

# Large-scale synchrony and inter-annual variability in roach recruitment in the Rhône River: the relative role of climatic factors and density-dependent processes

G. GRENOUILLET,\* B. HUGUENY,† G. A. CARREL,‡ J. M. OLIVIER\* and D. PONT\*

\*Laboratoire d'écologie des Hydrosystèmes Fluviaux, Université Lyon I, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne cedex, France

†Antenne IRD, Laboratoire d'écologie des Hydrosystèmes Fluviaux, Université Lyon I, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne cedex, France

‡CEMAGREF-Groupement d'Aix en Provence, B.P. 31 Le Tholonet, 13612 Aix en Provence Cedex 1, France

## SUMMARY

1. We report patterns of temporal variation in the recruitment of roach (*Rutilus rutilus*). The data consist of the annual abundance of the first 2 year-classes, 0+ and 1+ fish, at four sites in the Rhône River (France) between 1987 and 1997. Over this 11-year period both 0+ and 1+ fish fluctuated strongly.
2. Cross-correlation indicated high spatial synchrony in 0+ dynamics, although correlations among sites in 1+ dynamics were weaker. No clear pattern was apparent in the relationship between the level of synchrony and distance between pairs of sites.
3. The spatial synchrony in 0+ fish could be attributable to large-scale variations in weather, influencing water temperature. Total body length of 0+ roach was correlated with water temperature (expressed in degree-days over 12 °C), and water temperature was the main factor explaining inter-annual variation in 0+ cohort size. Monthly variation in abiotic factors (measured by standard deviation in water temperature and discharge) did not influence 0+ fluctuations. Correlations with June water temperature suggest that year-class strength was mainly determined by abiotic factors during the first few months of life.
4. The absence of spatial synchrony in 1+ fluctuations suggests little correlation between survival and abiotic conditions during the first year of life, other factors influencing survival.
5. Survival in the first year was density-dependent. Intraspecific competition within the 0+ cohort could thus influence the fluctuations in recruitment to older age-classes.
6. The implications of age- or stage-dependent synchrony in temporal variation for species with complex life histories are discussed. Studying spatial synchrony for the different life history stages could enhance our understanding of the population dynamics of spatially structured species.

*Keywords:* climatic factors, density-dependence, river fish dynamics, *Rutilus rutilus*, spatial synchrony

## Introduction

Animal populations fluctuate both spatially and temporally (e.g. Connell & Sousa, 1983; Glazier, 1986; Pimm & Redfearn, 1988) and ecologists have long been interested in factors that determine these varia-

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Correspondence: G. Grenouillet, Bat. 401 C, Ecologie des Hydrosystèmes Fluviaux, Université Lyon I, 43 Bd du 11 novembre 1918, 69622 Villeurbanne cedex, France.  
E-mail: grenouil@cismisun.univ-lyon1.fr

tions. A central idea in population ecology is that temporal variability is the result of combined effects of density-dependent and density-independent factors (Rothery *et al.*, 1997), which are diverse and operate at different scales (Pimm, 1991). Despite an extensive literature, these factors have been under debate for several decades. The question of the relative importance of both processes remains unresolved (Murdoch, 1994) and the concepts of density-dependence, population regulation and temporal variability are still continually debated (Hanski, 1990).

The fact that populations fluctuate in synchrony over large spatial scales is now considered a common ecological phenomenon (Ranta, Kaitala & Lindström, 1998). Two major factors are involved in synchronizing population fluctuations: climatic perturbations and the dispersal of individuals. So, assessing the degree of spatial synchrony and determining if climate is involved in the process should clarify the nature of population dynamics. Myers, Mertz & Bridson (1997) addressed this question in fish populations by focusing on inter-annual recruitment variability in marine, anadromous and freshwater species. They observed that the spatial scale of recruitment correlations for marine species was approximately 500 km compared with less than 50 km for freshwater species, and concluded that climate is a more important factor in determining recruitment in marine environment than it is in freshwaters. However, only five freshwater species were studied, some of them in lakes, and a general pattern in riverine species remains to be revealed.

