



Effects of regime shifts on the population dynamics of the grey-sided vole in Hokkaido, Japan

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ABSTRACT: We explored the effects of regime shifts (drastic changes usually observed in marine ecosystems, corresponding to climatic variability) in a terrestrial system focusing on a key event that occurred in 1976-77. We used data on the gray-sided vole *Clethrionomys rufocanus* (Sundevall, 1846) from 89 time series covering 31 yr (1962–1992), recorded in Asahikawa, Hokkaido, Japan, where both cyclic and non-cyclic populations occur. Wavelet analyses demonstrated a clear shift of dynamic patterns in the mid-1970s, presumably resulting from the Aleutian Low Pressure (as measured by the Aleutian Low Pressure Index). The vole populations exhibited erratic fluctuations until the mid-1970s, and then changed their pattern to cyclic fluctuations at a 4 yr interval. The structure of density dependence changed during the regime shift. Although the strength of direct density dependence was similar, delayed density dependence became stronger after the shift. Altogether these findings suggest that changing climate may affect the ecological interactions among voles, predators and resources.

KEY WORDS: Aleutian Low Pressure · *Clethrionomys rufocanus* · Cycle · Density dependence · Hokkaido

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1. INTRODUCTION

Drastic changes in marine ecosystems, called regime shifts, have been observed worldwide in response to climate change. Three major regime shifts have been recognized during the 20th century (1920s, 1940s and 1970s) in the North Pacific Ocean based on various meteorological indices (Minobe 2000). Other shifts occurred in the South Pacific Ocean in the late 1960s and the mid-1980s (Alheit & Niqen 2004) as well as the North Sea after 1987 (Reid et al. 2001, Beaugrand 2004). Among them the regime shift in the North Pacific Ocean in 1976-77 is regarded as a key event because of its profound effects on marine ecosystems (Kawasaki 2002; see also Wooster & Zhang 2004). Most

major flat fish species in the Gulf of Alaska and the Bering Seas increased from the mid-1970s to the mid-1980s in concert with other ground fish (Clark et al. 1999). Annual catches of many salmon populations in Western Alaska were abundant during that period (Hare & Mantua 2000). In addition to these observations in east of the North Pacific, similar patterns have been observed in sardine, tuna and salmon population in the west of the North Pacific (Kawasaki 2002).

Changes in population dynamics corresponding with climate modification have also been found in various other organisms (including additional fish species, shrimps, oysters, plankton, sea birds and others), that make up the bulk of the marine ecosystems of several oceans covering a large spatial scale (Hare & Mantua

2000 [Pacific], Reid & Croxall 2001 [Antarctic], Reid et al. 2001 [North Sea], Jenouvrier et al. 2005 [Antarctic]). Marine biologists have considered the concept of regime shifts as a breakthrough explanation for the dynamics of marine ecosystems. For example, although it had been assumed that many fish populations are in equilibrium with fishing effort under average environmental conditions, fluctuations in fish populations have recently been explained more effectively by global climate change than by fishing effort, because a common fluctuation pattern occurring at scales greater than one hemisphere cannot be explained without the presence of a factor operating on a global scale. Sardine populations simultaneously fluctuate in the Northeast Pacific, the West Pacific, the South Pacific and the Atlantic (Kawasaki 2002) and the dominant species in the fishery has shifted from anchovy to sardine in the Pacific Ocean (Chavez et al. 2003).

If the impact of climate modification is so widespread, we might expect some similar major changes to happen in terrestrial ecosystems in concert with oceanic regime shifts. In rodent and ungulate populations, the effects of climatic variation on their dynamics has already been demonstrated (e.g. Grenfell et al. 1998, Lima et al. 1999, 2001, 2002, Coulson et al. 2001, Forchhammer et al. 2002, Stenseth et al. 2002a,b), although regime shifts have not been implicated in these studies.

Using time series of the grey-sided vole *Clethrionomys rufocanus* (Sundevall, 1846) in Hokkaido, Japan, and focusing on the key event in 1976–77, we explored the effects of oceanic regime shift on terrestrial ecosystems. We aimed to determine whether there was a shift in vole populations that was equivalent to shifts detected in marine ecosystems. The Hokkaido vole is well suited to these analyses, as the basic features of its dynamics have already been thoroughly analyzed, and because time series of wide spatial extent are available over several decades (Stenseth & Saitoh 1998).

2. MATERIALS AND METHODS

2.1. Study animals and data

Hokkaido is the northernmost island (41° 24' to 45° 31' N, 139° 46' to 145° 49' E) of Japan and covers 78 073 km². It neighbours the Asian continent and is surrounded by the Sea of Okhotsk, the Pacific, and the Sea of Japan. Hokkaido represents the easternmost extent of the geographic distribution of the grey-sided vole (*Clethrionomys rufocanus*). The westernmost edge of their range lies in Fennoscandia (see Kaneko et al. 1998).

Forestry is a major industry of Hokkaido, where large stands of larch *Larix leptolepis* and todo fir *Abies sachalinensis* are planted every year. Because the grey-sided vole sometimes seriously damages plantations, the Forestry Agency of the Japanese government has conducted censuses of vole populations in forests for management purposes (such as for determining volumes of poisonous bait used for pest control).

