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Special feature
Population Ecology of
Clethrionomys rufocanus

The Population Dynamics of the Vole *Clethrionomys rufocanus* in Hokkaido, Japan

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Abstract. Population dynamics of the gray sided-vole, *Clethrionomys rufocanus,* in Hokkaido, Japan were described on the basis of 225 time series (being from 12 to 31 years long); 194 of the time series have a length of 23 years or longer. The time series were classified into 11 groups according to geographic proximity and topographic characteristics of the island of Hokkaido. Mean abundance varied among populations from 1.07 to 21.07 individuals per 150 trap-nights. The index of variability for population fluctuation (*s*-index) ranged from 0.204 to 0.629. Another index for population variability (amplitude on log-10 scale) ranged from 0.811 to 2.743. Mean abundance and variability of populations were higher in the more northern and eastern regions of the island. Most populations, except for the southernmost populations, exhibited significant direct density-dependence in population growth. Detection rate for delayed density-dependence varied among groups from 0% to 22.6%. Both direct and delayed density-dependence tended to be stronger in the more northern and eastern populations. The proportion of cyclic populations was higher in the northern-eastern areas than that in the southern-western areas. There was a clear gradient from the asynchronous populations in southwest, to the highly synchronized populations in the northeast.

Key words: cycle, density-dependence, geographic gradient, population variability, spatial scale, regional synchrony.

Introduction

Population dynamics of small rodents have been of focal interest to ecologists ever since Elton (1924). Our appreciation and understanding of the pattern of fluctuation has improved greatly during the last few decades, partly due to the accumulation of relatively long time series (Saitoh 1987; Turchin 1990; Hörnfeldt 1994; Saucy 1994; Bjørnstad et al. 1995; Stenseth et al. 1996a, 1998a; Saitoh et al. 1998). The most extensive set of data on any small rodent species is the census data on the gray-sided vole (*Clethrionomys rufocanus* (Sundevall, 1846)) in Hokkaido, Japan. The part of these data that covers the northern region of Hokkaido, have already been analyzed and reported (Saitoh 1987; Bjørnstad et al. 1996, 1998a; Stenseth et al. 1996a; Saitoh et al. 1997, 1998). Within this northern area, Saitoh et al. (1997, 1998) documented direct density-dependence in the growth rate of all populations and delayed density-dependence in a significant proportion of them. Stenseth et al. (1996a) uncovered a geographic gradient in temporal variability and in strength of delayed density-dependence. Northeastern and inland populations are more variable than populations along the northwestern coast, and this correlates with an increase in the lags in regulation. Both aperiodic and multiannually periodic fluctuations were observed with 2–5 years between peaks (Bjørnstad et al. 1996; Stenseth et al. 1996a; see also Bjørnstad et al. 1998b). Bjørnstad et al. (1996) found that the gradient in variability reflected a geographic transition in cyclicity. Geographic synchrony was found to be extensive, and the spatial scale of synchrony in dynamics was found to be of the order of 50 km (Bjørnstad et al. 1998a).

Here we provide a comprehensive account of the population dynamics of the gray-sided vole using an extended set of time series covering the entire island of Hokkaido. We also synthesize much of the earlier work on this species

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in Hokkaido. Specifically we describe the basic characteristics of population dynamics of the species in Hokkaido (abundance, variability, density-dependence, cyclicity, and spatial synchrony). We show that the pattern observed in the northern area of Hokkaido is part of a larger island-wide pattern. Our discussion is throughout put into the more general framework of geographic patterns in fluctuating microtine populations (particularly that seen in Fennoscandia; cf. Hannson and Henttonen 1985; Henttonen et al. 1985).

Materials and methods

Hokkaido, the study area

Hokkaido is the northernmost island of Japan (41°45′–45°31′ N, 139°53′–145°49′ E) and covers 78,073 km^2. It neighbors the Asian continent (Fig. 1a), and is surrounded by the Sea of Okhotsk, the Pacific, and the Sea of Japan. A southern warm current prevails in the Sea of Japan along the western shore of Hokkaido, whereas northern cold currents prevail in the Pacific along the northern and eastern shores (Fig. 1a). Mountain ridges run north-south through the middle of the island; in the south-western part there is another mountain-ridge (Fig. 1b). Hokkaido represents the easternmost part of the gray-sided voles' distribution ranging from its westernmost edge in Fennoscandia (see Kaneko et al. 1998).

Except for the southwestern peninsula that harbors temperate deciduous forest, most of the natural forests in Hokkaido is classified as the 'pan mixed forest' with conifers and broad-leaved trees. This may be regarded as the transition between the temperate and the subarctic zones (Tatewaki 1958; Fig. 1c). The dominant tree genera are *Abies, Acer, Betula, Picea* and *Quercus* (Tatewaki 1958).

Many vole predators inhabit in Hokkaido: mustelids (*Mustela nivalis, M. itatsi, M. vison, Martes zibellina* and *Mustela erminea* in the order of assumed importance), the red fox (*Vulpes vulpes*), owls (*Strix uralensis* and *Asio otus*) and snakes (*Elaphe climacophora, E. conspicillata, E. quadrivirgata* and *Agkistrodon blomhoffii*). Even though the main predators in Hokkaido (*M. nivalis* and *V. vulpes*) are the same as those in northern Fennoscandia, more generalist predators (e.g. snakes) are found in Hokkaido (Henttonen et al. 1992). A rich alternative prey community (hares, grouse, and frogs) also characterizes Hokkaido (Henttonen et al. 1992). Most predators, however, selectively take the gray-sided vole (Yoneda 1979; see also Kaneko et al. 1998). With respect to flora and fauna, Hokkaido thus bears some resemblance to the southern transition zone in Fennoscandia (Hansson and Henttonen 1988). Notice, however, that no *Microtus* is found in Hokkaido.

In Hokkaido the gray-sided vole is a pest species on plantations of larch (*Larix kaempferi* (Lambert)) and todo-fir (*Abies sachalinensis* Fr. Schmidt) (Kaneko et al. 1998). It is also abundant in natural forests (Ota 1984). The data used for this paper is the direct results of census of the gray-sided vole for the purpose of pest control and outbreak forecasting (for further discussion, see Kaneko et al. 1998).

Census methods and data arrangement

Since 1954 the Forestry Agency of the Japanese Government has carried out monitoring censuses of vole populations for management purposes at approximately 1,000 sampling stations in forests all over Hokkaido. The forests managed by the Forestry Agency cover 28,400 km^2 (21,500 km^2 natural forests, and 6,900 km^2 planted forests; 1992-figures). These forests were in 1992 managed by 76 District Offices, which were themselves subdivided into several Ranger Offices, giving a total of 433 Ranger Offices. The censuses were carried out by the individual Ranger Office which also represents our basic unit of analysis; personnel at the Ranger Offices were regularly trained for performing the censuses, including species identification (see Kaneko et al. 1998).

Trapping was carried out three times a year (spring (May/June), summer (July/August) and fall (September/October)) on 0.5 ha (50 × 100 m) grids, where 50 snap traps were set at 10 m intervals for three nights (i.e. 150 trap-nights; but see below for exceptions). Since abundances usually reach their maxima in fall in Hokkaido (Saitoh 1987; Saitoh et al. 1998), fall data were used in this study (as used in Bjørnstad et al. 1996, 1998a, b; Stenseth et al. 1996a; Saitoh et al. 1997, 1998).

Each Ranger Office censused 2-6 separate grids. Census grids were located in fixed preselected habitats (planted forest and natural forests neighboring a plantation, which together constituted a unit). The census grids were occasionally relocated within the area of a given Ranger Office. With a few exceptions (see below), we only used data from natural forests (pesticides were occasionally applied to the plantations). These natural forests represent the indigenous habitat of the species.

