more or less the same on all cruises except that observations north of Goa were made only on SK148 and SK149d, and only the cross-shelf transect off Goa was worked during SK138a. The shallower transect off Goa was regularly sampled (on 15 occasions) during August–December for three years (1997–1999).

Water samples during the cruises were collected using Seabird CTD (conductivity–temperature–depth) rosette systems, and hydrocasts were made with Niskin bottles for observations in shallow waters off Goa. O_2 and H_2S analyses were performed by titrimetric (Winkler) and colorimetric (methylene blue) techniques, respectively[29], within three hours of collection. Nutrients were analysed using an autoanalyser[29]. N_2O concentration was determined[25] by head-space extraction with helium followed by injection into a Hewlett-Packard 5890 Series II gas chromatograph equipped with an electron capture detector (precision ~4%). Percentage saturation was computed with reference to the solubilities given in ref. 30. For incubation experiments subsamples from a 20-litre Go-flo bottle were transferred into polyethylene-lined, airtight bags (10 litre), previously flushed with helium, avoiding any atmospheric contamination and incubated in the dark on board ship close to the *in situ* temperature. Aliquots were analysed periodically for NO_3^-, NO_2^- and N_2O.

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Microseismological evidence for a changing wave climate in the northeast Atlantic Ocean

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One possible consequence of a change in climate over the past several decades is an increase in wave heights, potentially threatening coastal areas as well as the marine industry[1–4]. But the difficulties in observing wave heights exacerbates a general problem of climate-change detection: inhomogeneities in long-term observational records owing to changes in the instruments or techniques used, which may cause artificial trends[5,6]. Ground movements with periods of 4–16 seconds, known as microseisms, are associated with ocean waves and coastal surf[7–10], and have been recorded continuously since the early days of seismology. Here we use such a 40-year record of wintertime microseisms from Hamburg, Germany, to reconstruct the wave climate in the northeast Atlantic Ocean. For the period 1954–77, we detect an average of seven days per month with strong microseismic activity, without a significant trend. This number increases significantly in the second half of the record, reaching approximately 14 days of strong microseisms per month. The implied increase in northeast Atlantic wave height over the past 20 years parallels increased surface air temperatures[11] and storminess[12] in this region, suggesting a common forcing.

Observations of the Earth's near-surface temperature show a global increase since 1901, occurring from 1925–1944 and 1978–1997. Over these periods global temperature rose by 0.37 and 0.32 K, respectively[11]. The temperature change over the past decades is unlikely to be entirely due to internal climate variability[13–15] and has been attributed to changes in the concentration of greenhouse gases caused by human activity[16,17]. There are, however, basic physical relationships between temperature, air pressure and wind fields[17,18] (and hence wave fields[4,19]). Consequently, many people are concerned about the possibility of an intensification of extratropical storms[20,21]. However, because of inhomogeneities in historical data sets, the impact of climate changes on the temporal evolution of the storm and wave climate is difficult to reveal.

In climatology, homogeneity and therefore quality of data is essential[5,6]. A climatological time series is termed homogeneous[22] if the variations exhibited by the series are solely the result of the vagaries of the weather and climate. Therefore, the methodological challenge with the analysis of historical data sets is the discrimination between signals that reflect real changes and signals that reflect changes that are attributable to improved instrumental accuracies, altered environmental conditions, observational practices, data coverage and analysis routines. In terms of wave height, data are available from reports of visual assessments from ships of opportunity and lighthouses, from river buoys and shipborne wave recorders at ocean weather stations; wave height maps have also been constructed for the purpose of ship routing from wind analyses. Analyses of these data have revealed a substantial worsening of the wave climate in the north Atlantic Ocean[1–3]. However, these data are sparse and suffer from various inhomogeneities[23].

In the late nineteenth century seismologists started to record movements of the ground continuously. In addition to ordinary earthquakes seismographs almost always record small movements in the Earth's crust, called microseisms. It has rapidly been recognized that several parts of microseisms (periods of 4 to 16 s) are strongly correlated with oceanographic forcing and atmospheric disturbances. In 1904 Wiechert[7] considered the surf to be the main cause of microseisms produced by extratropical low-pressure areas. Many authors confirmed this idea by experimental data[8,24,25]. However, microseismic energy could also be generated in the oceans away from coastal areas[9,26,27] and Gutenberg[9] showed that microseisms could be used in weather forecasting, especially in locating tropical disturbances. Later a mathematical theory was established[10,27] that explains the generation of microseisms by standing ocean waves and coastal surf. Although this permitted ocean wave heights to be calculated from seismometer data[28], most seismologists considered microseisms primarily to be noise in seismic recordings. Today, however, these data can be re-examined to assess the wave climate of the twentieth century.