These censuses have provided 225 time series datasets of varying lengths (see Saitoh et al. [1998] for census methods). Asahikawa, a region that includes both cyclic and non-cyclic vole populations (Bjørnstad et al. 1998, Saitoh et al. 1998), has the richest dataset (89 time series), taken from natural forests where pest control has never been carried out, and spanning 31 yr (1962–1992).

Based on our previous studies, the features of population dynamics of the Hokkaido vole can be summarized as follows (Saitoh 1987, Bjørnstad et al. 1996, 1998, 1999, Stenseth et al. 1996, 1998, 2002a, 2003, Saitoh et al. 1997, 1998, 1999, 2003):

- Populations fluctuated with large amplitude (10 to 100 fold); some populations exhibit clear periodicity, with the major interval of the cycle being 3 to 4 yr
- Areas of high abundance are found in northern, central and eastern Hokkaido
- Abundance of populations in central and northeastern regions is highly variable
- Cyclic patterns of abundance are found in central and northeastern regions
- Direct density dependence is significant in all populations, though it is stronger in northeastern populations
- Significant delayed density dependence is specifically detected in populations of the northeastern region
- Density dependence is stronger in winter than in summer
- In general, cyclicality, density dependence and variability are stronger in northeastern populations (colder areas).

Based on the data set of these populations, we looked for temporal changes in the abundance fluctuation pattern. We used the data on the 89 populations in Asahikawa, because they had the longest time series (31 yr, 1962–1992) and were free from the rodent control. The populations were grouped into 3 areas, based on topography (Fig. 1).

2.2. Aleutian Low Pressure Index and the North Pacific Regime

Major climate changes in the North Pacific have been linked to the Aleutian low-pressure system (Minobe 2002). Hence, we analyzed changes in population dynamics in relation to the Aleutian Low Pres-

sure Index (ALPI), defined as the mean area (km^2) with sea level pressure ≤ 100.5 kPa, averaged over December to March, and expressed as an anomaly from the 1950–1997 mean. A positive index value reflects a relatively strong Aleutian low, which may cause a severe winter in Japan, in association with its location, due to strong northwest winds from Siberia (R. Rikiishi & S. Miyahata pers. comm.). The ALPI time series is shown in Fig. 2, and is available from www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/downloads/indices/alpi.txt.

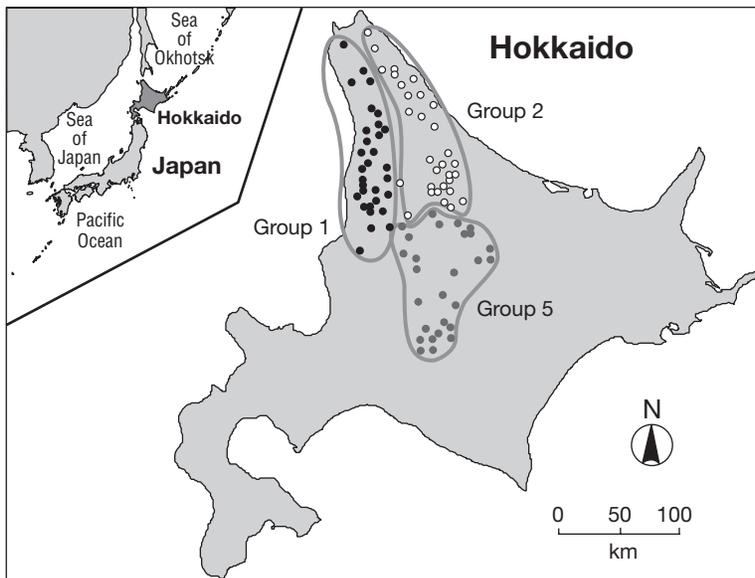


Fig. 1. Study area: vole populations were studied in the northern region of the island, in which national forests are managed by Asahikawa Regional Office, Forestry Agency of Japanese Government. The populations were grouped into 3 based on the topography. Solid circles: Group 1 ($n = 31$); open circles: Group 2 ($n = 31$); shaded circles: Group 5 ($n = 27$)