The ranger offices belong to five Regional Offices, which provide time series of different length: Asahikawa, 31 years (1962–1992) for 89 populations (Groups 1, 2 and 5; see below); Kitami, 27 years (1966–1992) for 20 populations (Group 3); Hokkaido, 23 years (1970–1992) for 50 populations (Groups 4, 7 and east half of Group 6); Hakodate, 23 years (1970–1992) for 50 populations (Group 8 and west half of Group 6); and Obihiro, 12 years (1981–1992) for 31 populations (Groups 9, 10 and 11). Since census data in natural forests of Obihiro region were

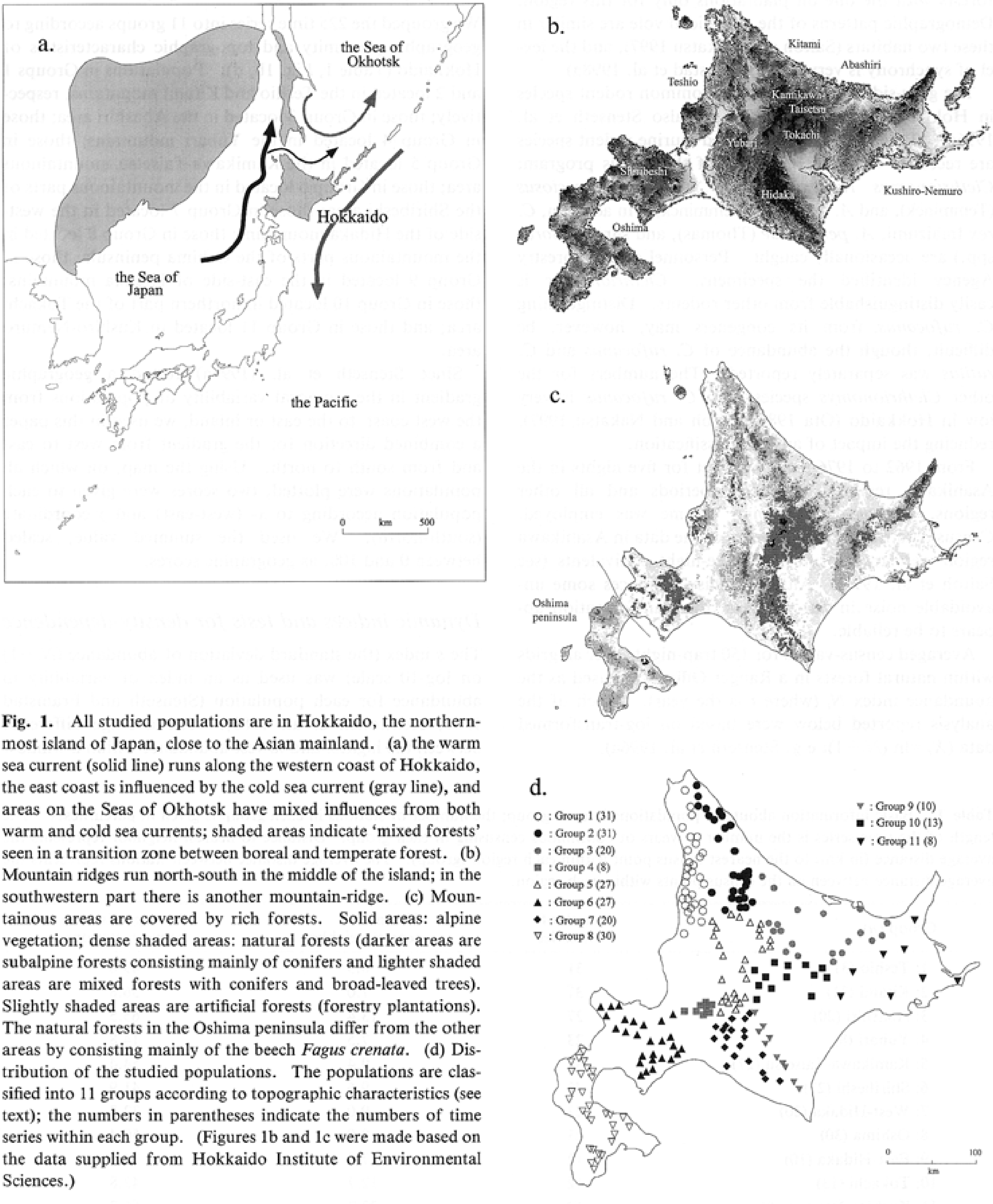

Fig. 1. All studied populations are in Hokkaido, the northernmost island of Japan, close to the Asian mainland. (a) the warm sea current (solid line) runs along the western coast of Hokkaido, the east coast is influenced by the cold sea current (gray line), and areas on the Seas of Okhotsk have mixed influences from both warm and cold sea currents; shaded areas indicate 'mixed forests' seen in a transition zone between boreal and temperate forest. (b) Mountain ridges run north-south in the middle of the island; in the southwestern part there is another mountain-ridge. (c) Mountainous areas are covered by rich forests. Solid areas: alpine vegetation; dense shaded areas: natural forests (darker areas are subalpine forests consisting mainly of conifers and lighter shaded areas are mixed forests with conifers and broad-leaved trees). Slightly shaded areas are artificial forests (forestry plantations). The natural forests in the Oshima peninsula differ from the other areas by consisting mainly of the beech *Fagus crenata*. (d) Distribution of the studied populations. The populations are classified into 11 groups according to topographic characteristics (see text); the numbers in parentheses indicate the numbers of time series within each group. (Figures 1b and 1c were made based on the data supplied from Hokkaido Institute of Environmental Sciences.)

very fragmented, we combined the census data in natural forests with the one on plantations only for this region. Demographic patterns of the gray-sided vole are similar in these two habitats (Saitoh and Nakatsu 1997), and the level of synchrony is very high (Bjørnstad et al. 1998a).

The gray-sided vole is the most common rodent species in Hokkaido (Ota 1958, 1984; see also Stenseth et al. 1996a). Three other microtine and murine rodent species are recorded as an integral part of the census program: *Clethrionomys rutilus* (Pallas), *Apodemus speciosus* (Temminck), and *A. argenteus* (Temminck). In addition, *C. rex* Imaizumi, *A. peninsulae* (Thomas), and shrews (*Sorex* spp.) are occasionally caught. Personnel of the Forestry Agency identified the specimens. *Clethrionomys* is easily distinguishable from other rodents. Distinguishing *C. rufocanus* from its congeners may, however, be difficult, though the abundance of *C. rufocanus* and *C. rutilus* was separately reported. The numbers for the other *Clethrionomys* species than *C. rufocanus* is very low in Hokkaido (Ota 1984; Saitoh and Nakatsu 1997), reducing the impact of any misclassification.

From 1962 to 1976 traps were set for five nights in the Asahikawa region. For other periods and all other regions, a three-day trapping scheme was employed. Census data for the first 15 years of the data in Asahikawa region were transformed to three-night equivalents (see Saitoh et al. 1997). Although this introduces some unavoidable noise in our analyses, the transformation appears to be reliable.

Averaged census-values for 150 trap-nights over all grids within natural forests in a Ranger Office were used as the abundance index N_t (where t is the year). Much of the analysis reported below were based on log-transformed data ($X_t = \ln(N_t+1)$; e.g. Stenseth et al. 1996a).

Grouping and geographic scoring of the time series

We grouped the 225 time series into 11 groups according to geographic proximity and topographic characteristics of Hokkaido (Table 1, Fig. 1b, d). Populations in Groups 1 and 2 located in the Teshio and Kitami mountains, respectively; those in Group 3 located in the Abashiri area; those in Group 4 located in the Yubari mountains; those in Group 5 located in the Kamikawa-Taisetsu mountainous area; those in Group 6 located in the mountainous parts of the Shiribeshi area; those in Group 7 located in the west-side of the Hidaka mountains; those in Group 8 located in the mountainous parts of the Oshima peninsula; those in Group 9 located in the east-side of Hidaka mountains; those in Group 10 located in northern part of the Tokachi area; and those in Group 11 located in Kushiro-Nemuro area.

Since Stenseth et al. (1996a) found a geographic gradient in the temporal variability of populations from the west coast to the east or inland, we used in this paper a combined direction for the gradient from west to east and from south to north. Using the map, on which all populations were plotted, two scores were given to each population according to x- (west-east) and y-coordinate (south-north). We used the summed value, scaled between 0 and 100, as geographic scores.

Dynamic indices and tests for density-dependence

The s-index (the standard deviation of abundance (N_t+1) on log-10 scale) was used as an index of variability in abundance for each population (Stenseth and Framstad 1980; Henttonen et al. 1985). The average difference between the highest and lowest abundance within a window

Table 1. Basic information about the populations in each group; the number of stations in each group is given in parentheses. The length of the time series is the number of years of continuous censusing in each group. Distance to nearest neighbor represents the average distance (in km) to the nearest census point within each region (group). The average distance between stations represents the average distance between all the census points within each region.

Group (n)	Length of time series	Distance to nearest neighbor	Average distance between stations
1: Teshio (31)	31	8.5	49.8
2: Kitami (31)	31	7.0	56.8
3: Abashiri (20)	27	13.4	65.5
4: Yubari (8)	23	7.5	14.8
5: Kamikawa-Taisetsu (27)	31	9.4	54.4
6: Shiribeshi (27)	23	9.6	41.9
7: West-Hidaka (20)	23	9.0	32.3
8: Oshima (30)	23	8.0	50.4
9: East-Hidaka (10)	12	7.5	34.9
10: Tokachi (13)	12	12.7	42.8
11: Kushiro-Nemuro (8)	12	23.3	66.2

corresponding to the dominating cyclic period (4 years; see below) was used as an index of amplitude of the fluctuations. An equivalent index for amplitude was also calculated based on abundance (N_t+1) on log-10 scale.