Many studies have observed large temporal variations in fish species abundance, and recruitment variability is one of the most important factors affecting population fluctuations (Houde, 1997a). Understanding recruitment variability is, therefore, central and remains one of the major objectives in fish ecology (Gulland, 1982; Houde, 1987; Hilborn & Walters, 1992). Most studies of recruitment variability have examined marine fishes, in which density-independent factors and dynamics in the early larval stage play a dominant role in determining recruitment (Houde, 1994). Factors determining year-class success are of particular interest to ecologists, and processes acting on early life-stages have long been investigated.

Many studies have examined the mortality and growth of larval and juvenile fishes. These rates,

which are high and variable during early life, are of major importance in generating year-class fluctuations (Houde, 1997b). Defining factors that determine these rates therefore is essential for understanding recruitment variability.

Experimental studies have demonstrated that growth rate depends upon water temperature and population density, and it is also recognized that growth rate and year-class strength are positively correlated (Mann, 1991). Although both are involved in recruitment dynamics, density-dependent and environmental factors have rarely been examined together (Henderson & Corps, 1997). Despite the great interest in the early life of fish in recent years, the mechanisms underlying recruitment and the processes influencing juvenile dynamics are still poorly known: recruitment variability, therefore, is still not well understood (Henderson & Corps, 1997; Houde, 1997a).

In contrast to marine species, freshwater fish larvae are characterized by a relatively large size at hatching, a short larval-stage duration, and low mortality rate (Houde, 1994), and fish density appears to be 10–1000 times greater than in marine systems (Horn, 1972). Trophic interactions, competition for resources and overwinter mortality during the juvenile stage, may therefore be the dominant factors affecting the level and variability of recruitment in freshwater fishes (Houde, 1994). However, freshwater studies are frequently restricted to lacustrine fishes and recruitment fluctuations in flowing waters remain poorly investigated.

In flowing waters, most studies have focused on the effects of environmental factors, and hydroclimatic events are known to influence survival during the early life of fishes. In rivers, water temperature and hydrology are the two main factors that affect fish dynamics and mainly determine annual variations in fish abundance (Schlosser & Angermeier, 1990). The close correlation between water temperature and the growth of 0+ group cyprinids is now well demonstrated (Mann, 1991). Reviewing data for river populations, Mills & Mann (1985) have pointed out two characteristics: (1) a correlation between year-class strength of some cyprinids and water temperature in the months following spawning, and (2) a significant relationship between growth and subsequent year-class strength. Density-dependent interactions, although strongly evident from aquaculture

data and experimental studies (Backiel & Le Cren, 1978) have only recently been examined in field studies and remain hard to detect.

In this study, we present the results of an 11-year study on inter-annual variability in the recruitment of roach (*Rutilus rutilus* (L. 1758)) in the Rhône River. We focus on the analysis of inter-annual dynamics of juvenile fish. Focusing on these age-classes is justified for two main reasons: (1) mortality rate is highest in young fish; and (2) in the Rhône River, the roach is a highly fecund species, with no fishing pressure, and mature fish can spawn several years in succession. The inter-annual fluctuations in juvenile age-classes are thus not likely to be determined by fluctuations in the spawning stock, and the roach constitutes a good target species for the study of inter-annual recruitment variability.

To the best of our knowledge, there is no long-term study that documents fish recruitment at several sites on the same river system. A key feature of this study is that our long-term data come from four similar sites, and allow us to investigate synchrony in recruitment dynamics. We addressed the following questions: (1) how do the number of juvenile fishes fluctuate with time? That is, do they fluctuate in synchrony, are there cyclic variations? And (2) why do juvenile fish numbers fluctuate? In other words, which abiotic or biotic factors determine these fluctuations?

## Methods

### Study area

With an 812-km length and a drainage area of approximately 97800 km<sup>2</sup>, the Rhône River is the fourth largest European river and the fifteenth in the world. The Lower River Rhône, between Lyon and the delta, is 280 km long. Mean annual discharge is 1000 m<sup>3</sup> s<sup>-1</sup> downstream from Lyon and 1700 m<sup>3</sup> s<sup>-1</sup> upstream from the delta. Embankments built in the 19th century, construction of hydroelectric schemes and simultaneous channelization have profoundly modified the Lower River Rhône. As in many other large rivers, regulation has decreased spatio-temporal heterogeneity of the hydrosystem which has become a slow flowing lowland river (Fruget, 1992).