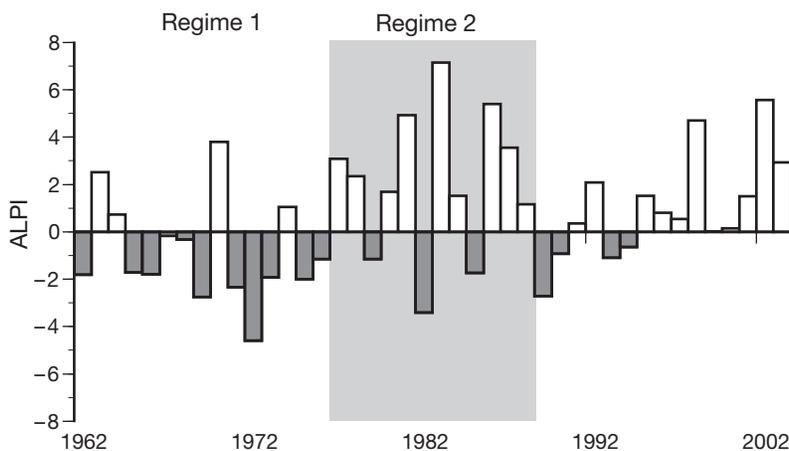


Fig. 2. Yearly change in Aleutian Low Pressure Index (ALPI), defined as the mean area (km^2) with sea level pressure ≤ 100.5 kPa, averaged over December to March and expressed as an anomaly from the 1950–1997 mean. A positive index value reflects a relatively strong Aleutian Low. A major regime shift is recognized in 1976–77 and a minor one in 1988–89 (Minobe 2000)

During the study period of the vole populations (1962–1992), a major regime shift occurred in 1976–77. Here, we denote the period between 1962 and 1976 as Regime 1 and the period between 1977 and 1988 as Regime 2, because a minor regime shift has been recognized in 1988–89 (Minobe 2000; see Beamish et al. 1997). There is no Regime 3 because it is not possible to define the end of the period that follows Regime 2.

2.3. Wavelet analysis

We applied a wavelet analysis to account for non-stationarities in population dynamics. By decomposing a time series simultaneously into time and frequency domains, the wavelet analysis can determine both the dominant modes of variability, and how those modes vary in time (Torrence & Compo 1998, Klvan et al. 2004, Jenouvrier et al. 2005). Due to a 31 yr maximum duration for time series, low frequency components having periods greater than 8 yr (corresponding to one fifth of the total length of time series) may not be well resolved. Therefore, before performing the wavelet analysis, we removed low frequencies (i.e. the trend) in our time series using a high-pass Gaussian filter, and focused then on periods between 2 and 8 yr.

We used the Morlet wavelet function Ψ_0 that is essentially a damped complex exponential function, which can quantify local cyclic fluctuations in the time series. The frequency/time range over which it does this is set by a scale parameter, (s), relating to the conventional Fourier period of oscillations, and a translation parameter η . The Morlet wavelet function is defined as $\Psi_0(\eta) = \pi^{1/4} \exp(i\omega_0\eta) \exp(-\eta^2/2)$, where ω_0 is the non-dimensional frequency (Torrence & Compo 1998). With $\omega_0 = 6$, the wavelet scale s is inversely proportional to the central frequency of the wavelet, and the frequency is equal to $1/s$, or the period p is equal to s .

The continuous wavelet transformation $W_n(p)$, of the time series X_n is calculated as the convolution of X_n with $\Psi_0(\eta)$. Local matching of wavelet function for a period p at a time point η with the signal X_n leads to a high value of $W_n(p)$. Conversely, with no matching, one obtains a low value for $W_n(p)$. The wavelet transform coefficient $W_n(p)$ represents the contribution of the scale p to the signal at a different time posi-

tion η . By taking into account a range of p and η values, one can decompose fluctuations in the signal with respect to period and time. The wavelet power spectrum (or 'scalogram') is given by $|W_\eta(p)|^2$ and gives a measure of the variance distribution of the time series at time point η and period p . The wavelet power spectrum may be averaged over time for comparison with classical spectral methods.

The significance of the high values of wavelet power spectra have been tested using bootstrapping. We have considered the null hypothesis as the temporal distribution of the variance in the observed time series being different from that expected through chance alone. We constructed 500 bootstrapped data sets, and calculated for each bootstrapped series the wavelet power spectra (see Klvana et al. 2004, Jenouvrier et al. 2005). Based on these bootstrapped series, the distribution of the wavelet power spectra can be constructed under the null hypothesis. These distributions are then used to establish the 5% significance levels.

2.4. Variability

Variability of a population is frequently measured by the s -index, which is defined as the standard deviation of logarithmic (base 10) abundance:

$$s = \sqrt{\sum (X_i - \bar{X})^2 / (n - 1)} \quad (1)$$

where $X_i = \log(N_i + 1)$, $\bar{X} = \sum X_i / n$, N_i is the number of voles caught per 150 trap-nights in year i , and n is the number of years. Standardized abundance (per 150 trap-nights) for each time series (89 populations) was divided into 2 (i.e. Regime 1: 1962–1976; and Regime 2: 1977–1988). The s -index was calculated for Regimes 1 and 2 of each time series. The s -indices were compared between the regimes for each group using paired sample t -test, because variances did not differ between the regimes.

2.5. A model for density dependence

Typically, small rodent populations exhibit an order-two autoregressive structure on an annual basis (e.g. Bjørnstad et al. 1995, Stenseth 1999). We let x_t correspond to the log-transformed 'true' abundance in year t , then, ignoring higher-order terms, the abundance in year t may be expressed using density dependence parameters α_1 and α_2 , defining the direct and delayed density dependence (Stenseth et al. 2003, Viljugrein et al. 2005):

$$x_t = (1 + \alpha_1)x_{t-1} + \alpha_2 x_{t-2} + \varepsilon_t \quad (2)$$

where ε_t is a sequence of independent and distributed random variables with a constant variance (σ^2).