Testing for density-dependence was done according to Saitoh et al. (1997). Three methods were used: (1) Bulmer's autocorrelation method (R; Bulmer 1975), (2) the bootstrap test of Dennis and Taper (1994) employing a Gompertz model as the alternative hypothesis, (3) the bootstrap method for delayed density-dependence based on an extension of Dennis and Taper (1994, see Holyoak 1994; Saitoh et al. 1997), also employing the Gompertz model as the alternative.

The effects of time series length on the tests of direct and delayed density-dependence were examined by plotting the detection rate of density-dependence against the length of time series (Fig. 2). Although the detection rates increased with the length of time series, the rate leveled off around 20 years in both tests for direct density-dependence, in particular for Bulmer's test. The detection rate of the extended Dennis and Taper' test for delayed density-dependence also gradually increased with the length. The power for the tests appears to be acceptable for series with a length of 20 years or longer (details of the analyses can be obtained from the first author; see also Woiwod and Hanski 1992).

Linear autoregressive modeling (on a log-scale) was performed according to Stenseth et al. (1996a), to give an estimate of the strength of the direct and delayed density-dependence.

Bjørnstad et al. (1998b) analyzed the patterns of cyclicity, by estimating all the 225 individual spectral density functions. The spectral densities were subsequently subjected to a *functional data analysis* (Ramsay and Silverman 1997), to describe the dominant differences in periodic behavior between the populations. We provide a summary of the results in this paper. Bjørnstad et al. (1998b) should, however, be consulted for details of this analysis.

The level of synchrony in the different regions was

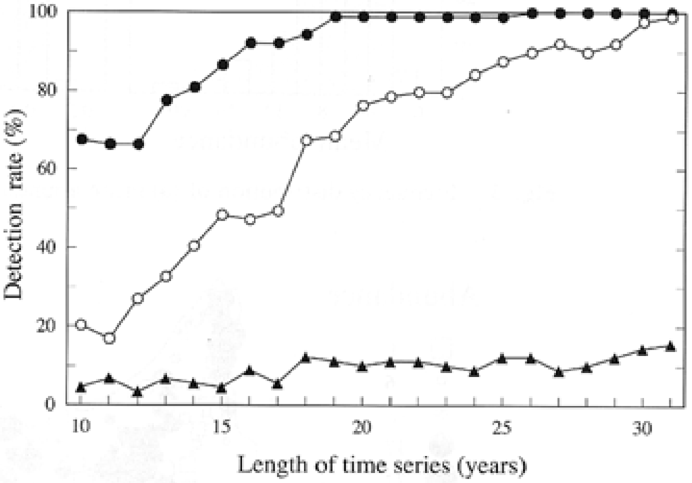

Fig. 2. Percentage of time series in which the null hypothesis for direct or delayed density-dependence was rejected at 5% level for the each length of time series using the three methods: (●) Bulmer's test for direct density-dependence; (○) the test of Dennis and Taper (1994) using the Gompertz model for direct density-dependence; (▲) the extended Dennis and Taper's test using the Gompertz model for delayed density-dependence. The length of time series was elongated backward from 10 years (1983–1992) to the full years (1962–1992) by one year step using the data on 89 populations covering 31 years (1962–1992) in Asahikawa Regional Office. A one-tailed test was applied to the direct density-dependence tests, whereas the two-tailed test was applied to the delayed density-dependence test.

Table 2. Basic statistics (average ± SD) for three population dynamics features. Abundance is the mean abundance (N_t) of time series, *s*-index is the standard deviation of abundance (N_t+1) on log-10, amplitude was calculated based on abundance (N_t+1) on log-10 (see text for details); each value was averaged within each group. Figures in parentheses (n) are the number of time series in each group.

Group (n)	Abundance	*s*-index	Amplitude
1: Teshio (31)	8.23±3.78	0.340±0.043	0.663±0.101
2: Kitami (31)	7.74±1.49	0.418±0.046	0.876±0.119
3: Abashiri (20)	7.01±2.36	0.465±0.051	0.947±0.107
4: Yubari (8)	4.95±2.12	0.414±0.039	0.860±0.125
5: Kamikawa-Taisetsu (27)	8.86±3.43	0.424±0.050	0.865±0.107
6: Shiribeshi (27)	5.05±2.27	0.367±0.072	0.718±0.155
7: West-Hidaka (20)	6.48±3.87	0.414±0.046	0.857±0.120
8: Oshima (30)	5.21±2.17	0.340±0.063	0.560±0.132
9: East-Hidaka (10)	4.64±3.24	0.379±0.038	0.796±0.104
10: Tokachi (13)	8.67±5.22	0.453±0.095	0.910±0.193
11: Kushiro-Nemuro (8)	11.56±4.09	0.360±0.129	0.750±0.228

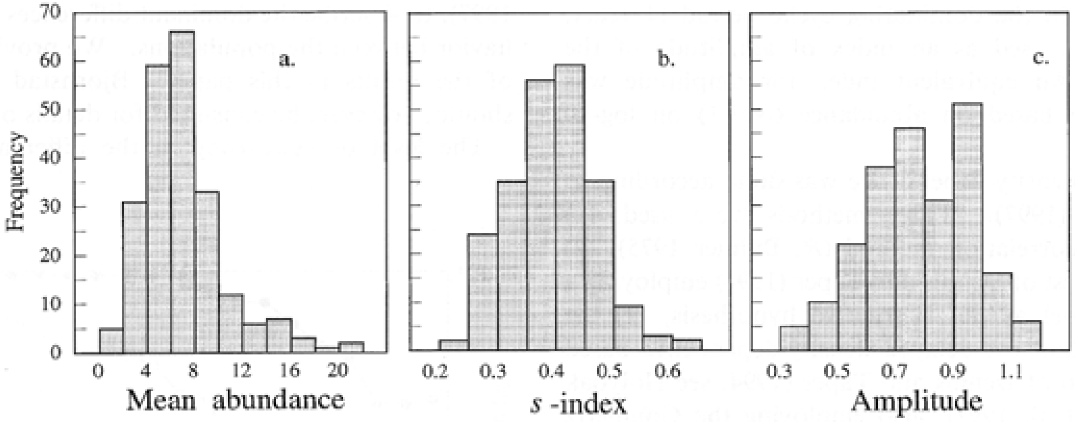

Fig. 3. Frequency distribution of (a) mean abundance, (b) *s*-index and (c) amplitude for the 225 time series.