This study included four sites in the main channel of four hydroelectric schemes, in the regulated part of

the Lower River Rhône (Fig. 1). Each hydropower scheme had the same structure, with a diversion canal parallel to the old channel, which is blocked by a diversion dam. The four sites, typical of the artificially modified main channel, were thus similar in their physical characteristics, with low structural diversity and a highly uniform environment: very low slope (from a few to 20 cm km<sup>-1</sup>), low flow velocity (mean velocity around 0.3 m s<sup>-1</sup>), channel over 150 m wide and absence of nearby backwaters. Throughout the period 1987–97, the four sites were sampled once per season (176 samples).

At each sampling site, the mean daily water temperature (data from the Electricité De France) and mean daily discharge (data from the Compagnie Nationale du Rhône) were obtained from continuous recordings.

### Fish data

In large rivers, electrofishing is the most suitable sampling technique available for studying fish and this technique is considered to be particularly well adapted for the capture of juvenile fishes (Copp & Garner, 1995). Fish data were obtained by one of two electrofishing procedures depending on site: point abundance sampling (PAS, Persat & Copp, 1990) at site 1 and continuous sampling (CS, Allardi, Duguet & Leynaud, 1975) at the other three sites. Both methods allowed the abundance of fish to be expressed as catch-per-unit-effort (CPUE). We used the equivalence found between the two procedures (20 min, CS = 20 points PAS, Pont, Changeux & Torre, 1993) to compare all time series.

In the main channel of the lower Rhône River, the roach is one of the three ubiquitous Cyprinidae (with bleak *Alburnus alburnus* (L. 1758) and chub *Leuciscus cephalus* L. 1758) which dominate the fish fauna (Carrel & Rivier, 1996). In the Rhône River basin, roach spawn in late May (Chappaz, 1986). From June to May the fish are underyearling or 0+; from June to May of their second year they are 1+, and so on. According to Chappaz (1986), roach in the Rhône River basin all mature in their third year (2+) and may live up to 10+ or more. Thus, the variability in roach recruitment is probably due to fluctuations of 0+ and 1+ fish.

In some cases, 1+ abundance in year  $t+1$  ( $N(1+)_{t+1}$ ) was greater than 0+ abundance in year

