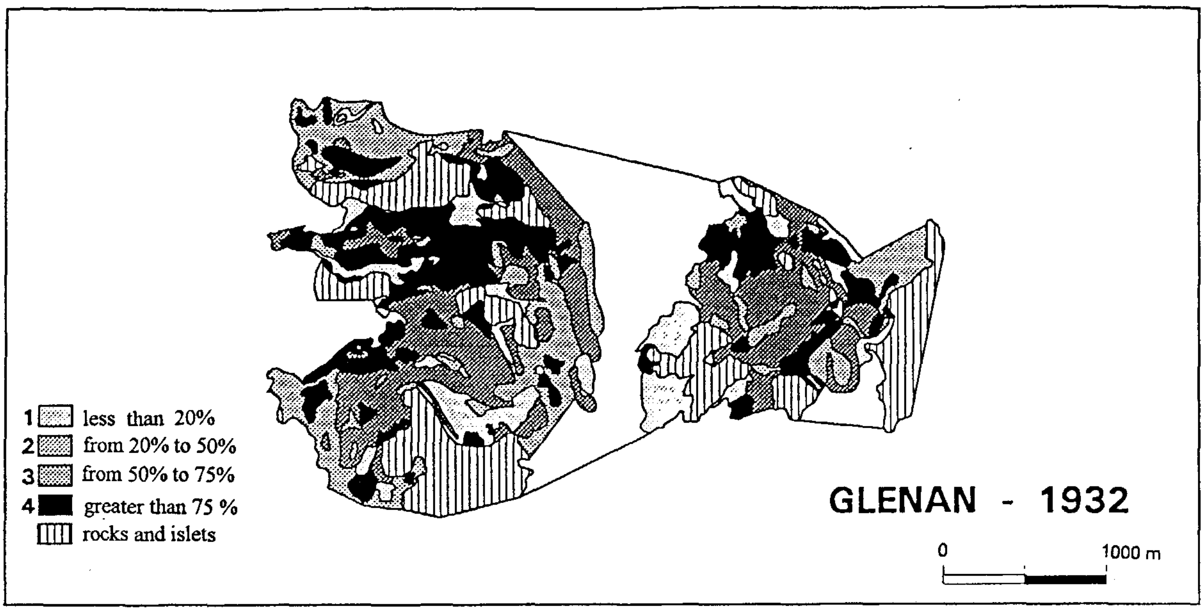
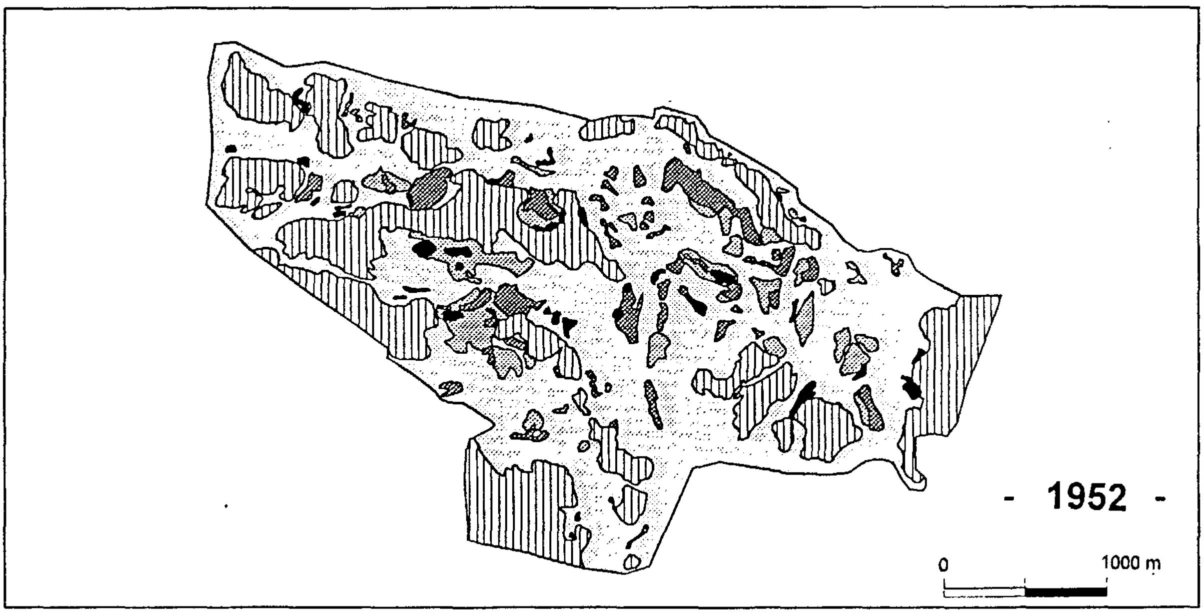
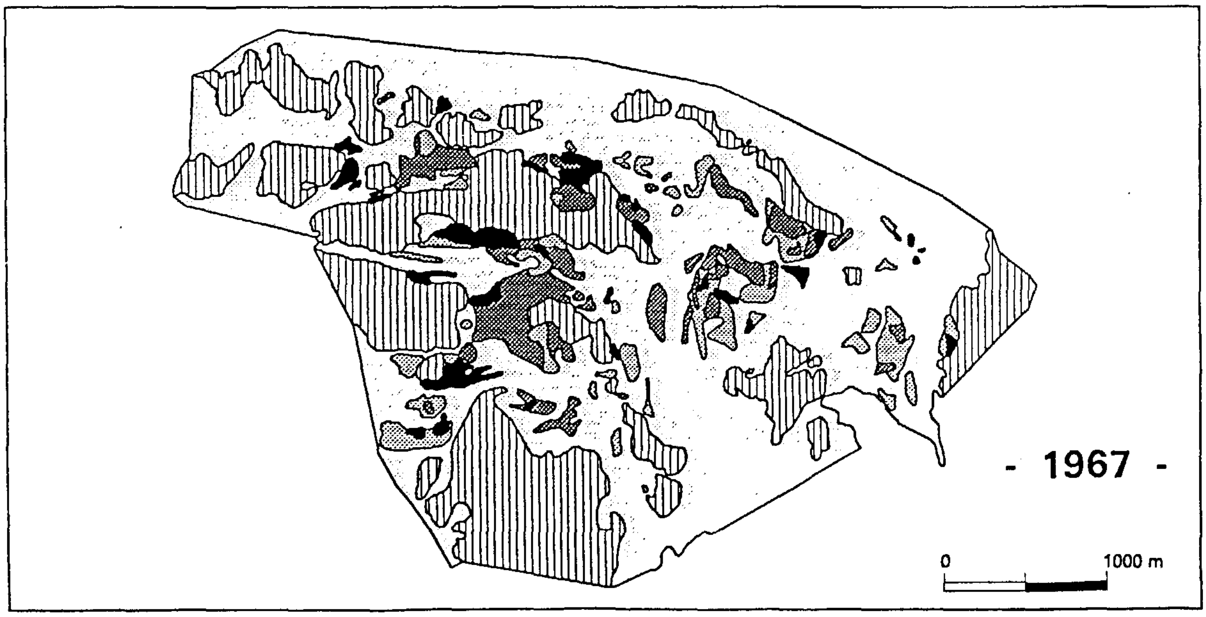