The presence of sampling error may lead to substantial bias in estimates of density dependence (e.g. Kuno 1973, Bulmer 1975, Rothery 1998, Shenk et al. 1998, Solow 2001). In a previous study (Stenseth et al. 2003), sampling error was explicitly accounted for by incorporating both an ecological process model and an observation model (i.e. a state-space model; see de Valpine & Hastings 2002). By using the WinBUGS v1.4.1 software package (Spiegelhalter et al. 2003), a Bayesian approach was taken to estimate coefficients for density dependence (for detailed methodology see Stenseth et al. 2003). We estimated the coefficients for each individual population as well as for a group. In the estimation for a group, assuming a common dynamic structure within a group, the density dependence model was simultaneously fitted to each population within a group. Here, we used the mean of the posterior distributions as representatives of the parameters.

3. RESULTS

3.1. Abundance

As in a preceding study on regime shift (Hare & Mantua 2000), we present temporal changes in abundance as deviation from the average (Fig. 3). As can be seen, abundance did not show a clear shift during the study period, though average abundance in Regime 2 was slightly higher than that in Regime 1 in Groups 1 and 2 (8.34 and 9.27 for Group 1, paired sample t -test, $n = 31$, $t = 1.239$, $p = 0.225$; 7.78 and 8.95 for Group 2, $n = 31$, $t = 1.978$, $p = 0.058$). These figures were nearly equal in Group 5 (9.52 and 9.26, $n = 27$, $t = 0.313$, $p = 0.756$).

3.2. Variability

Variability was significantly higher in Regime 2 than in Regime 1 in all 3 groups; the s -index was 0.301 and 0.359 for Regime 1 and Regime 2, respectively, in Group 1 (Paired sample t -test, $n = 31$, $t = 2.57$, $p = 0.007$); 0.341 and 0.460 for Regime 1 and Regime 2, respectively in Group 2 ($n = 31$, $t = 8.08$, $p < 0.0001$); and 0.357 and 0.459 for Regime 1 and Regime 2, respectively in Group 5 ($n = 27$, $t = 5.21$, $p < 0.0001$).

3.3. Cyclicity

Wavelet analysis revealed a significant shift of the dynamic pattern in all 3 groups (Fig. 4). The scalogram

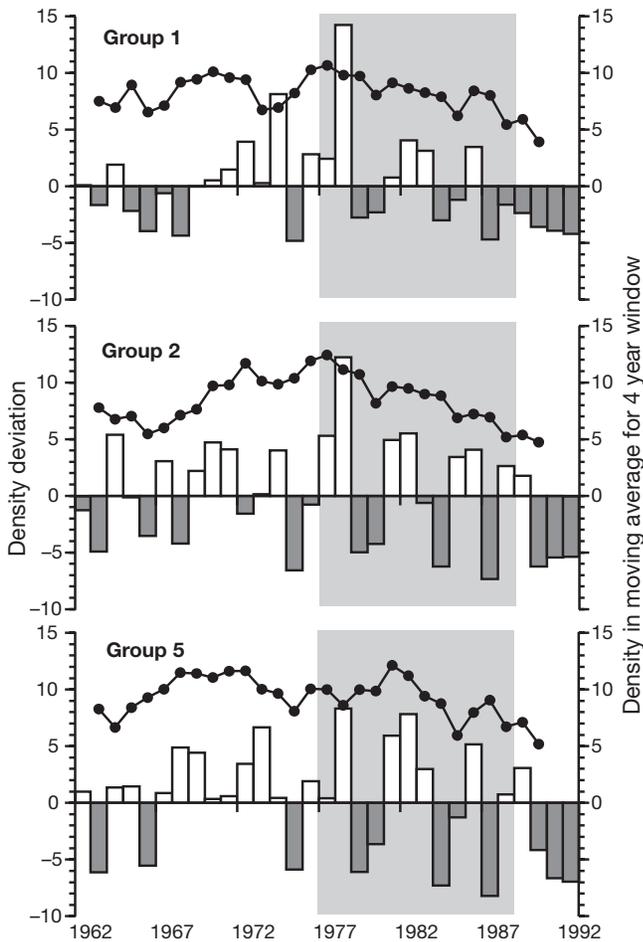


Fig. 3. *Clethrionomys rufocanus*. Yearly change in abundance of vole populations. Abundance was measured by catches per 150 trap-nights in autumn census. Abundance (bars) is represented by a deviation from the average for each group. Moving average (line), which was calculated by averaging abundance for each 4 yr, is also presented. See Section 2.1. and Fig. 1 for method of grouping studied populations. The study period was divided into 2 regimes: Regime 1, 1962–1976; Regime 2, 1977–1988 (shaded zone)

shows that the periodicity was significantly dominant around a 4 yr period between 1975 and early 1980s in Group 1, while the periodicity was unclear before 1975 and after 1985. The periodicity was clearer and lasted longer in Groups 2 and 5 than Group 1. Significant periods were around the 4 yr mode from the mid-1970s to the late 1980s for Group 2, while from early 1970s to the late 1980s for Group 5.