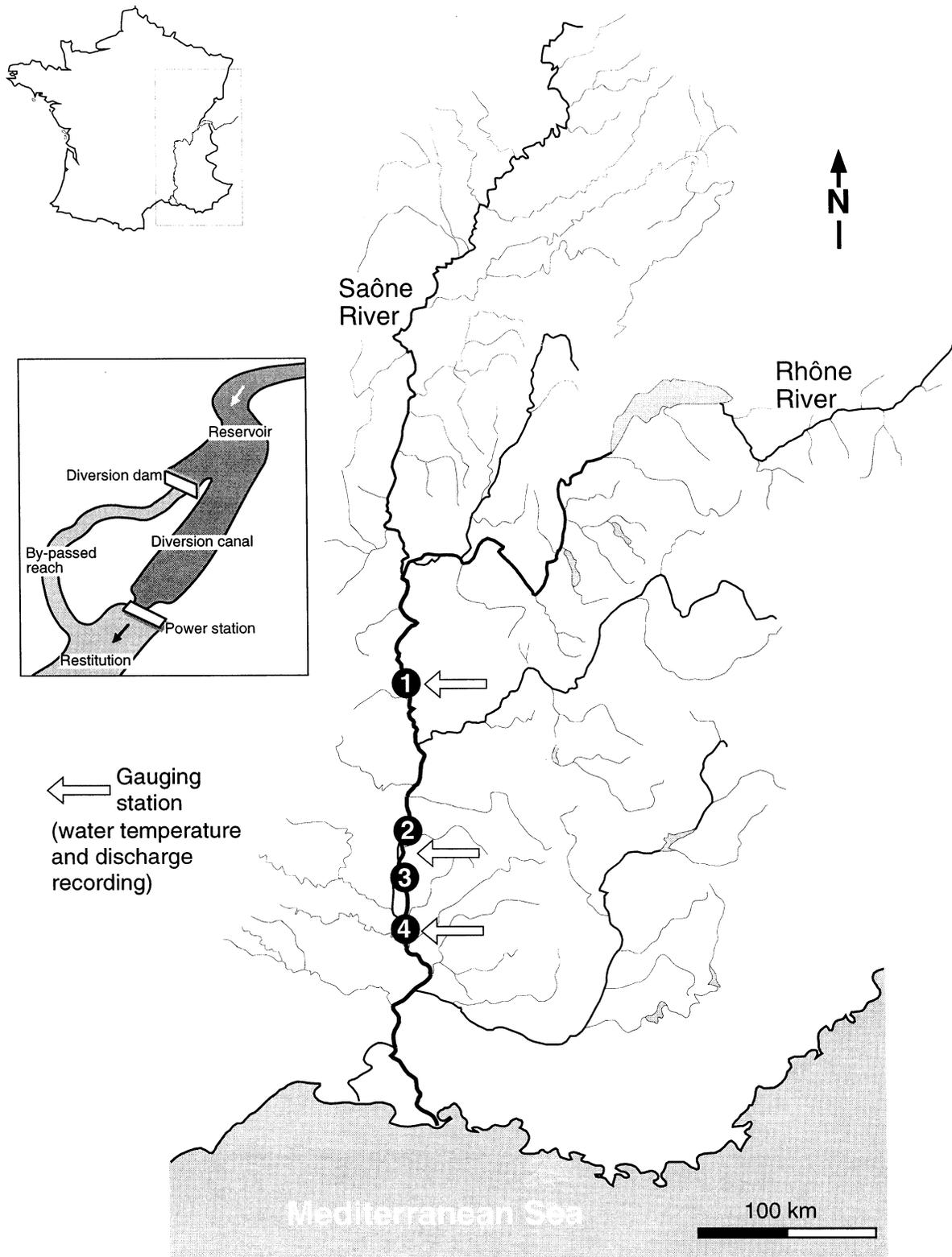


Fig. 1 Location of the four sampling sites in the lower Rhône River.

$t(N(0+)_i)$ . In fact, the  $N(1+)_{i+1}/N(0+)_i$  ratio takes into account not only survival rate but also includes the emigration and immigration likely to occur at each site between the by-passed reach and the channelized canal (see Fig. 1). This ratio will be interpreted as an apparent survival index.

Mean annual abundance was calculated for 0+ and 1+ fish on two or three samples depending on sampling dates. To prevent possible confusion between 0+ and 1+ groups, samples used to determine 0+ abundance were taken from September to February (from the end of the growing season to the beginning of the next), whereas 1+ abundance was determined using spring and summer samples.

From the simple linear relationship between water temperature WT (expressed as degree-days over 12 °C) and total length  $L_T$  (in mm) in 0+ cyprinids (Mills & Mann, 1985; Mann, 1991), we used samples from years and sites where juvenile catches were sufficient to provide good estimates of  $L_T$  ( $n > 30$ ). We used the regression model:

$$L_T = 0.038WT + 22.04 \quad (R^2 = 0.64, P < 0.0001, n = 5141),$$

to estimate a maximum length for 0+ fishes at each sampling date, and we used this maximum length to separate 0+ and older groups.

From previous results from a similar system, the Seine River (Boughida, 1992), a maximum length of 160 mm (mean length of 140 mm) was assumed for 1+ roach.

#### Data analysis

Prior to the analyses, a log-transformation was applied to fish data and weather-related parameters. All transformed variables were normally distributed (Liliefors test).

In accordance with Grossman, Down & Crawford (1990), we calculated the coefficient of variation (CV) among annual means to quantify the temporal variability in abundance of the 0+ and 1+ groups.

To test for synchrony in 0+ and 1+ inter-annual variability, we used Robson's variance test generalized to handle population density data and first proposed for detecting species associations (Schluter, 1984). In this test, each population is one age-group at one site, and the observed variance in the total number of individuals per year ( $\sigma_T^2$ , all populations combined) is compared with the sum of the variance of

individual population densities ( $\sum \sigma_i^2$ ). The statistic:

$$W = \sigma_T^2 N / \sum \sigma_i^2$$

(with  $N$  the number of years) is then, under the null hypothesis of no synchrony ( $H_0$ ), distributed approximately as  $\chi_N^2$ .

Cross correlation coefficients with a time-lag of zero years,  $r_0$ , were used as a measure of spatial synchrony (Ranta, Lindström & Linden, 1995a). The observed level of synchrony between any pair of sites was then related to geographical distances between the sites.