Figure 2

Glenan archipelago. Position of Zostera *beds in 1972 in relation to the principal geomorphological units. Isobaths of 5 and 10-m depth are outlined.*


1 less than 20%
2 from 20% to 50%
3 from 50% to 75%
4 greater than 75 %
rocks and islets
GLENAN - 1932
0
1000 m


- 1952 -
0
1000 m


- 1967 -
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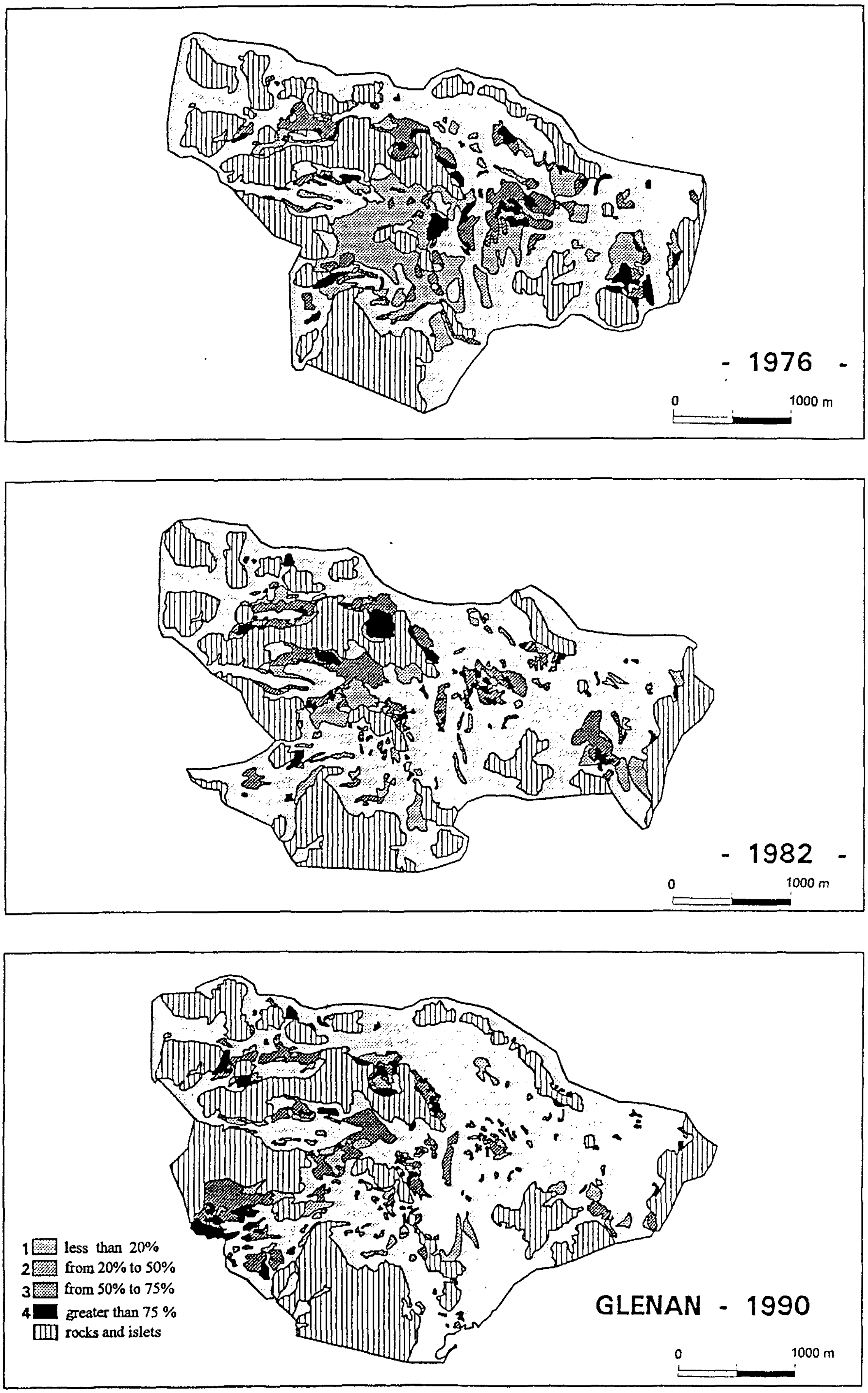

Figure 3

Development in time of the Zostera *beds in Glenan archipelago. Relative importance of the coverage indexes classes 1 to 4.*

Methodology

To establish a geographical database, we selected the most distinct photographs from a series of ten aerial surveys done between 1932 and 1990. These images were obtained by the French *Institut Géographique National* during summer between June and September, except for those of 1987, which was obtained in March by the French Navy. On the basis of the photographs, changes in the cover of the seagrass beds could be described. Interpretation of the photographs and the integration of results into the geographical database were performed as described below.

Analysis of seagrass density

The quality of the photographs, and in particular those taken before 1950, was very heterogenous, due to specular reflection and mist. It was therefore not possible to use automated methods to establish a relation between the different grey levels on the photographs and density levels of *Zostera*. Consequently, photo-mapping and transfer of results to polyester films were performed by hand. Using these techniques, *Zostera* cover was estimated and normalized to the total surface area within the study area. The results were grouped according to four coverage indices (C.I.) describing the percentage of the surface covered by *Zostera*.

- C.I.1: less than 20 %.
- C.I.2: from 20 to 50 %.
- C.I.3: from 50 to 75 %.
- C.I.4: greater than 75 %.

Integration of results into the database

The polyester films were digitalized using a scanner with a resolution of 300 dots per inch. For a scale of 1/30 000, the spatial resolution is estimated to 2.5 m × 2.5 m, and the minimum size of mapped *Zostera* patches is evaluated to 6.3 m^2. The Arc/info software package was used to integrate the data and transform them from raster mode to vector mode.