Altogether, all 3 groups showed similar erratic dynamics until the early 1970s, and after which changed to a cyclic pattern at 4 yr intervals in the early- or the mid-1970s. Subsequently, Group 1 returned to its previous dynamics, whereas Group 2 and 5 sustained their cyclic periodicity until the late 1980s. The shift of the dynamics patterns corresponded well to the shift in

ALPI, and the cyclic period in Groups 2 and 5 was concordant with the time period of Regime 2 (Fig. 4).

3.4. Density dependence

The estimation of density dependence coefficients (α_1 and α_2) converged successfully for 25 out of 31 time series both for Regime 1 and 2 of Group 1, and for all time series of Group 2 ($n = 31$) and Group 5 ($n = 27$). The density dependence coefficients were plotted on the parabola diagram of Royama (1977, 1992), where the relationship between the structure of density dependence and cyclicity can be shown (Bjørnstad et al. 1995). Under the parabola, where delayed density dependence is relatively strong, periodical dynamics emerges, and the strength of direct density dependence affects the interval length of the periodicity (Fig. 5).

The structure of density dependence changed between Regime 1 and Regime 2 (Fig. 5). Most points for Regime 1 in the populations of Group 1 were distributed on an upper (non-cyclic) region outside of the parabola, while most of those moved within the parameter space down into the cyclic region in the parabola in Regime 2. Similar shifts were observed in Group 2, though the points were distributed in the lower part of the panel as a whole, in comparison with Group 1. Such a shift was less clear in Group 5; points for Regime 1 were widely scattered both inside and outside of the parabola, while most points for Regime 2 were distributed in the cyclic region under the parabola.

The 95% credible intervals of the mean direct density dependence coefficient (α_1) of the two regimes substantially overlapped within an individual population. In all populations the 95% credible intervals of the difference (α_1 for Regime 1) – (α_1 for Regime 2) included zero. The mean α_1 of the common model for Group 1 was $-0.999 (\pm 0.060 \text{ SD})$ and $-0.789 (\pm 0.105 \text{ SD})$ for Regime 1 and Regime 2, respectively. Although the direct density dependence appeared stronger in Regime 1 than in Regime 2, the 90% credible intervals of the common α_1 of Regime 1 overlapped with those of Regime 2 and the 95% credible intervals of the difference (α_1 for Regime 1) – (α_1 for Regime 2) included zero. The common α_1 values ($\pm \text{SD}$) were very similar between the regimes in Groups 2 and 5—Group 2: $-1.214 (\pm 0.051)$ and $-1.147 (\pm 0.082)$ for Regime 1 and Regime 2, Group 5: $-1.064 (\pm 0.054)$ and $-1.006 (\pm 0.095)$ for Regime 1 and Regime 2, respectively. The 80% credible intervals of the difference included zero in Group 2, while even the 50% credible intervals of the difference included zero in Group 5.

Delayed density dependence was generally stronger in Regime 2 than in Regime 1. Though the 95% credible intervals of the mean delayed density dependence