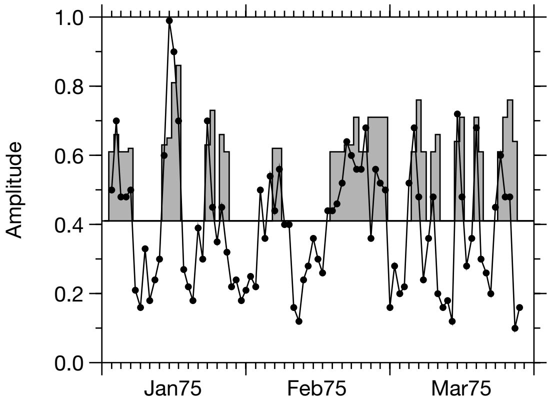

Figure 1 Correlation between daily microseism data (periods 6–8 s) from an old Wiechert pendulum and a modern Sprengnether seismometer for January–March 1975. Grey shaded areas indicate days with significant microseismic ground motions derived from the Sprengnether seismometer. The threshold amplitude for the Wiechert pendulum was changed until both instruments provided a common trend.

We have shown that microseisms at the seismological station HAM (Hamburg, Germany) are related to the northeast Atlantic wave climate[24]. Large-amplitude microseismic ground motions occurring at HAM are primarily related to secondary microseisms[10,26,27] with periods of 6–8 s. Here, we present historical microseismic data recorded between 1954 and 1998. This period covers the time where other climatological data sets detected major changes in, for example, the surface air temperature[11], the wintertime north Atlantic oscillation (NAO) index[18] and the northwestern European storm climate[4,12]. The seismic records used are those from a Wiechert vertical seismograph (1,300 kg pendulum) and a Sprengnether long-period vertical seismometer. The instruments were operated from 1954–1975 and 1974–1998, respectively. To yield absolute ground motion from different seismometers the recordings have to be convolved with an instrument-dependent response function. Historical seismological data, however, are analogue recordings. In the analysis of microseisms it is not feasible to digitize 40 years of continuously recorded data. The standard approach to obtaining daily statistics of microseisms from analogue data is to read the amplitude and frequency of the strongest microseismic ground motions over a fixed time window of 1–2 hours per day[29]. Using digital data from the wintertime microseisms of the years 1992 to 1998 (ref. 24) we were able to show that this technique provided reliable averages. In addition, we introduce a measure called the microseismic index that should be independent

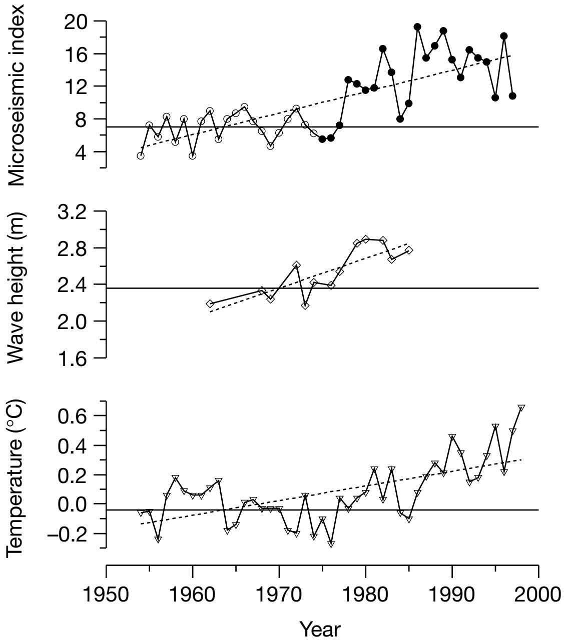

Figure 2 Time series of the wintertime microseisms recorded at the station HAM (Hamburg, Germany) over the last four decades. Microseisms at HAM are produced by waves in the northeast Atlantic and coastal surf along northern Europe's coastlines[8,10,24]; thus, they could be used to assess changes of the wave climate. Solid dots are from a Sprengnether seismometer and open dots are from a Wiechert seismometer. Also shown are the mean annual significant wave heights at the Seven Stones Light Vessel off Land's End[1] and the Northern Hemisphere temperature anomaly[11]. Horizontal lines are the 1954–1977 averages and broken lines indicate linear trends revealed by the time series.

of the instrumental response within the narrow band of periods considered in our analysis. To characterize days with strong microseisms, we define a threshold amplitude of ground movements which is significantly above the noise level and above the average microseisms recorded during summer seasons. If this threshold is reached, we consider the day to be affected by microseismic activity. Thus, the microseismic index defines the number of days per month affected by strong microseisms and is therefore more a qualitative measure indicating overall changes of the wave climate rather than a quantitative measure yielding absolute changes of wave height.