Geographical coverages

An aerial photograph is not directly superimposable on maps or other photographs. A geometrical transformation was necessary to obtain data referenced in the Lambert geographical projection normally used by the IGN. To this end, a set of wedging points on photographs and on the Glenan map, (1/25 000 IGN), with an homogeneous distribution on the study area, was selected. The mathematical transformation in X and Y between the photograph and the map were then calculated. These transformations were estimated using functions of polynomial order 2. Point coordinates were then referenced with the same geographical projection.

The final stage of the production of geographical information coverages involved associating the areas with or without *Zostera* meadows, as represented by their outlines, and the thematic information. A label was placed at the gravity centre of each polygon and a thematic code was associated with each label. The topology of the coverage was then calculated, furnishing for each polygon the following parameters:

- area of each polygon;
- perimeter of each polygon;
- thematic attributes, *i.e.* density levels.

Each polygon was then defined using any of the above attributes (C.I. classes) and if necessary with reference to the attributes of the neighbourhood polygons. These properties permit the use of advanced spatial analysis functions.

Temperature fluctuations

To interprete climatic fluctuations, we used the COADS-NOAA database (Comprehensive Ocean Atmosphere Data Set) where sea-water temperatures are regularly collected by merchant ships. From this database, we selected data collected in the geographic area within 46° N-48° N and 4° W-6° W, which is a square of convenient size to obtain a significant amount of data. In a previous paper (Glémarec, 1979), we justified the use of average temperatures from September and October to express the cumulative effects of spring and summer warming each year. To describe local air temperature changes, data from the nearest signal station – the *semaphore* of Benodet, 20 km distant – were used. All the signal station data collected before the 1950s are lost today.

RESULTS

Fluctuations in the seagrass meadows

It is possible to discern from the series of aerial photographs six situations which permit description of the general scenario of temporal fluctuations of the eelgrass (Fig. 3). Taken together, the ten surveys permit calculation of the area of the variable cover from year to year, especially in terms of clouds, and the evaluation of the respective percentages of each C.I. (Fig. 4, Table 1).

Table 1

Total surface suitable for eelgrass growth, investigated for each aerial survey and relative percentages of each C.I. class.

Year	Total surface in km^2	Percentage of each class			
		Cl 1	Cl 2	Cl 3	Cl 4
1932	5.12	15.0	24.7	33.8	26.5
1952	7.41	83.6	6.6	7.7	2.1
1961	9.15	77.5	14.3	4.0	3.6
1967	9.25	81.0	7.0	8.4	3.6
1969	7.34	76.4	7.0	10.6	6.0
1976	7.34	67.0	18.8	10.0	4.2
1978	7.13	73.8	10.7	11.8	3.7
1982	7.34	78.2	8.6	10.0	3.2
1987	6.23	80.7	8.5	7.6	3.2
1990	8.12	81.1	6.1	9.6	3.2