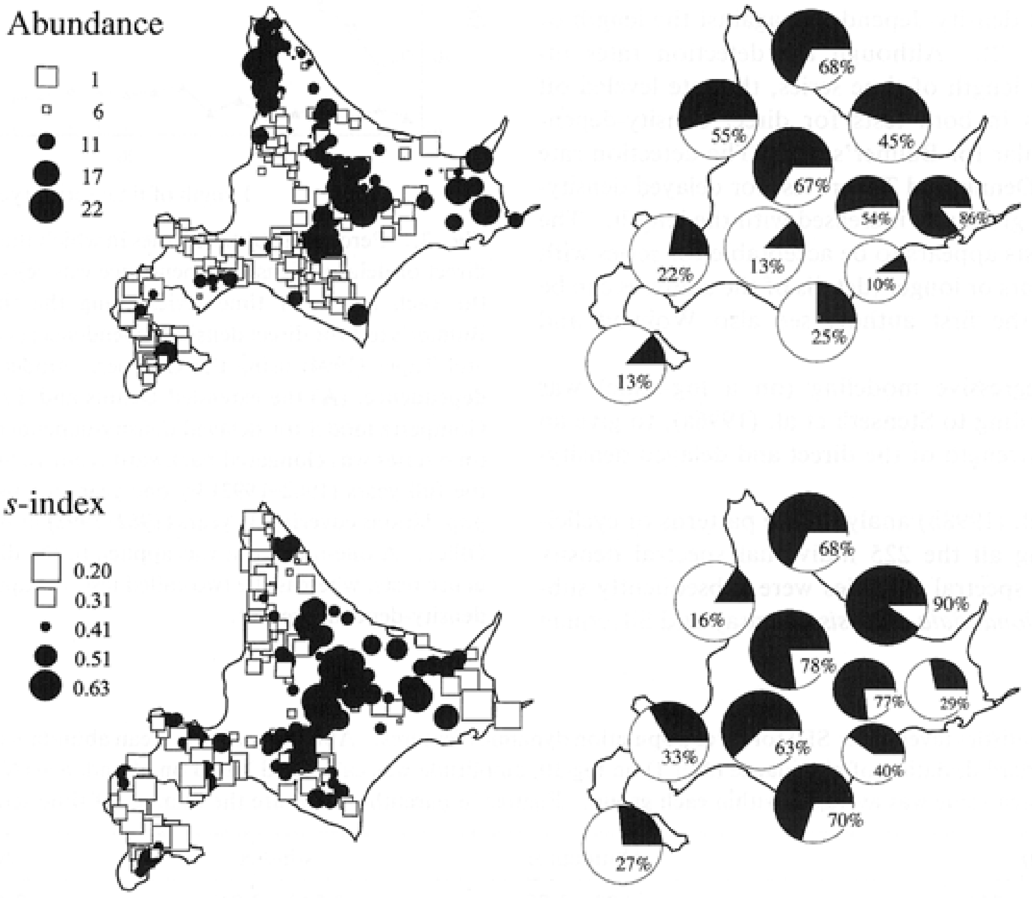

Fig. 4. Mean abundance (upper-left) and a *s*-index (lower-left) of the 225 time series plotted at their spatial co-ordinates. Filled circles represent values that are larger than the grand average, open squares represents values that are smaller. The size of symbols is proportional to the deviation from the average (grand average in abundance is 7.1, average *s*-index is 0.39). The pie-charts represent the proportion (percentage) of time series in each group having higher values than the grand average (upper-right for mean abundance; lower-right for *s*-index).

quantified by the average Spearman rank correlations between the time series of growth rates (1st differenced log-abundances) within a region (Bjørnstad et al. 1998a; see also Hanski and Woiwod 1993). We also quantified the average correlation between neighboring populations (to correct for any differences in interspersion of stations or size of regions; see Table 1).

Table 3. The test results of comparisons of mean abundance (upper matrix) and amplitude (lower matrix) between groups by Wilcoxon-Mann-Whitney test. *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$.

Group (*n*)	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Group 9	Group 10	Group 11
Group 1 (31)		—	—	**	—	***	*	***	**	—	*
Group 2 (31)	***		—	**	—	***	**	***	***	—	**
Group 3 (20)	***	*		*	—	**	—	**	*	—	**
Group 4 (8)	***	—	—		**	—	—	—	—	—	*
Group 5 (27)	***	—	**	—		***	**	***	***	—	—
Group 6 (27)	—	***	***	*	***		—	—	—	*	***
Group 7 (20)	***	—	*	—	—	**		—	—	—	**
Group 8 (30)	**	***	***	***	***	***	***		—	**	***
Group 9 (10)	**	*	**	—	*	—	—	***		*	**
Group 10 (13)	***	—	—	—	—	**	—	***	—		—
Group 11 (8)	—	—	*	—	—	—	—	—	—	—	

Results

Abundance and variability

Mean abundance, *s*-index and amplitude were calculated for all 225 time series (Table 2, Fig. 3). Mean abundance varied among populations from 1.07 to 21.07 individuals per 150 trap-nights. Abundance often exceeded 20 individuals per 150 trap-nights in a peak year. The highest abundance (74 individuals per 150 trap-nights) was observed in Muri Ranger Office of Group 3 in 1986, while the lowest abundance (zero catches per 150 trap-nights) was sometimes observed in most census sites. The grand mean (±SD) of the mean abundance for 225 time series was 7.08 ± 3.47 individuals per 150 trap-nights; the distribution was skewed to the right (Fig. 3a; skewness$=2.63$, kurtosis$=1.38$, $n=225$). The shape of the distribution of the mean abundances was similar to that of individual data for abundance for each year and population, though the overall distribution of all data was more skewed to the right (mean$=7.13$, SD$=8.05$, skewness$=8.13$, kurtosis$=2.28$, $n=5{,}626$).

The variability index for population fluctuation (*s*-index) ranged from 0.204 to 0.629. Its mean (±SD) for 225 time series was 0.393 ± 0.073; the distribution was similar to the normal (Fig. 3b; skewness$=0.149$, kurtosis$=0.125$). The percentage of highly variable populations (>0.5, see Henttonen et al. 1985) was 6.2%. The amplitude ranged from 0.352 to 1.191. Its mean (±SD) for 225 time series was 0.782 ± 0.178; the distribution was somewhat skewed towards the left (Fig. 3c; skewness$=-0.515$, kurtosis$=-0.184$).

The highest average abundance was found in the Kushiro-Nemuro area (Group 11; Table 2; Fig. 4a); the generally lower abundances were found in the south-western part of Hokkaido. Variability, as measured by the *s*-index, was clearly highest in the central mountainous part of Hokkaido, even though populations towards the northeastern part of the island generally varied more than the island-wide average (Fig. 4b).

The statistics on abundance and its variability is further evaluated in Tables 2 and 3. Groups 1, 2, 3 and 5 had similar mean abundances. Their mean abundances were significantly different from those of Groups 4, 6, 8 and 9 with low mean abundance. The mean abundance of Group 7 was intermediate, it appeared to be close to that in the latter groups. Mean abundance of Group 11 was high, whereas Group 10 appeared very heterogeneous. The variability was the highest in Group 3, whereas that of Groups 1, 6 and 8 was conspicuously low. The variability in other groups showed less clear patterns; in particular Group 11 seemed very heterogeneous.

Encouraged by the suggestion of a gradient going southwest to northeast, we depicted the changes in mean abundance (on log scale, X_t; Fig. 5a), variability as measured by the *s*-index (Fig. 5b) and by the amplitude (Fig. 5c) as functions of the geographic score. As can be seen, the mean abundance, the variability (*s*-index) and the amplitude increased along this gradient. The trend was fitted by a quadratic curve ($y=(1.541 \pm 0.126)-(0.0099 \pm 0.0071)x+(0.0002 \pm 0.00009)x^2$; adj. $R^2=0.129$, $P<0.001$ for mean abundance; $y=(0.302 \pm 0.022)+(0.0040 \pm 0.0012)x-(0.00004 \pm 0.00001)x^2$, adj. $R^2=0.087$, $P<0.001$ for variability; $y=(0.414 \pm 0.0484)+(0.0160 \pm 0.0027)x-(0.00015 \pm 0.00004)x^2$, adj. $R^2=0.253$, $P<0.001$ for amplitude); the x being equal to the geographic score and the y equal to the statistics. The *s*-indices of most time series in Groups 1 and 11 were lower than the values expected from the geographic trend (see Fig. 4). The geographic trend was clearer in amplitude than in *s*-index.

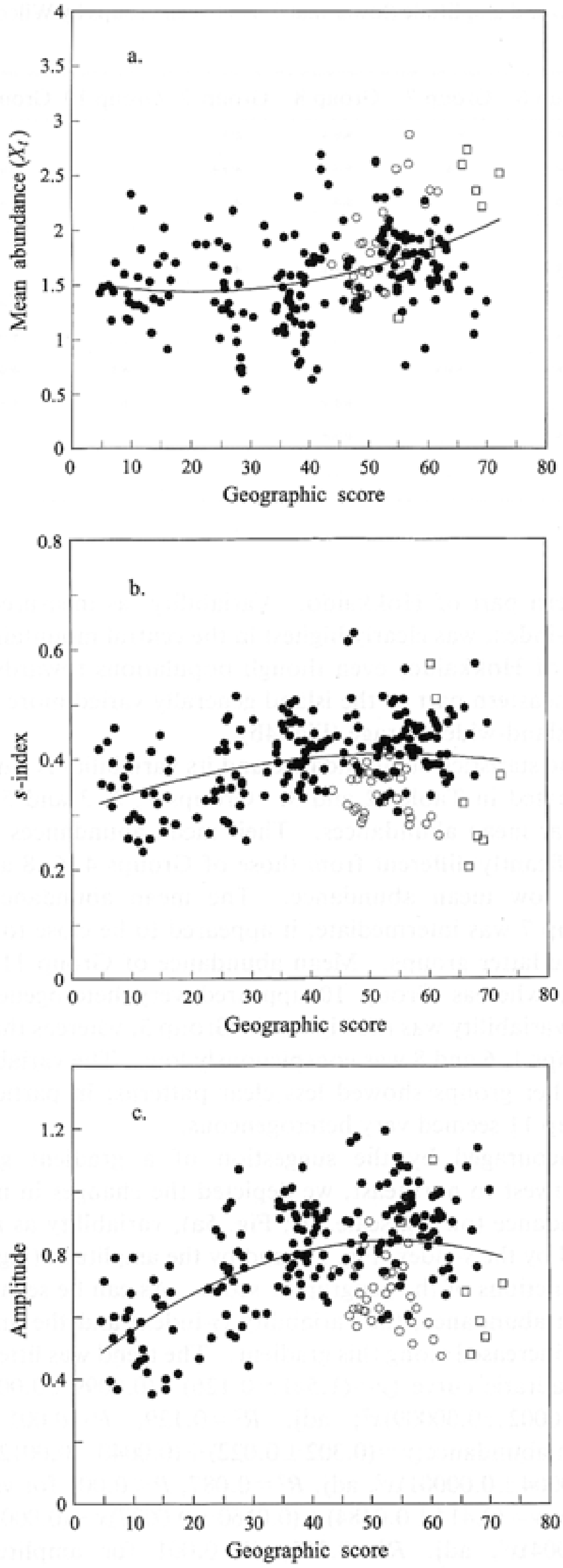

Fig. 5. The relationship between three statistics of population dynamics and geographic score. (a) mean abundance (X_t), (b) temporal variability (s-index) and (c) amplitude. Solid circle: 186 populations for Groups 2, 3, 4, 5, 6, 7, 8, 9 and 10; open circle: 31 populations for Group 1; open square: 8 populations for Group 11.