Two models were used to answer the following questions: (1) What factors determine inter-annual fluctuations in 0+ cohort size? (2) What factors determine inter-annual fluctuations in survival?

In each model, we assessed whether the variable 'site' was significant. To identify the relative importance of density independent and density dependent processes, both abiotic and biotic factors were used together in each model. Water temperature and discharge were thus examined taking into account biological considerations: summer conditions are known to affect early life-stages, whereas autumn-winter conditions are expected to affect overwinter survival.

*Model 1: inter-annual 0+ fluctuations.* In this model, the contribution of weather-related parameters (water temperature and discharge) and biotic factors (1+ abundance) in explaining 0+ abundance was analysed using the following multiple regression:

$$N(0+) = a + b(\text{site}) + c(WT_i) + d(Q_i) + e(N(1+)) + \varepsilon_i,$$

where  $WT_i$  and  $Q_i$  are the mean water temperature and mean discharge in the month  $i$ , respectively. The same multiple regression was then repeated for each month from April to September. We hypothesized that biotic interactions with 1+ fish would have an eventual effect (by competition or predation) on 0+ abundance of the same year.

As temporal variation in water flow can strongly affect 0+ abundance in stream (Schlosser, 1985), we investigated the effects of environmental variability in 0+ fluctuations. Standard deviation (SD) was used as a measure of temporal variation and we calculated SD for environmental variables (water temperature WT and discharge Q) for each month from April to September. We incorporated SD(WT)

and  $SD(Q)$  in model 1 and we tested significance of these two additional variables by testing if the observed increase in the explained variance was significant (significance test for additional independent variables, Sokal & Rohlf, 1995).

*Model 2: inter-annual fluctuations in survival.* We investigated the effect of 0+ abundance and autumn-winter weather conditions (mean weather conditions from October to March) on the 1+ abundance in the following year, using the parametric bootstrap test of Dennis & Taper (1994) modified to cope with environmental variables and two age-classes. This test, based on a discrete time stochastic logistic model, uses a likelihood ratio to detect density dependence in time series observations of population abundances.

If  $N(0+)_t$  is the population size of 0+ at time  $t$ , and  $N(1+)_t$  is the population size of 1+ at time  $t$ , a density-independent survival rate is:

$$\ln[N(1+)_t/N(0+)_t] = a + \varepsilon_t, \quad (1)$$

where  $a$  is apparent survival rate between 0+ and 1+ (including emigration and immigration),  $\varepsilon_t$  is a normal random variable (with mean zero and variance  $\sigma^2$ ).

If density-dependence occurs:

$$\ln[N(1+)_t/N(0+)_t] = a + b \ln[N(0+)_t] + \varepsilon_t, \quad (2)$$

where  $a$  is a constant trend parameter and  $b$  ( $b < 0$ ) is the slope of the linear function determining the strength of the density dependence. This is a variation of the Gompertz model (Dennis & Taper, 1994). We modified this model to incorporate weather factors:

$$\ln[N(1+)_t/N(0+)_t] = a + b \ln[N(0+)_t] + cWT + dQ + \varepsilon_t. \quad (3)$$

Given this framework, testing for density dependence means testing for  $b < 0$ . This was done as described in Dennis & Taper (1994) by using Monte Carlo simulations for assessing the distribution of the  $t$ -test associated with  $b$ ,  $t(b)$ . Parameters of eqn 1 ( $a$ ,  $\sigma^2$ ) and 2 ( $a$ ,  $b$ ,  $\sigma^2$ ) were estimated from the observed data by linear regressions and observed  $t(b)$  computed accordingly. Then  $N(1+)$  values were generated from eqn 1 and observed  $N(0+)$  values to generate a simulated time series, and simulated  $t(b)$  was computed. One thousand time series were gener-

ated this way giving 1000 simulated values of  $t(b)$  under the hypothesis of no density dependence. If less than 5% of the simulated  $t(b)$  values were lower than the observed value we concluded that there was density-dependence.

Parameters  $c$  and  $d$  were estimated by linear regression and we tested if they jointly contributed significantly to the observed survival rate in the following way.  $N(1+)$  values were generated from eqn 2 and observed  $N(0+)$  values to generate a simulated time series, and the residual sum of squares (RSS) was computed. One thousand time series were generated this way giving 1000 simulated values of RSS under the hypothesis of no weather effect. If less than 5% of the simulated RSS values were lower than the observed value we concluded that there was a significant weather effect. In all analyses, the four sites were studied jointly, assumed that parameters of eqn 1–3 did not differ among sites.