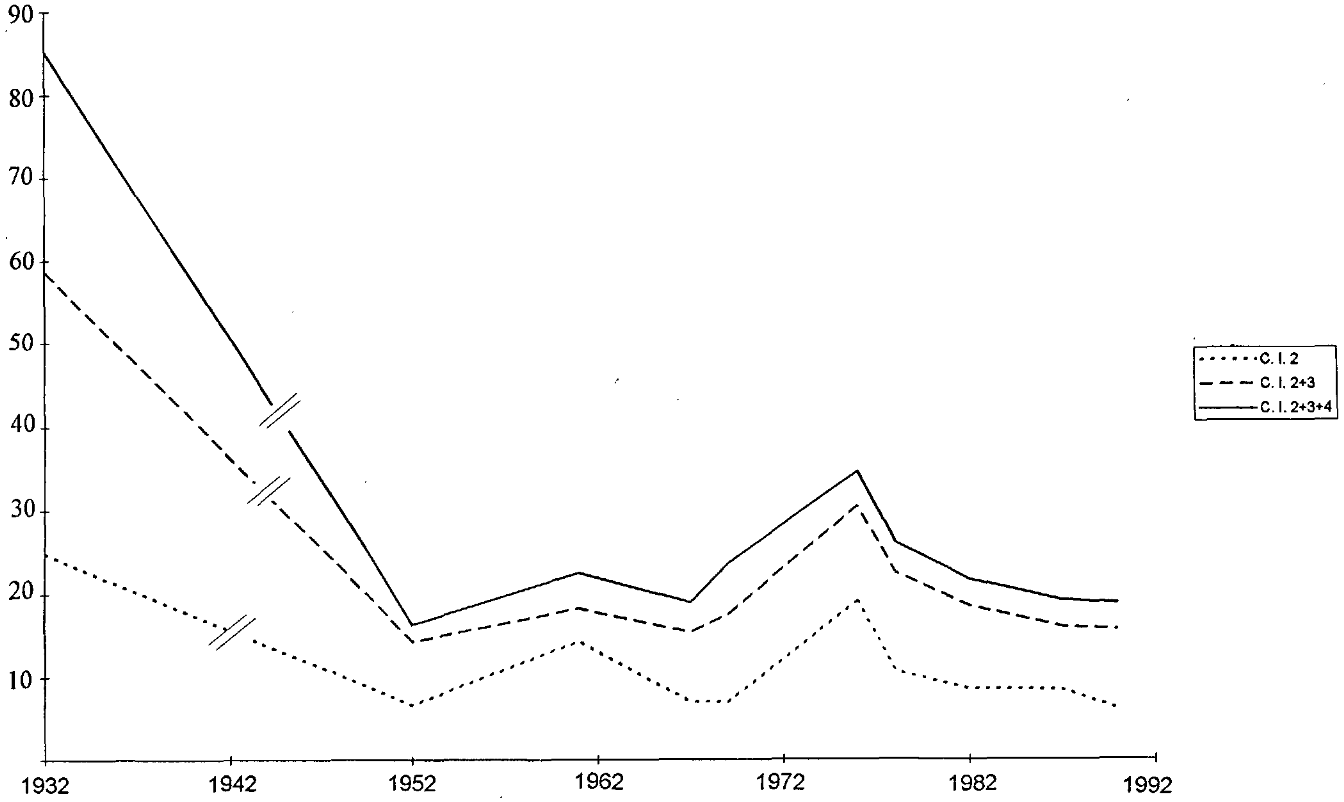

Figure 4

Relative importance of the coverage indexes 2, 3 and 4 as a function of time. Class 2 illustrates the extension phase of meadows, in 1976 for example.

1932. The situation is considered as exceptional. Practically all the suitable sediment surfaces are covered by eelgrass, with just a few bare sandy areas in the intertidal. The eelgrass appears to be in good health, and more than 25 % of the surfaces have a high frequency of coverage index 4 (C.I. 4) (Fig. 4). Unfortunately, a large part of the area is hidden by cloud cover.

1952. The situation has changed dramatically, with a minimum surface covered by *Zostera* meadows, and the index C.I. 4 covering only 2 % of the surface, while C.I. 1 represents nearly 84 % (Table 1); practically all the surfaces of sands and gravels are bare and just some residual areas of meadow appeare. The relative frequency of C.I. 3 and 4 account for less than 10 % of the total surface area.

1967. The extent of C.I. 4 is still very limited (less than 4 % of the total surface). The respective percentages of each class suggest a situation very comparable to that of 1952. Meanwhile the total surface investigated has increased, from 7.4 km^2 in 1952 to 9.2 km^2 in 1967.

1976. An intensive recovery appears to have taken place and colonization to the east is evident. The C.I.2 index dominates in comparison with the C.I.3 and 4, which suggests that the first step in colonization at this site appears on the bare surfaces of sands and gravels in the eastern part of the archipelago. The meadows are not as abundant as in 1932, however, as is demonstrated by the low frequency of areas of C.I.4. The C.I.1 index accounts for 67 % of the surfaces compared to 15 % in 1932 (Table 1).

1982. A new decline of the meadows is evident. The meadows are strictly limited to small areas essentially located in the western part of the archipelago (Fig. 3). The situation is very similar to those pertaining in 1952 and 1967.

1990. The last of the series of pictures reveals a new decline of the eelgrass. Large surfaces are bare, more than 80 %. Residual areas, characterized by the indices C.I. 3 and 4, appeared to be in the same locations as in 1967. C.I. 2 is particularly reduced, as in 1952.

After the important flourishing of the meadows in the 1930 and, to a lesser extent, in 1976, it seems that the C.I.2 index indicates meadow recovery and that the relative importance of the C.I.2 index is a means of evaluating interannual fluctuations of the meadows (Fig. 4).