Tests for density-dependence

Bulmer's test and the bootstrap test of Dennis and Taper (1994) for direct density-dependence were performed on time series spanning 23 years or more (i.e. 194 populations in Groups 1–8); Thirty-one time series (Groups 9–11) were omitted from this part of the analysis due to too short length (see Fig. 2). Bulmer's test detected direct density-dependence in all time series in Groups 2, 3, 4, 5 and 7 and detection rates were also high in Group 1 and 6 (Table 4). However, more than one-third of the populations in Group 8 did not exhibit significant density-dependence. The results obtained by Dennis and Taper's test were similar, though the detection rates were generally lower than for the Bulmer's test.

Regional variation was found for delayed density-dependence (depending on density in two year before) by the extended Dennis and Taper's test. In five groups (Groups 1, 2, 4, 5 and 7) detection rate was around 10% or higher, whereas the rate was low in three groups (Groups 3, 6 and 8; Table 4, Fig. 6).

Assuming an order two processes (justified by the analysis reported by Stenseth et al. (1996a, b)), the first and second autoregressive coefficients were estimated to measure intensity of density-dependence. Both the first and second

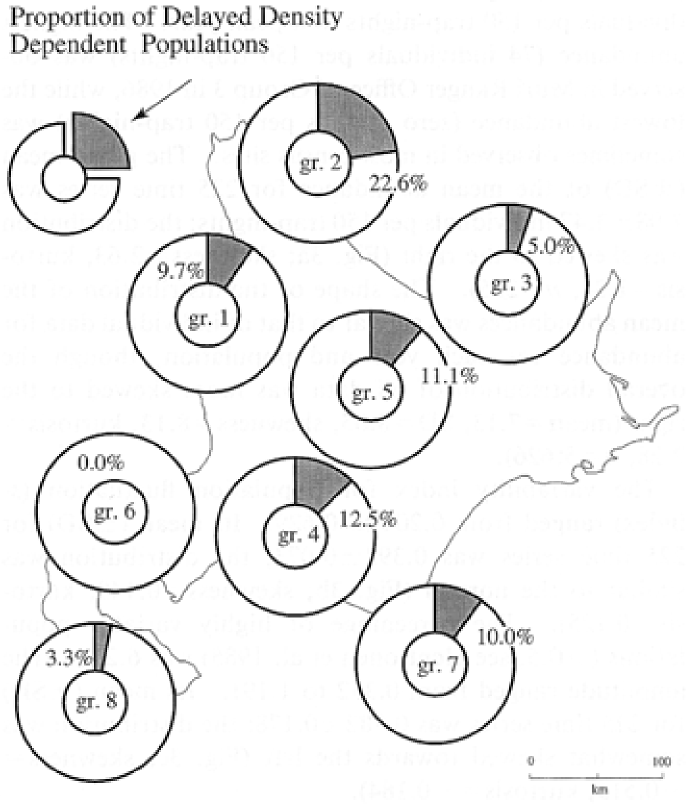

Fig. 6. Proportion of delayed density-dependent populations for each group. Groups 9, 10 and 11 were omitted because of the short length of these time series.

Table 4. Test result of direct and delayed density-dependence. For the time series with length longer than 23 years (i.e. Groups 1, 2, 3 and 5), density-dependence was tested at two different length (23 years and the full length; 31 years for Groups 1, 2, 5 and 27 years for Group 3).

Group (*n*)	Direct density dependence Bulmer's test (*R*)				Delayed density dependence Dennis & Taper's test	
			Dennis & Taper's test			
	23 years	full	23 years	full	23 years	full
Group 1 (31)	96.8%	100%	67.7%	96.8%	9.7%	9.7%
Group 2 (31)	100%	100%	90.3%	100%	12.9%	22.6%
Group 3 (20)	100%	100%	90.0%	95.0%	5.0%	5.0%
Group 4 (8)	100%	—	80.0%	—	12.5%	—
Group 5 (27)	100%	100%	81.5%	100%	11.1%	11.1%
Group 6 (27)	96.4%	—	92.9%	—	0%	—
Group 7 (20)	100%	—	90.0%	—	10.0%	—
Group 8 (30)	63.3%	—	46.7%	—	3.3%	—

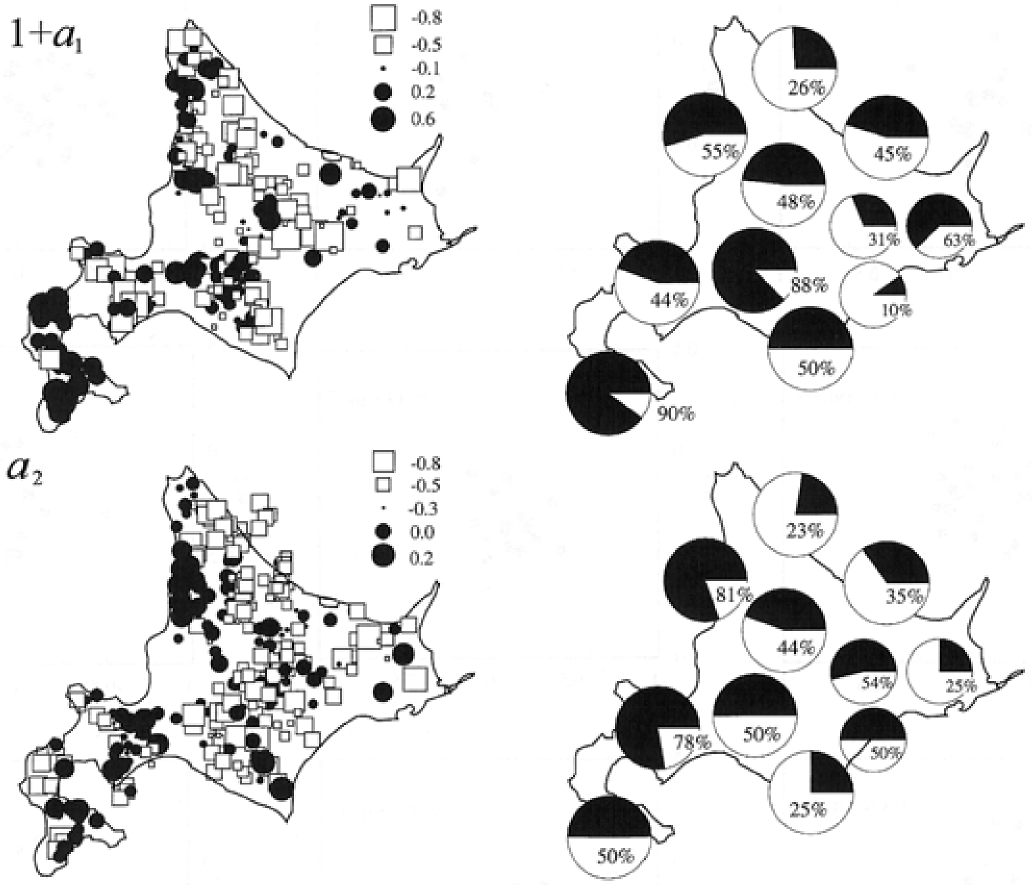

Fig. 7. First order ($(1+a_1)$; upper-left) and second order (a_2; lower-left) autoregressive coefficients of the 225 time series plotted at their spatial co-ordinates. Positive estimates are represented by filled circles, negative estimates are represented by open squares. The size of the symbol is proportional to the absolute value of the estimate. The pie-charts represent the proportion (percentage) of time series in each group having higher values than the grand average (upper-right: $(1+a_1)$, grand average$=-0.13$; lower-right: a_2, grand average$=-0.29$).

coefficient were plotted on the map (Fig. 7). Both coefficients showed a similar geographic gradient; thus, both sources of density-dependence were stronger in the more northern and eastern populations.