## Results

### *Environmental variation*

The environmental variables, water temperature and discharge were negatively correlated (monthly mean data,  $r = -0.54$ ,  $P < 0.0001$ ). Mean annual water temperature (in degree-days over 12 °C) ranged from  $984 \pm 112$  in 1987 to  $1498 \pm 218$  in 1997. Mean annual discharge (in  $\text{m}^3 \text{s}^{-1}$ ) ranged from  $931 \pm 124$  in 1989 to  $1760 \pm 277$  in 1995 (Fig. 2). Water temperature and discharge fluctuated significantly between years ( $F_{10,44} = 3.615$ ,  $P = 0.003$  and  $F_{10,44} = 4.004$ ,  $P = 0.001$ , respectively; year effect in repeated-measures ANOVA).

### *Inter-annual variability in recruitment*

Over the 11-year study period, the mean annual abundance (expressed in CPUE) of 0+ and 1+ groups fluctuated broadly, ranging from 0.1 to 575.7 individuals per 20 sampling points, and from 0.1 to 127.6 individuals per 20 sampling points, respectively (Table 1). No alternation of strong and weak year-classes was evident: the mean annual abundance of neither group showed any clear cycle (Fig. 3).

The CV of annual abundance was high for all four data sets (Table 1). According to the classification scheme proposed by Freeman *et al.* (1988), both 0+

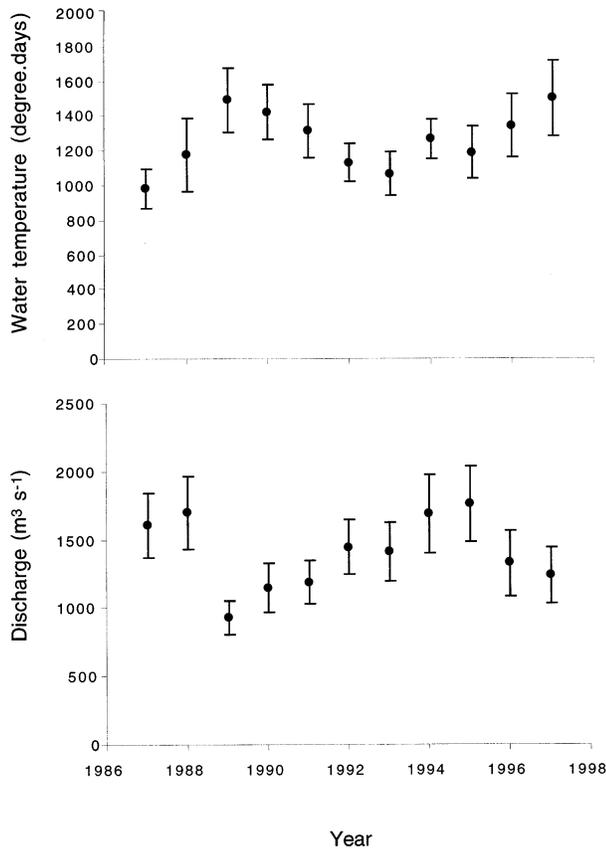


Fig. 2 Annual variation in weather conditions for the four study sites during the 1987–97 study period. Mean annual data are shown (mean  $\pm$  1 SE).

and 1+ groups were strongly fluctuating (CV > 75%). The four sites did not differ in their degree of variability (df = 3,  $P = 0.538$ ; Kruskal–Wallis test). CV values tended to be smaller for the 1+ group (mean  $111 \pm 19.2$ ) than for the 0+ group (mean  $142.8 \pm 31.7$ ), but the difference was not statistically significant ( $\chi^2 = 2.08$ , df = 1,  $P = 0.15$ ; Kruskal–Wallis test).

### Synchrony

The  $W$  statistic was calculated for the 0+ and 1+ groups. Synchrony was evident in 0+ inter-annual variability ( $W = 23.01 > \chi^2_{0.05;11} = 19.675$ ), but not in 1+ fluctuations ( $W = 18.84 < \chi^2_{0.05;11} = 19.675$ ).