Temperature fluctuations

Using the COADS-NOAA database, it is possible to confirm a general warming trend for the area 46° N-8° N and 4° W-6° W. The mean temperatures for September and October, as demonstrated elsewhere (Glémarec, 1979), show that 1922 and 1923 are the coldest years of this century. In the 1930s, warming begins, reaching its maximum at the end of the 1940s (1948 and 1949) and of the 1950s (1958, 1959). The 1960s and 1970s are characterized by an inverse trend. Cooling is maximum during the 1970s (1972 and 1974). From the mid-1970s temperatures increase until 1980 and remain more or less constant until 1990. On a more local scale, air temperature data of the nearest signal station (Fig. 6) show similar anomalies. Records before 1955 are unfortunately unavailable, everywhere in the Glenan neighbourhood. The five-year running averages (Figs. 5, 6) show more clearly the changes in the warming trend, notably in the mid-1970s. Temperatures are higher in the final than in the first quarter of this century.

Following the cool period at the beginning of the 20th century, eelgrass beds are at their maximal development. With the warming in the mid-1930s, a general decline sets in, and the situation in 1952 illustrates the minimum state of development of the cold-origin species, *Zostera marina* at such a temperate latitude as in Brittany. The double events of cooling in 1972 and 1974 coincide with an outburst of eelgrass. In the 1980s, however, a new decline becomes evident, which can be attributed to the global warming trend that seems to characterize the end of the century (Fig. 5).

DISCUSSION

In the 1930s, eelgrass beds in the North-Atlantic coastal waters were dramatically destroyed. The locally total disappearance of eelgrass has been described in numerous papers and Rasmussen (1973, 1977) was alone in evoking a warming climate as the reason for the general breakdown of this *Zostera marina* in European temperate latitudes. Many papers mention the "wasting disease" which appeared in the 1930s, and the pathogenic agent *Labyrinthula zosterae* was identified (Muehlstein *et al.*, 1988, 1991). More recently,