Periodic and aperiodic fluctuations

Figure 8 summarizes the estimated autoregressive coefficients for the various geographic groupings. As can be

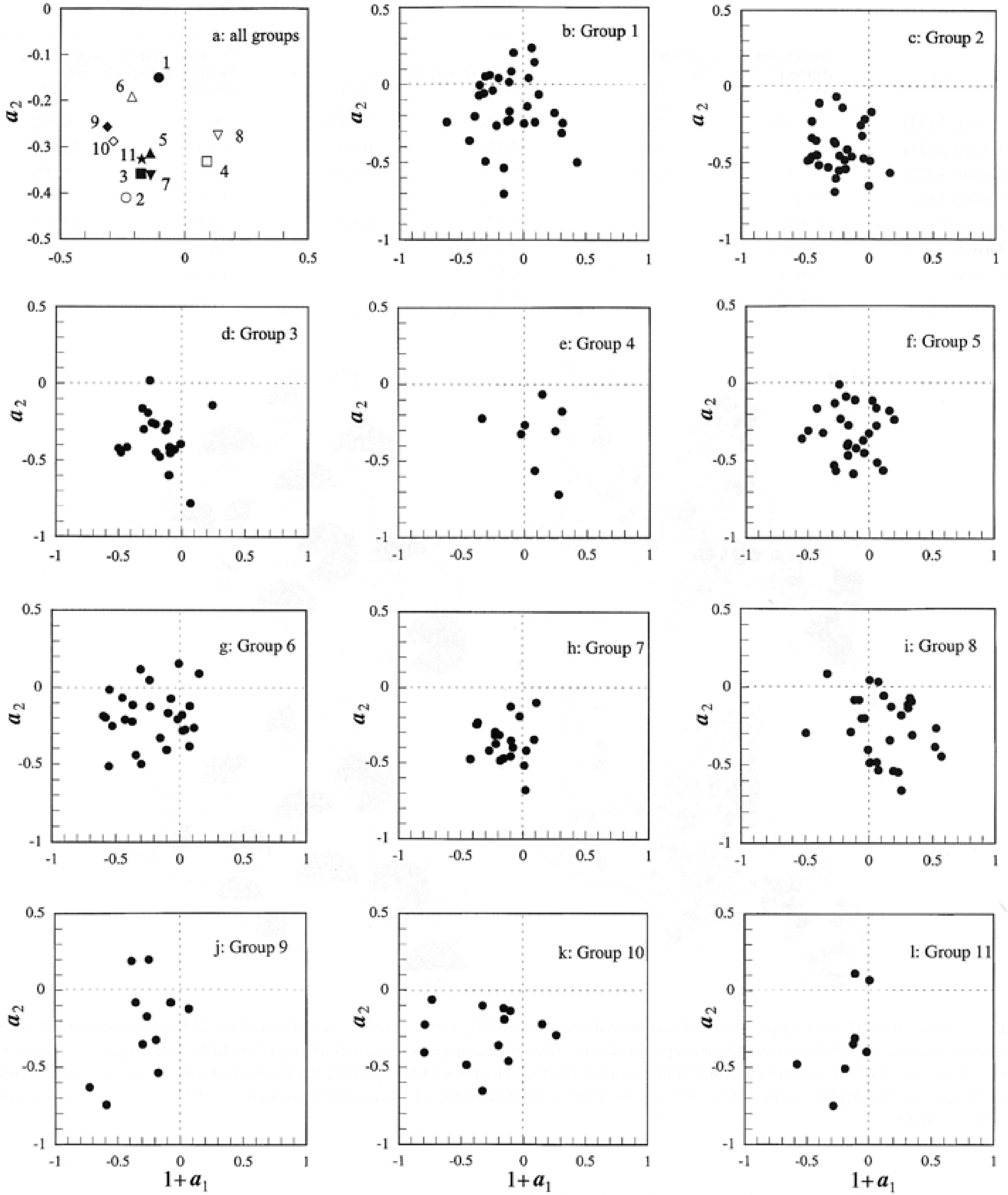

Fig. 8. Scatter plot of first order ($1+a_1$) versus second order (a_2) autoregressive coefficients for each group. Panel (a) represents the average values of the coefficients within each of the groups.

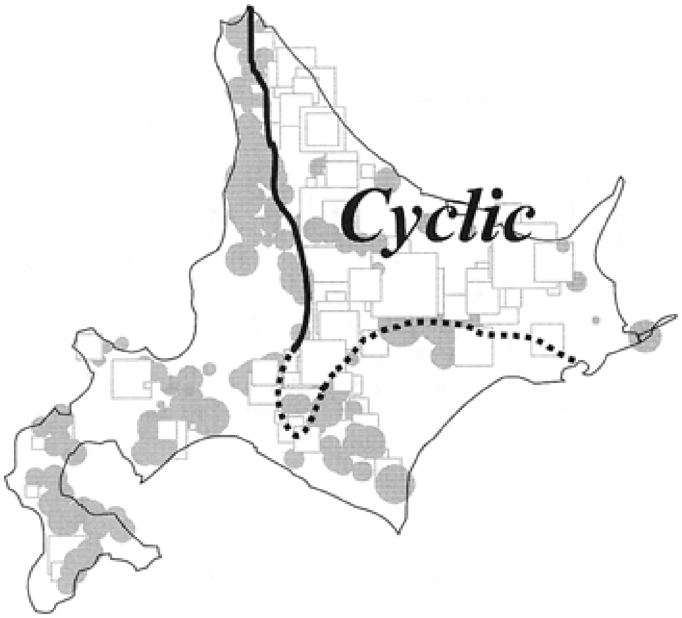

Fig. 9. A crude demarcation of the area where populations exhibited multiannual cycles (in the 3.5–4.5 year range) according to the analysis of Bjørnstad et al. (1998b). The grey symbols represents the 2nd rowscores of the functional data analysis upon which the demarcation is based. Open squares represents time series that showed evidence of 3–4 year cyclicity (see Bjørnstad et al. 1998b for methodology and analyses).

seen, Group 1 (Fig. 8b) and Group 6 (Fig. 8g), both of which neighbor the Sea of Japan, were somewhat different from the others in the sense that they all fell more or less around the origin (0,0). Group 4 (Fig. 8e) and Group 7 (Fig. 8h) were somewhat similar in the sense that they scattered along the line running on the zero point of the first order. Points in each group fell more or less in the same region of the parameter space. With the possible exception of Groups 1 and 6 (cf. Stenseth et al. 1996a, 1998b), these were all expected to show some degree of cyclicity, with Groups 4 and 8 having the longer periods (note, however, that the amplitude and variability in these two regions were very low (see also Bjørnstad. 1998b)); the remaining was expected to have periods around 3–4 years (see Bjørnstad et al. 1995; Stenseth et al. 1998b).

Bjørnstad et al. (1998b) studied the cyclic behavior of the 225 time series. They demonstrated a transition between the populations in the northeast, east and central that exhibited a 3–4 year cyclicity and the remaining populations that did not. A summary of the pattern detected by Bjørnstad et al. (1998b) is given in Fig. 9.

Examples of the range of dynamics in the populations are shown in Fig. 10. The population at Heian in Group 2 oscillated with a clearcut 4 year period (Fig. 10a). Although its mean abundance was relatively low (6.75 individuals per 150 trap-nights), it was quite variable and exhibited both direct and delayed density-dependence (s-index$=0.466$). The population at Tokusawara in Group 3 also varied regularly at 4–5 year period with both direct and delayed density-dependence (Fig. 10b; mean abundance$=7.76$ individuals per 150 trap-nights; s-index$=0.493$). The population at Chikubetsu in Group 1, which exhibited only direct density-dependence and fluctuated irregularly (Fig. 10c; mean abundance$=7.67$ individuals per 150 trap-nights; s-index$=0.335$). The population at Nagatoyo in Group 8 did not exhibited direct nor delayed density-dependence, and both mean abundance and s-index were low (Fig. 10d; mean abundance$=4.76$ individuals per 150 trap-nights; s-index $=0.379$).