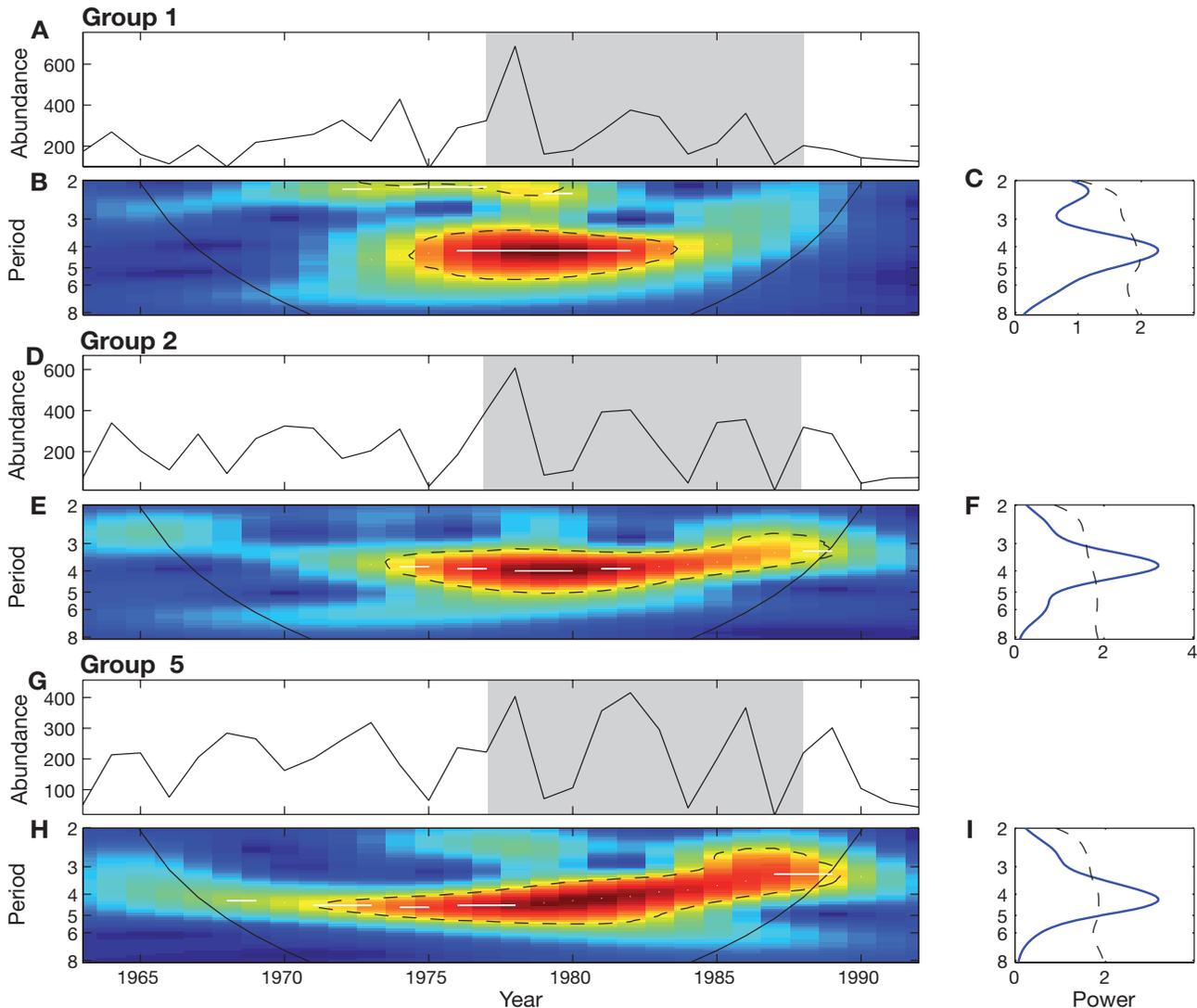


Fig. 4. *Clethrionomys rufocanus*. Wavelet analysis of average vole abundance in each group (see Fig. 1 for explanation of groups). (A–C) Group 1; (D–F) Group 2; (G–I) Group 5. (A,D,G) Vole abundance, measured by catches per 150 trap-nights in autumn census, was summed for each group. (B,E,H) Local wavelet power spectrum (scalogram). Power is coded from low values (dark blue), to high values, (dark red). Black dashed lines: bootstrapped 5% significance contours. White lines materialize maxima of the undulations of the wavelet power spectrum. Area within cone of influence (solid line): region not influenced by edge effects. (C,F,I) Global wavelet power spectrum (solid lines). Dashed lines: $p = 0.05$. Years 1962–1976 are denoted as Regime 1, and years 1977–1988 as Regime 2 (shaded in abundance panels).

coefficients of the two regimes substantially overlapped within an individual population and the 95% credible intervals of the difference (α_2 for Regime 1) – (α_2 for Regime 2) included zero in all populations but one, the common α_2 showed clear differences. The coefficient α_2 (\pm SD) of the common model for Group 1 was 0.115 (\pm 0.063) and -0.321 (\pm 0.114) for Regime 1 and Regime 2, respectively. The lower limit of the 95% credible intervals of the difference (α_2 for Regime 1) – (α_2 for Regime 2) was 0.173 and thus the probability that those were not different was very low. Similarly in Group 2, α_2 (-0.506 ± 0.087) for Regime 2 was lower than that for Regime 1 (-0.258 ± 0.054) with high prob-

ability ($>97.5\%$). Although the difference was small in Group 5 (α_2 of the common model was -0.163 ± 0.058 and -0.272 ± 0.094 for Regime 1 and Regime 2, respectively), the probability that α_2 for Regime 2 was lower than that for Regime 1 was $>75\%$.

To illustrate changes in the structure of density dependence between Regime 1 and Regime 2, we connected 2 points obtained from α_1 and α_2 of the common model for each regime by an arrow (Fig. 5). The structure of density dependence moves into a deeper area of the cyclic region in all 3 groups. These results are consistent with those obtained by wavelet analyses (cf. Fig. 4).