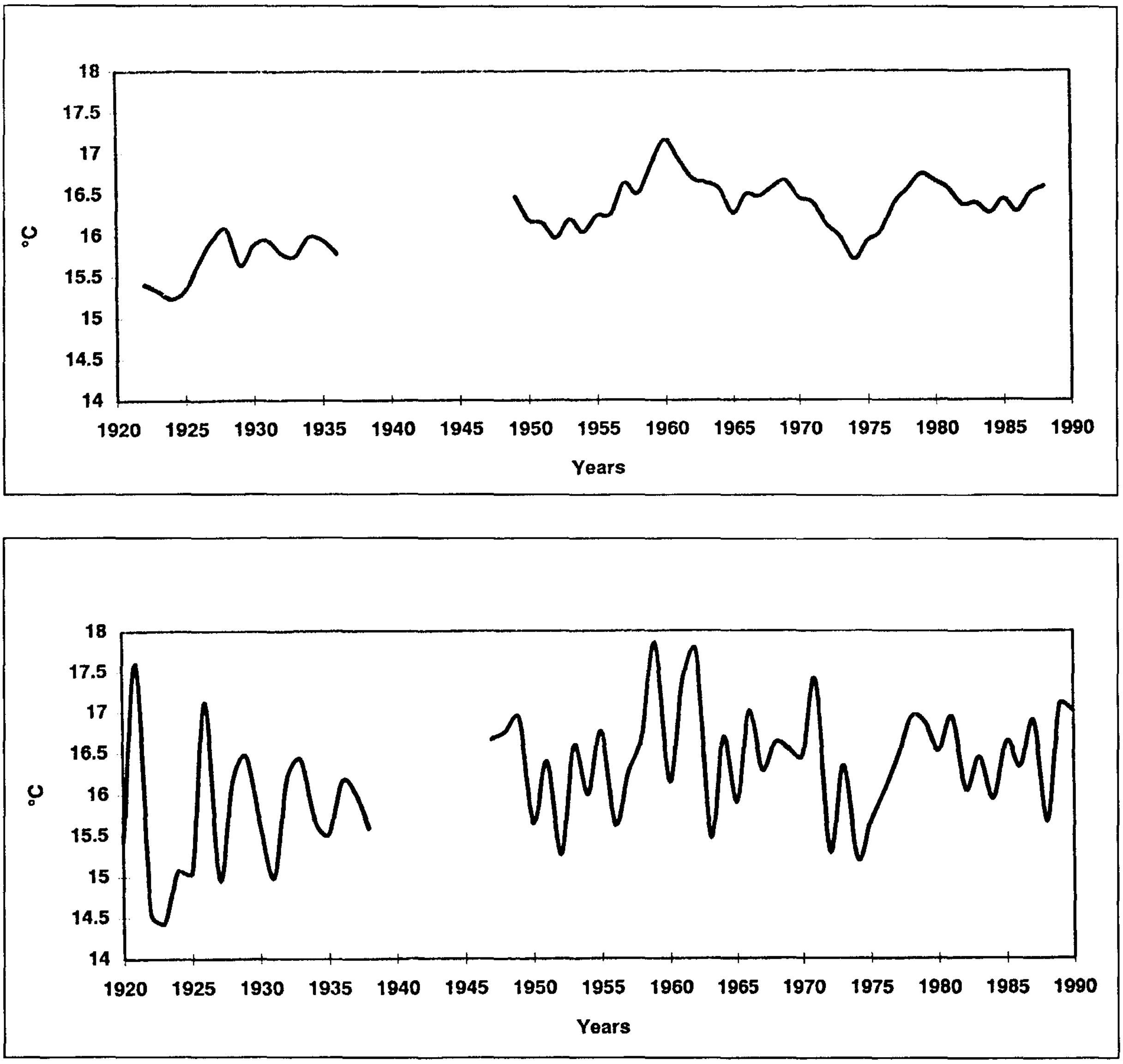

Figure 5

Below, sea-surface temperature evolution in the 46°N-48°N and 4°W-6°W square from COADS-NOAA database. Means of September and October months. Above, five-year running average.