Spatial synchrony

The patterns of average within-group synchrony (and average nearest-neighbor synchrony) in population growth rates are summarizes in Fig. 11. There was a clear gradient from the essentially asynchronous populations in southwest (Group 8) to more highly synchronized populations in the northeast (Group 2). Thus, the degree of synchrony correlated with both degree of variability and the presence of multiannual cycles in abundance. The overall pattern is the same when focusing on the nearest-neighbor synchrony.

Discussion

Abundance and variability

Even though the survey data do not allow us to properly estimate abundance, applying Tanaka's (1960) method, peak densities in areas with the highest abundances may be from 100 to 200 (or more) individuals per hectare. The low densities are presumably close to zero. Thus, the range of abundance seemed to be similar to that of other fluctuating small rodent populations (e.g. Krebs 1993). The degree of variability in abundance, as measured by the s-index, was lower than the most extremely cyclic populations in Fennoscandia (e.g. Henttonen et al. 1985; Ostfeld 1988); however, several populations had an s-index above 0.5 (being considered as a cutoff point by, for instance, Henttonen et al. 1985).

The gradient in fluctuation in the Hokkaidian gray-sided vole

Previously, it has been shown that both aperiodic and multiannual periodic fluctuations occur in populations of the gray-sided vole in northern Hokkaido (Bjørnstad et al. 1996): along the coast of the northwestern part of Hok-

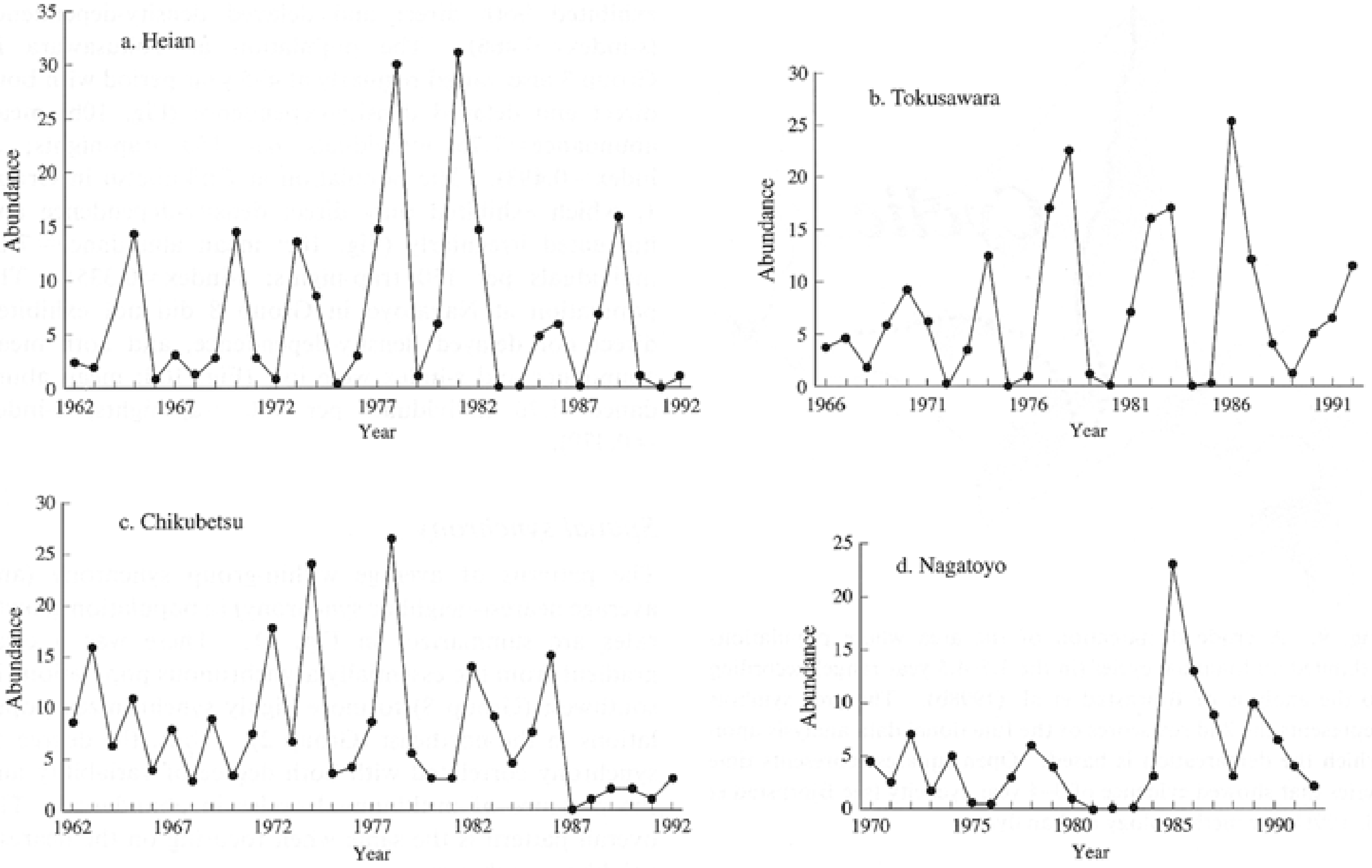

Fig. 10. Examples of population fluctuation pattern. (a) the population with 4 year cycle at Heian in Group 2; (b) the population with 4–5 year cycle at Tokusawara in Group 3. Examples of aperiodic fluctuation are shown in (c) the population at Chikubetsu in Group 1; and in (d) the population at Nagatoyo in Group 8.

kaido the species exhibits primarily aperiodic fluctuations, whereas populations in the interior and the east exhibit periodic fluctuations with a period of 3.5–4 years. We hence extended these earlier results by demonstrating that both aperiodic and multiannual periodic fluctuations were also found for other populations than the northern ones, but the proportion of cyclic populations appeared to be higher in the more northern and eastern parts of the island (Fig. 9).

A geographic gradient was found in the temporal variability indices (*s*-index and amplitude) of all 225 time series (Figs. 4, 5b, c). More northern and eastern populations showed higher variability. Regional variation in the magnitude of density-dependence (both direct and delayed) appear to be a proximate cause for the gradient in Hokkaido. Alongside with the cline in variability there were corresponding changes in degrees of cyclicity and synchrony. We will return to this below.

A similar geographic gradient is found as going from north (periodic multiannual fluctuations) to south (stable) in Fennoscandia. This is often explained by predator-prey interactions (Hansson and Henttonen 1985, 1988; Henttonen et al. 1985). Specialist predators are thought to destabilized vole densities through delayed density-dependence effects (Hassell and May 1986; Hanski et al. 1991; Hanski and Korpimäki 1995). Hansson (1987) argued that snow may interact with predation rates such that mustelids (being specialist predators capable of finding rodent prey under the snow cover) may, on a relative scale, be more important than the large generalist predators wherever the snow cover last for a longer part of the year (see also Yoneda 1983; Lindström and Hörnfeldt 1994; Sittler 1995; Saitoh and Takahashi 1998). In Hokkaido, however, the geographic variation in average snow depth and the duration of snow cover does not correlate directly with the pattern of dynamics, since, roughly speaking, the snow and its duration is deeper and longer in northern and western areas of Hokkaido (Masuda 1983), where vole populations are relatively stable.

Contrary to the snow cover, temperature appears to change in a parallel manner to the vole dynamics; average temperature becomes lower as going north and east. The trend in temperature will affect the breeding season of the vole and the growing season of plants (Kaneko et al. 1998). Although the breeding season of the gray-sided vole generally last from April to October with a summer pause

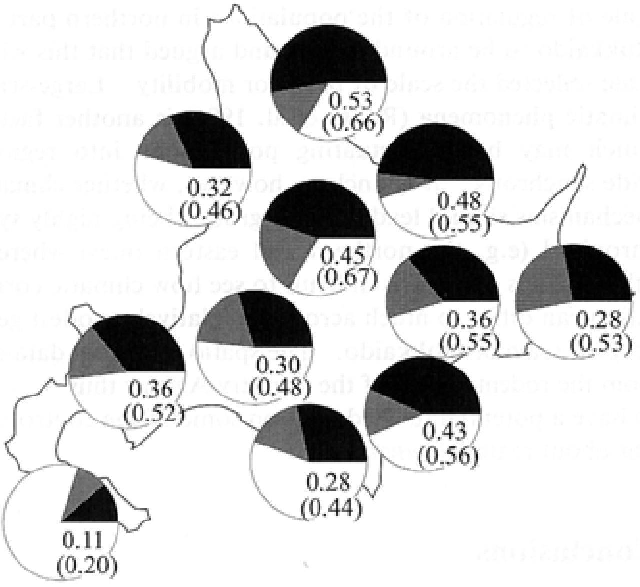

Fig. 11. Within-group synchrony in population growth rates. The synchrony was calculated as the average Spearman rank correlation between the 1st differenced log-transformed time series. The black symbol and first number is the average correlation coefficient between all populations in each group. The combined area with black and gray symbol and number in parentheses represent the average correlation between the nearest neighboring populations within each group (see Table 1).