The threshold amplitude itself might be in some way arbitrary. Another value, however, merely produces a linear shift of the time series, without affecting the overall trend revealed by the data. To correlate and normalize recordings from the Sprengnether and the Wiechert seismometer we used the daily measurements and changed the threshold amplitude for the Wiechert until both instruments supported a common trend during the time of overlap. Within the relatively narrow frequency band of secondary microseisms, any bias due to differences in the response of the seismometers should be minimized. This is demonstrated by the excellent correlation between the two time series (Fig. 1). This approach provided a data set covering 40 years which has no substantial inhomogeneities. However, because most storms and the resulting strong microseisms are generally restricted to the wintertime[29], we only rely on the months October to March.

Figure 2 shows the annual averages of the microseismic index. Like other climatological time series it displays a considerable degree of year-to-year variability. There is a noticeable increase (estimated by a linear trend calculated using least squares) in the frequency of microseismic storms, that is, the number of days per month affected by microseisms increases by 0.26 per year. However, the data clearly indicate two different periods; from 1954–1977 the number of microseisms that occur increases only slightly, settling at a steady rate of 7 days per month, but increases significantly from 1978–1998 to 14 days per month. This fact is visible even in the data obtained from the Sprengnether seismometer alone; operated since 1974, it provided the lowest values in its first years. Thereafter, values double within a few years.

The same trend could be observed at the Seven Stones Light Vessel off Land's End[1] (Fig. 2). It was the first site in the world where a wave recorder was installed; annual mean values of significant wave height were used[1] to examine whether the northeast Atlantic has become rougher in recent years. The measurements published cover the years 1962 to 1985. We note that, just as for the microseismic index, annual means obtained before 1978 are always lower than those obtained thereafter. Unfortunately, there is no homogeneous data set available for comparison. However, problems of inhomogeneities were overcome by feeding a numerical wave model (WAM)[19] with historical surface pressure and wind distribution data. This simulation[19] suggested, for the Norwegian Sea at the weather station OWS Mike, an increase of significant wave heights over the period 1955–1994 of the order of 8 cm yr^{-1} for the annual maxima. The increase in wave height was even more significant in the second part of the simulated period, 1975–1994. During that time the maxima of significant wave height increased by more than 17 cm yr^{-1}. A formal correlation of microseisms and wave hindcast data gave a regression coefficient of $r = 0.4$ which increases to 0.61 when using data smoothed with a five-year gaussian filter. Even the 99 and 90 percentiles indicate similar trends. In general, however, a two-step evolution is not evident in the simulations of the WASA project. Nonetheless, the model output suggests that statistics of significant wave height in the northern North Sea and the Norwegian Sea have undergone a steady increase since 1954 (refs 4, 19). Thus, in addition to previous studies, microseisms at HAM present a new and homogeneous data set that suggests and supports a worsening of the northeast Atlantic wave climate over the last two decades.

If we compare microseisms with the Northern Hemisphere (or global) temperatures (Fig. 2) we observe a similar trend; temperatures remaining nearly at a constant level between 1954 and 1977 and a warming of 0.32 K from 1978–1997 (ref. 11). Similar trends are also revealed by the NAO index and the northwestern European storm climate[12]. A two-phase evolution, however, is not evident; but in terms of an overall increase the correlation between the time series is statistically significant. The similarities between the different climatological records strongly suggest a common forcing. Recent simulations and analyses of the Earth's temperature pattern exclude purely natural forcing and attribute it largely to changes in the concentration of greenhouse gases and aerosol loading due to human activity[13,17]. Therefore, it seems reasonable to propose that greenhouse forcing affects the ocean's wave climate and hence coastal surf and storm surges along northern Europe's coastlines, which in turn produced the observed increase of microseisms. However, large ocean waves and hence significant microseisms are generally related to the very high wind speed of storms. The storm climate itself seems to be comparable with that at the beginning of the twentieth century[4,12], though. Work is now required to backtrack microseisms and hence the wave climate into the early twentieth and late nineteenth century. Such a time series will allow us to understand the interaction between the NAO index, surface air temperature, storm frequency and intensity and the north Atlantic wave climate on a longer timescale. ☐

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Fine-scale genetic structuring on *Manacus manacus* leks

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Leks have traditionally been considered as arenas where males compete to attract females and secure matings. Thus, direct fitness benefits mediated through competition between males to fertilize females have been considered to be the primary force driving the evolution of lekking behaviour[1,2]. Inclusive fitness benefits mediated through kin selection[3] may also be involved in lek formation and evolution[4,5], but to date this theory has been largely ignored. According to kin-selection theory, both reproducing and non-reproducing males may gain indirect inclusive fitness benefits. If females are attracted to larger leks, non-reproducing males add attractiveness to a lek, and therefore, in a genetically structured population, boost the reproductive success of kin. Theory predicts that the attractiveness of leks is plastic, and that males establish themselves on a lek in which the top male, in terms of reproductive success, is a close relative[6]. Here we show that in white-bearded manakins (*Manacus manacus*), for which larger leks are more attractive to females[7,8] and so secure the maximum number of matings, there is extraordinary fine-scale genetic structure, with leks being composed of clusters of related kin. We propose that males establish themselves where they find relatives to such an extent that they form groups within leks, and that such behaviour is consistent with kin-selection theory to maximize reproductive success of the group.