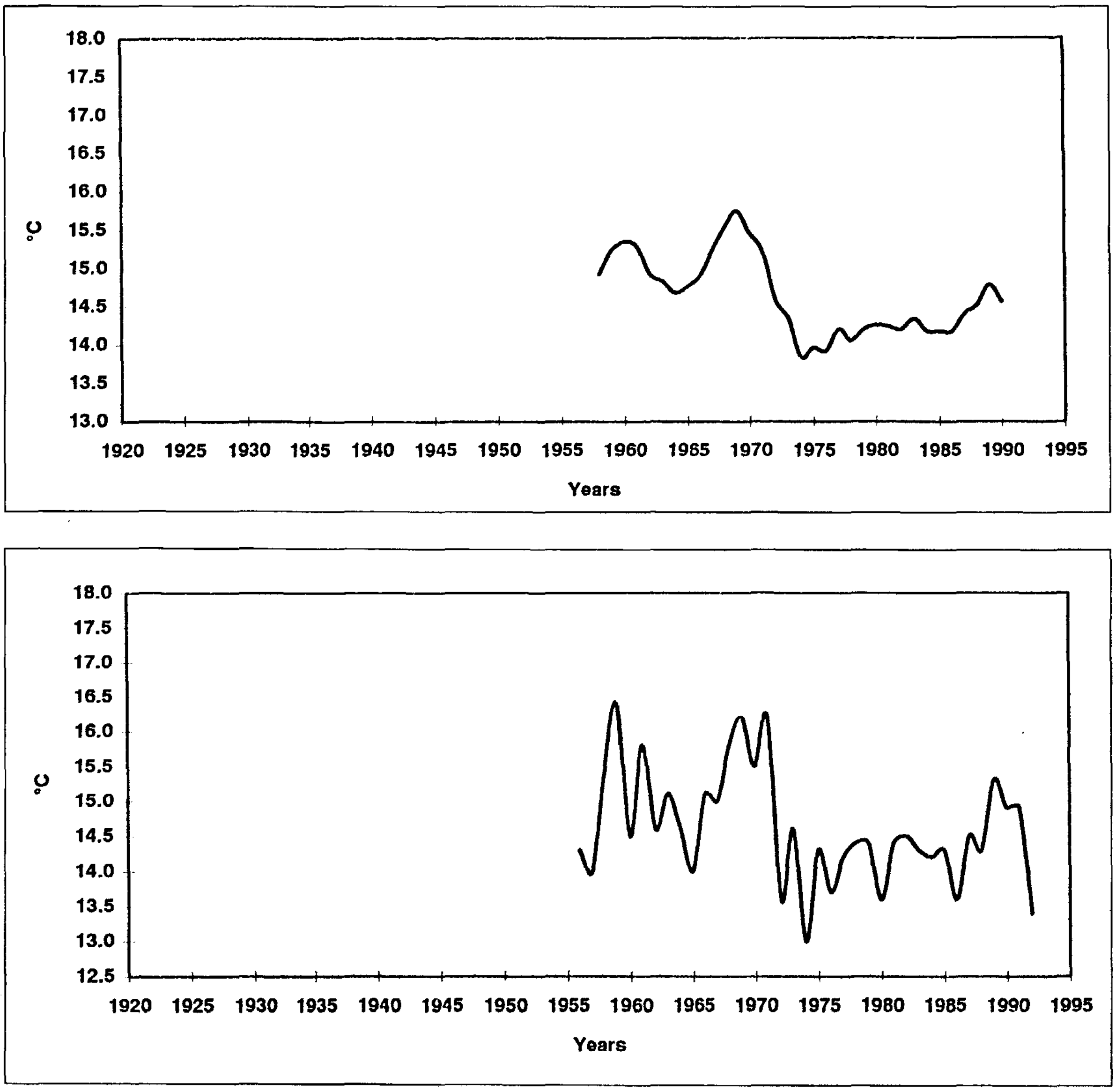

Figure 6

Below, air temperatures at the Benodet signal station from 1956 to 1992. Means of September and October. Above, five-year running average.

Den Hartog (1989) and Giesen *et al.* (1990) reconsider the role of this pathogenic agent, which plays an important role in the initial decomposition of aged plant parts. In fact, high stress (sunshine deficits, increasing turbidity) and temperature fluctuations may have placed *Z. marina* under continuous stress and this may have weakened the plants, rendering them susceptible to disease and allowing *Labyrinthula* to develop a large-scale epidemic. So the pathogenic agent is not the first cause of decline. This provides us with the opportunity to reaffirm, after our paper in 1979, the essential role of climatic factors. Jones *et al.* (1986), in describing the global warming of the planet, show the trend in global mean annual air temperature: a rise of ≈0.7 °C since 1960. From 1940 to 1960, a stagnation in the trend towards a warmer planet occurred, but only in the northern hemisphere. Farmer *et al.* (in: Houghton *et al.*, 1990) followed the evolution of sea-surface temperatures, and demonstrated that, after the evident warming from the1940s to the 1960s, cooling of the surface temperatures occurred in the 1970s. These fluctuations were described in the same manner by Billiet and Servain (1979), who examined the sea-surface temperatures on a local scale similar to ours (Marsden square 145) and identified negative and positive anomalies (between 1910 and 1970). These anomalies are negative in the mid 1910s and 1920s, becoming positive at the end of 1930s, in the 1940s and the 1950s. Warming in the mid-1930s weakened *Z. marina*; conversely, cooling at the beginning of the 1970s can explain the sudden and general outburst of eelgrass, as at Roscoff, in the Bay of Morbihan and the Glenan archipelago.

In the Roscoff area in 1909, eelgrass covered 11.6 km^2, which appears to be its maximum recorded development. After an almost total disappearance in the 1930s, which persisted up to 1957, an outburst was described in 1976 at a level equivalent to that of 1909 (12.7 km^2). But in 1977 and 1978, a new decline was observed by Jacobs (1982).