(Ota 1984), breeding in the southern areas begins earlier (middle of March) and extend until later in the year (October; Fujimaki 1972, 1973, 1975). The breeding season is short but intensive without a summer pause in the northern and eastern populations (Fujimaki 1972, 1973, 1975). The geographic variation may therefore be seen as paralleling the suggestion of Stenseth (1985, 1986) that the short breeding season destabilizes a population (see Stenseth et al. 1998b).

The geographic pattern of population dynamics and its relation to the phenology cycle is further discussed by Stenseth et al. 1998b).

The variability indices (*s*-index and amplitude) for Group 1 and Group 11 were low compared to that expected from the geographic trend (Fig. 5b, c). Since a warm sea current runs along the west coast of Hokkaido in the Sea of Japan (Fig. 1a), the area including Group 1 is directly influenced by a warmer climate. Populations of Group 11 had the highest abundance with the lower temporal variability (Table 2): they rarely exhibited very low abundance (Saitoh and Takahashi 1998). Since the length of time series of this group is short (12 years), features of cyclicity and density-dependence are here unclear. Further studies are needed to understand populations in this region.

Stenseth et al. (1996a), studying the northernmost populations (corresponding to Groups 1, 2 and 5), concluded that a clinal gradient existed in variability of population (*s*-index) as going inland from the northwestern coast – a gradient which was seen as the result of more negative delayed density-dependence in the more inland populations. In the more extensive analyses reported here, we demonstrated that this previously observed gradient more properly may be seen as a segment of a gradient going from the southwestern part of Hokkaido to the northeastern part.

Cyclicity and density-dependence

Direct density-dependence was detected in essentially all populations of the gray-sided vole in our previous analyses (Saitoh et al. 1997, 1998). Delayed density-dependence was found in a more restricted subset of the populations. We have extended this conclusion by demonstrating that most populations, except for populations in the southernmost part of Hokkaido, exhibited direct density-dependence, but detection rate for delayed density-dependence varied from group to group: it tended to be higher in the more northern and eastern regions (Fig. 6).

Both in Fennoscandia and in Hokkaido, there is a clear clinal structure in density-dependence as expressed in the magnitude of the autoregressive coefficients (Bjørnstad et al. 1995, 1996; Stenseth et al. 1996b). However, differing from the gradient in Fennoscandia north of approximately 60°N, being a gradient in the direct density-dependence with non-varying but universally significant delayed density-dependence (Bjørnstad et al. 1995), the gradient in Hokkaido is a gradient in the both direct and delayed density-dependence (Fig. 7; Stenseth et al. 1998b for further discussion of this gradient).

Regional transitions in pattern of density fluctuations and density-dependence are features of the population dynamics of microtine rodents elsewhere (Hansson and Henttonen 1985, 1988; Hanski et al. 1991; Stenseth and Ims 1993; Bjørnstad et al. 1995): varying influence of both direct and delayed density-dependence appear to be quite general (Hörnfeldt 1994; Saucy 1994; Bjørnstad et al. 1995; Stenseth et al. 1996b). Self-regulation through spacing behavior and social interaction between voles is a plausible mechanism for the direct density-dependence (Saitoh et al. 1997, 1998; see also Stenseth et al. 1996b). Female gray-sided voles are generally territorial and commonly exhibit delayed maturation at high densities, both of which may cause direct density-dependency in the population growth rate. In Hokkaido territoriality in the gray-sided vole is commonly observed (Saitoh 1985); maturation rates are furthermore reduced at high densities (Abe 1976; Saitoh 1981; Nakata 1989).

The low detection rate for direct density-dependence in Group 8 is curious since this was the region with the lowest variability (Table 4). This may be a real phenomenon, but it may also be a statistical artifact: the tests for density-dependence are largely tests about the correlation between population growth and abundance (Pollard et al. 1987; Royama 1992; Dennis and Taper 1994), and correlations generally decrease as the range along the abscissa decreases even when the underlying relations are the same (e.g. Bhattacharyya and Johnson 1977). Low levels of variability generally makes it more difficult to uncover underlying relationships (see Schaffer et al. 1986).

Populations in Group 8 are distributed in the Oshima peninsula (Fig. 1d), of which the vegetation differs from that of the other regions in Hokkaido. Biogeographically, Hokkaido, of which forest is regarded as a transition between the temperate and the subarctic zones also found in Scandinavia (Tatewaki 1958), resembles the neighboring Asian mainland more than the other Japanese islands (Fig. 1a; Tatewaki 1958; Kondo 1993). However, the vegetation of the Oshima peninsula is similar to that of Honshu island, the southern neighboring island to Hokkaido, covered by temperate and cool-temperate deciduous forests (Tatewaki 1958). Although no large difference in predator fauna is known between the Oshima peninsula and other regions in Hokkaido, some specific ecological phenomena of the Oshima peninsula are found (Koaze et al. 1994). However, information about this ecological systems is still insufficient to relate the demographic features in the gray-sided vole populations to the community level.

Synchrony

Both the local and the group-wide synchrony in dynamics are very strong in the highly variable and cyclic northeastern area (see Bjørnstad et al. 1998a, b). In the relatively stable southwestern area, in contrast, even local synchrony is low. Theoretical models of spatial synchrony have demonstrated that the degree of spatial correlation between time-series is dependent on the degree of variability (Barbour 1990). The patterns we observed may therefore reflect such an effect. A word of caution is in order, though. There is a danger of confounding biological reality and statistical artifacts: decreasing the range along the abscissa (as one undoubtedly do when decreasing the variability in densities) will decrease the value of the correlation coefficient. Another hypotheses for the relatively wide ranging synchrony in cyclic species has been discussed by Bjørnstad et al. (1998a): cyclicity often involves interactions with specialist enemies that usually have greater mobility than its resource. Wide scaled synchrony in cyclic rodent populations may therefore be due to the populations being regulated at the spatial scale of its predators (see also Myers and Rothman 1995). Bjørnstad et al. (1998a) estimated that the spatial scale of regulation of the populations in northern part of Hokkaido to be around 50 km, and argued that this wide scale reflected the scale of predator mobility. Large-scale climatic phenomena (Ranta et al. 1995) is another factor which may bring fluctuating populations into region-wide synchrony. It is unclear, however, whether climatic mechanisms should lead to some groups being highly synchronized (e.g. the northern and eastern ones) whereas other groups not. It is difficult to see how climatic correlation can differ so much across the relatively modest geographic scale of Hokkaido. The spatio-temporal data-set from the rodent census of the Forestry Agency thus appears to have a potential to shed light on some of the controversies about regional synchrony.

Conclusions

In this paper we have demonstrated: (1) The abundance, variability, and amplitude of fluctuation in the gray-sided vole populations were higher in the more northern and eastern regions of Hokkaido. (2) Most populations, except for the southernmost ones, exhibited direct density-dependence. Detection rate for delayed density-dependence varied among groups from 0% to 22.6%. (3) Intensity of both direct and delayed density-dependence tended to be stronger (more negative) in the more northern and eastern populations. (4) Both periodic and aperiodic populations were found in Hokkaido. The proportion of cyclic populations was higher in northeastern areas than in southern areas. Dominant frequency of cycle was 4 year. (5) Most populations within a given group fluctuated in synchrony, except for in the southernmost group of populations.

These findings generally support previous findings based on a smaller subset of the data (corresponding to a smaller part of the island; Bjørnstad et al. 1996, 1998a; Stenseth et al. 1996a; Saitoh et al. 1997, 1998). On this basis we have been able to document a rather detailed mosaic for spatio-temporal dynamics of the gray-sided vole in the entire island of Hokkaido. Aperiodic populations are found in the southernmost part of the island whereas periodic (and cyclic) populations are found in the northern and eastern part of the island. The observed transition in dynamic properties may correspond to the one in Fennoscandia (e.g. Hansson and Henttonen 1988). However, the Hokkaidean gradient that spans about 460 km N-S and 500 km E-W is much more compact compared to the Fennoscandia spatial patterns.

The observed transition between aperiodic and periodic multiannual population fluctuations as well as the gradient in population dynamics features coincides with a gradient in the length of the breeding or winter season (corresponding again with gradients in climatic properties).

Changing seasonality may (cf. Hansson 1987) affect both the effect of predators as well as the interaction between voles and the vegetation they feed upon. A further study on effects of changing seasonality on population dynamics may be rewarding.

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