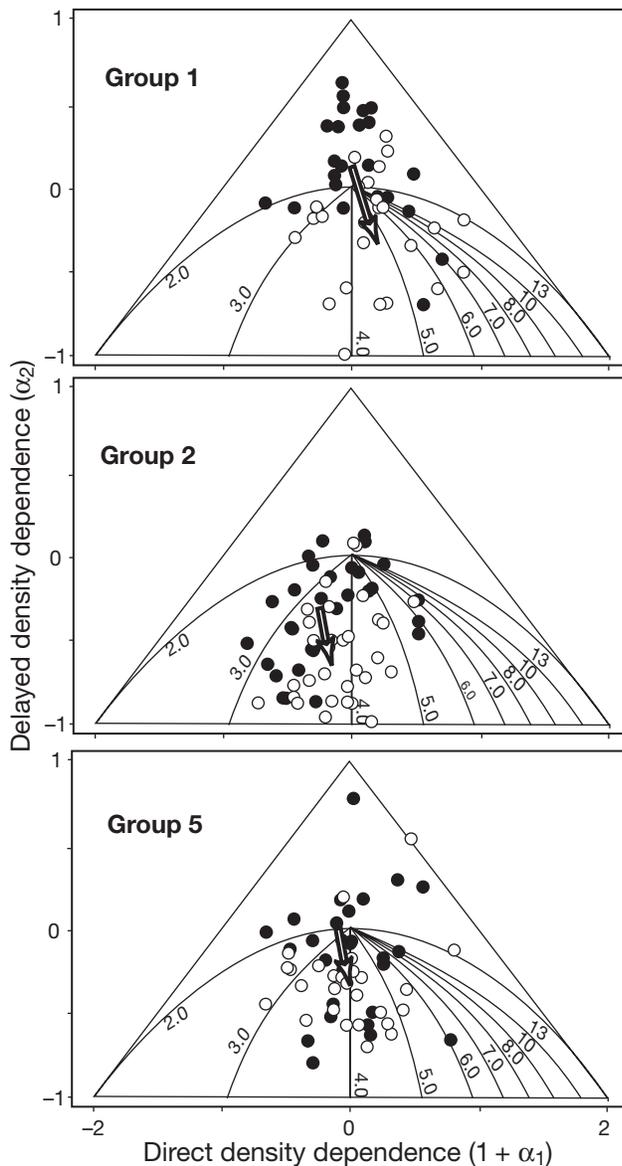


Fig. 5. *Clethrionomys rufocanus*. Structure of density dependence of vole populations for Groups 1, 2 and 5. Direct ($1 + \alpha_1$) and delayed (α_2) density dependence coefficients were plotted on the parabola diagram of Royama (1977, 1992). Solid circles: Regime 1; open circles: Regime 2. Outside the triangle the dynamics are divergent; below the parabola periodical dynamics are expected (Bjørnstad et al. 1995). Contour lines give periodicity (yr) of the cycle. Two points obtained from α_1 and α_2 of the common model for each regime are connected by arrows (see Section 3.4.), which show a shift in density dependence structure from Regime 1 to Regime 2

4. DISCUSSION

The gray-sided voles in Hokkaido changed their pattern of population dynamics during the time period corresponding to the regime shift (1976-77), from non-cyclic to cyclic dynamics, particularly in Groups 2 and 5

(Figs. 4 & 5). The density-dependence coefficients, which determine the dynamical pattern (Royama 1992), also shifted so as to increase the temporal variability of abundance (Fig. 5). However, they did not show a clear shift in their abundance over this time period (Fig. 3).

Geographic variation in the structure of density dependence of vole populations has been well studied in Fennoscandia (e.g. Stenseth et al. 1998) as well as elsewhere in Europe (Tkadlec & Stenseth 2001) and in Japan (Saitoh et al. 1997, Stenseth & Saitoh 1998, Stenseth et al. 2002a, 2003, Saitoh et al. 2003). Delayed density dependence is generally strong and prevails in Fennoscandia, whereas direct density dependence becomes weaker toward the north (Bjørnstad et al. 1995, Stenseth et al. 1998). On the other hand, a geographic gradient of the structure of density dependence of the Hokkaido vole can be characterized by variation of delayed density dependence. Delayed density dependence becomes stronger toward northeast (colder) areas of Hokkaido, where cyclic populations occur, and direct density dependence also becomes stronger toward northeast (Bjørnstad et al. 1998, Saitoh et al. 1998, Stenseth et al. 1998, 2002a). In central Europe, a similar gradient has been observed (Tkadlec & Stenseth 2001; but see Lambin et al. 2006). Based on those studies, we conclude that delayed density dependence is strong in cold areas with a short breeding season, where Hokkaido vole populations are cyclic. Thus, we may hypothesize that the increased cyclicity during Regime 2 is attributed to more severe winters in a period of generally positive ALPI (Figs. 2 & 4), resulting in stronger delayed density-dependence (Fig. 5). However, we were unable to detect such a worsening of winter climate in Hokkaido. Temperature and snow depth remained similar after the shift, although mean precipitation was lower in Regime 2. On the other hand, it is likely that vole ecology depends on temperature and precipitation in a highly nonlinear manner (e.g. being sensitive to episodes of freezing and thawing).

Predators are the most plausible agents for density dependence. The abundance of specialist predators which rely on rodent prey for reproduction are generally thought to track rodent densities with a time delay, whereas generalist predators are regarded as an agent of direct density dependence (Hassell & May 1986, Hanski et al. 1991, Hanski & Korpimäki 1995, Klemola et al. 2003). In Fennoscandia predator-prey interactions have been invoked to explain the geographic gradient (from cyclic to stable) in cycling periods and population amplitudes (Hansson & Henttonen 1985, 1988, Henttonen et al. 1985, Hanski et al. 1991, Turchin & Hanski 1997). Effects of generalist predators are reduced in the north, because the mammalian predator fauna is biased towards specialists and hunting by generalists is prevented by heavy snow in wintertime in northern Fennoscandia.