In the Bay of Morbihan, after the general decline which was evident everywhere at the beginning of 1960s (Glémarec, 1979), recovery reached its maximum in 1972, but a new decline was abrupt and dramatic (Denis and Mahéo, 1979). The coverage of 1,300-1,400/ha in 1972 subsequently decreased to 400 ha. On this site, anthropogenic actions were diversified and included clam and oyster dredging; turbidity increased as a result of eutrophication; in addition there was heavy grazing by birds in winter. It was for these reasons that we selected the Glenan archipelago, sufficiently remote from continental and anthropogenic disturbances. We attempted to separate the long-term and global warming change from the local and short-term oscillations. As the meadows are present in subtidal areas, this minimizes the short-term erosion/sedimentation cycles which affect essentially the upper meadows of *Z. noltii* in the intertidal zone. At this site, sailing school activities and tourism are well developed and the anchoring of sail boats is important but localized in time and place. Also, in the northern part of the archipelago, maerl dredging creates turbidity. Changes in the sediment composition are characteristic of short-term fluctuations. All these different disturbances are estimated to be of little importance in comparison with the obvious climate-mediated decline and sudden recovery of the seagrass beds.

Fluctuations in the zooplanctonic populations, known as the Russell cycle, are well documented. Although the cyclical nature of this phenomenon is questioned today, Southward (1980) clearly showed that a slight alteration in climatic conditions can be sufficient to account for important changes in the ecosystem. This concept of ecological amplification can be applied to the temporal fluctuations of seagrass throughout the northern hemisphere, and taken into account in making the essential point that as we reach the end of the century, *Zostera marina* has not regained the areal extent of the widespread cover observed in 1932.

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