Manacus manacus males aggregate on display grounds (leks) to attract females for the purpose of mating. Each male defends a small court on the lek where he performs an acrobatic display. Leks are present all year round, annual mortality is low and birds may live up to 15 years[9,10]. Birds remain at the same court all year and from one year to the next. Among these courts, however, male mating success is highly skewed[7].

It is assumed that all males on a lek aim to increase their individual fitness by fathering as many offspring as possible. There are, however, potential indirect inclusive fitness effects that could operate, which have largely been neglected as a cue for lek evolution. In many lekking species, females prefer to mate in larger male aggregations than in smaller aggregations or with single males[1], which for a number of species leads to the general positive relationship between lek size and number of mating females. This is certainly the case in *M. manacus*[7,8], for which larger lek sizes appear to attract more female visits (Spearman's coefficient of rank correlation (r_s) = 0.9, $n = 5$, $P = 0.037$; data from leks within our study in 1999 and 2000 and from two leks in ref. 7 where comparable data exist, female visits corrected for observational effort). As such, an individual could enhance his own inclusive fitness by joining a lek in which a relative is dominant and increasing the relative's reproductive success[4–6].

We used allele frequencies at four polymorphic microsatellite loci to estimate pairwise relatedness between males on two leks. Relatedness information[11] was combined with data on positions of male courts to delimit groups of related individuals. *M. manacus* males positioned themselves on a lek with relatives (Fig. 1). Furthermore, they positioned themselves in the lek to form spatially separated clusters of relatives, each with one or more reproductively successful male(s) (Fig. 2).

M. manacus females choose centrally positioned males in better physiological condition (L.S., unpublished data). Relatives may be more likely to gather around a top male and be accepted if they help in the initial attraction of females to the lek. By clustering near a top male, a family member may also improve his chances of acquiring a central court in the event of the death or injury of his successful relative. As suggested by our data, there may be more than one such family group on a single lek.

Related males may end up on the same lek by chance, as has been suggested in black grouse (*Tetrao tetrix*), for which male kin association on leks may be due to limited natal dispersal of males[4]. By forming related groups within leks, however, it seems that establishment on *M. manacus* leks cannot simply be attributed to limited male natal dispersal where males join the lek closest to their place of birth. Once on the lek, active choice among residential and newly arrived birds must take place[12], as we observed clusters of relatives within leks. Our data show that one group on each lek (group 2 in each case) consisted of individuals with a high average relatedness consistent with first-order relationships, whereas the other two groups consisted of individuals with lower average relatedness (Fig. 1). This suggests that the dynamics of reproductive sharing and competition could vary among groups within leks. Notably, the group showing the lowest average pairwise relatedness (r) (group 1 on lek 2) showed a more equal sharing of matings among the males (Fig. 2).

M. manacus individuals are unlikely to learn the characteristics of

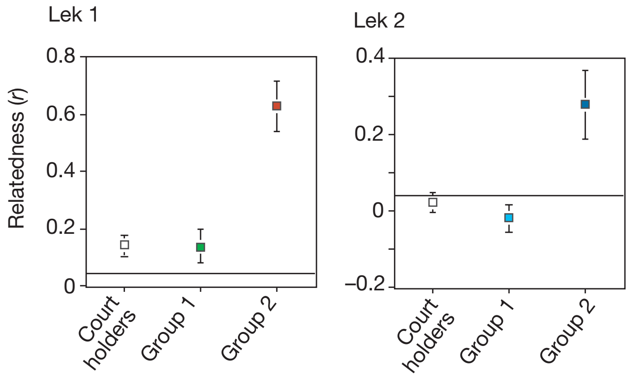

Figure 1 Mean relatedness values of male groupings. The line in each graph indicates the mean relatedness of both leks (bars indicate standard errors). Lek 1: green, group 1; red, group 2. Lek 2: light blue, group 1; dark blue, group 2. Statistical test, analysis of variance (ANOVA) in all cases. Lek 1: population versus court holders, $F_{1,2158} = 23.84$, $P < 0.0001$; population versus group 1, $F_{1,2082} = 3.95$, $P < 0.047$; population versus group 2, $F_{1,2088} = 153.3$, $P < 0.0001$. Lek 2: population versus court holders, $F_{1,2172} = 0.02$, not significant; population versus group 1, $F_{1,2094} = 1.13$, not significant; population versus group 2, $F_{1,2088} = 27.42$, $P < 0.0001$.