In Hokkaido, cyclic populations with strong delayed density dependence are also found in colder areas (northeastern parts). However, since there is no evidence of a different predator fauna in those areas, and heavy snow is frequently observed in non-cyclic regions, the geographic gradient in the Hokkaido vole cannot be explained by the predator community hypothesis of Hansson & Henttonen (1988), although specialist predators are still the most plausible agents of delayed density dependence in Hokkaido (Saitoh et al. 1999). Other proposed mechanisms of density dependence include social interaction, trophic interaction and disease (Lambin et al. 2000, 2006, Graham & Lambin 2002, Saitoh et al. 2003).

In marine ecosystem climatic variations are regarded as the driving force generating drastic changes in abundance of organisms. For example, it is thought that long-term variations in Japanese sardine catches are related to the interdecadal North Pacific ocean/climate variability (Yasuda et al. 1999). A plausible mechanism is as follows: the low sea-surface temperature (SST) in the migration route of the sardine may be a result of intensified westerly wind caused by an amplified Aleutian Low Pressure. Increased winds and low SST are usually accompanied by an increase in biological productivity because additional nutrients are brought to the surface in winter. This higher productivity might increase recruitment of the sardine. In marine ecosystems, regime shifts appears to influence productivity, and consequently the carrying capacity of various populations.

Terrestrial impacts of climatic variations appear to differ from those found in marine ecosystems. In the Hokkaido vole, the regime shift affected the structure of density-dependence rather than mean abundance, in contrast to what has been found in marine systems. Recently, temporal changes in fluctuation patterns have been observed in some vole populations of Fennoscandia (Hansen et al. 1999, Henttonen 2000, Hörnfeldt 2004), where density and amplitude of variation have declined from the 1980s. Many explanations have been suggested, but the causes remain unclear (Hörnfeldt 2004). Bierman et al. (2006) found a temporal change in fluctuation patterns in *Microtus agrestis* populations of England using long-term time series data (1984–2000). These populations exhibited a periodic cycle during the first half of the study period, while the periodicity became unclear by the end of their study. They hypothesized that the shortening of the winter season had reduced the period over which the delayed density dependent process worked, since the amount of snow cover and length of the winter season decreased during the study period. Although the severe winter hypothesis seems applicable to the regime shift, we cannot explain the shift of population

dynamics in the Hokkaido vole by this hypothesis, because there was no clear difference in local weather between the regimes as mentioned above.

A possible explanation, which has not been examined, is the effect of energy flow between ecosystems, to connect the regime shift in the ocean with the shift of population dynamics in the Hokkaido vole. Productivity in North Pacific rose during Regime 2. Salmon, minnow and other species, which use both ecosystems of the ocean and rivers, may have increased in their biomass in the ocean and returned to rivers. The river system of Hokkaido is very rich, with more than 2000 rivers of various sizes running through forests and fields (www.pref.hokkaido.jp/kensetu/kn-kasen/kasenkahome/coverp.htm; site in Japanese). Biomass in rivers of Hokkaido may have been enriched during Regime 2 owing to the energy flow from the ocean. Thus, generalist predators (e.g. the red fox *Vulpes vulpes*, the Japanese weasel *Mustela itatsi* and the American mink *M. vison*) may have depended more on resources from rivers (or sea shore) during Regime 2. According to the food shift of generalist predators, effects of specialist predators (e.g. *M. nivalis*), which is an agent of delayed density dependence, may have been more important in Regime 2 than in Regime 1, and consequently the vole populations in Hokkaido may have exhibited cyclic dynamics during Regime 2. Roth (2003) demonstrates that marine resources affect arctic fox abundance in Canada and suggests that they may delay the recovery of low lemming populations (see Rose & Polis 1998 for other examples). Inputs of allochthonous resources could modify food-web dynamics (Polis et al. 1997, Huxel & McCann 1998, Jefferies 2000).

Rodent cycles represent an enigma which has been puzzling many ecologists since Elton (1924). At least 22 hypotheses have been proposed on how the cycles are generated (Batzli 1992). Many of the hypotheses try to explain the cycle using a single factor and they have been tested by experiments in the field. However, there is still no hypothesis that is fully supported (e.g. Krebs 1996), though the predation-based explanation has recently gained many supporters (Turchin & Hanski 2001, Klemola et al. 2003). The rodent cycle may be more complex than expected. The rodent cycle should be considered as an ecological interaction, but not as simple response to a single factor (e.g. food or a climate factor), as the present results suggest.

The results reported in this paper suggest that climatic variation may change an ecological interaction governing the dynamic pattern of vole populations, yet have little effect on mean long-term abundance. Thus it may not be possible to predict the dynamics of vole populations directly by measures of climatic variability. However, if we could demonstrate that climatic

variations modify seasonality that is closely related to life history characteristics of voles (e.g. length of the breeding season or non-breeding winter period) and density dependence agents (e.g. predators, food and disease), we would be able to predict changes in dynamic pattern, since the structure of density dependence is influenced by seasonality (Stenseth et al. 1998, 2002a, 2003, Saitoh et al. 2003).

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