The cross-correlation emphasized high spatial synchrony in 0+ dynamics, with significant  $r_0$  values ranging from 0.657 to 0.897 (mean  $0.773 \pm 0.077$ ). For 1+ dynamics, cross-correlation coefficients were lower and more variable than for 0+ dynamics, ranging from 0.29 to 0.6 (mean  $0.442 \pm 0.119$ ).

In relating the level of synchrony in roach dynamics to the geographical distances among the four sites, a classical decrease in synchrony with increasing distance was not observed (Fig. 4). On the contrary, in both 0+ and 1+ dynamics, the highest  $r_0$  value was associated with the two most distant sites. Whatever the pair of sites used, cross-correlation coefficients  $r_0$  for 0+ fish were always greater than those for 1+ fish. For 0+ dynamics, each pair of sites fluctuated synchronously, whereas only three of the six pairs of sites were synchronous for 1+ dynamics, with  $r_0$  values near significance level.

### Determinants of recruitment variability

*Model 1: determinants of inter-annual 0+ fluctuations.* Multiple regressions of annual 0+ abundance and both annual 1+ abundance and mean monthly environmental data were performed for each month from April to September. For each regression, residuals were analysed and Durbin–Watson statistics showed no temporal autocorrelation (Table 2). Analysing the relationship between 0+ abundance and independent variables, neither site nor 1+ abundance appeared to affect 0+ variations. Only weather-related parameters were significantly correlated with 0+ abundance: results showed a negative correlation with April discharge, and positive correlations with water temperature in May and August.

When incorporating monthly standard deviation in water temperature and discharge in model 1, the increase in the explained sum of squares was not significant ( $F$  values ranging from 0.87 to  $4.05 < F_{\alpha/2, 37} = 5.23$ ;  $\alpha' = 0.01$  for Bonferroni's correction). Therefore, monthly standard deviation in environmental data did not significantly explain additional variance in 0+ cohort size.

In view of the apparent importance of water temperature, Pearson correlations were thus calculated between mean annual 0+ abundance and mean monthly water temperature. Correlation was significant with water temperature in May and June ( $R = 0.506$  and  $R = 0.742$ , respectively). Correlation with June water temperature (WT June), which accounted for 55% of the variance of annual 0+ abundance, could be modelled by the following linear regression:

$$\ln N(0+) = 5.413 \ln \text{WT June} - 25.74$$

$$(R = 0.742, P < 0.0001),$$

**Table 1** Fish data (mean annual abundance expressed in individuals per 20 sampling points and CVs (%)) for 0+ and 1+ groups\*

Fish data	Site	Year											CV
		1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	
0+	1	1.5	3.5	108.5	4	53	6	24.5	27.2	0.3	191.7	162.5	125
	2	0.1	7.4	119.6	23.5	4	4.1	3	47.5	5.8	115.2	117.5	119.7
	3	0.9	0.7	17.6	5.3	2.5	0.4	8.1	50.3	0.9	21.3	55.7	129.1
	4	0.2	1	85.7	5.7	8.7	13.5	24.4	133	0.1	51.2	575.7	197.4
Mean		0.7	3.1	82.9	9.6	17	6	15	64.5	1.8	94.9	228	138.4
$L_T$ max		79.4	86.8	98.8	96	91.9	85	82.6	90.2	87.2	93.1	99	
1+	1	9.7	7	3.2	96.7	4.5	51.5	8.5	3	20	1.7	9.5	142.2
	2	11.7	34.6	4	42.3	127.6	68.7	20.6	7.1	24.3	9.1	26.1	101
	3	7	12.7	2.8	52.6	7.2	10.8	3.9	30.7	15.7	5	29	90.9
	4	20.5	0	5.3	41.7	20	6.1	10.3	6.2	52.3	0.4	2.8	110.1
Mean		12.2	13.6	3.8	58.3	39.8	34.3	10.8	11.7	28.1	4.1	16.8	76.3

\* Maximum lengths,  $L_T$  max (in mm), were determined for 0+ fish according to the simple linear relationship between water temperature and total length,  $L_T$  (see 'Methods').

with residuals normally distributed (Lilliefors test:  $P = 0.376$ ) and homoscedastic (Fig. 5).

*Model 2: determinants of variability in inter-annual survival.* The modified Dennis & Taper's test showed that density dependence existed in the time series data (test of density dependence,  $P < 0.001$ , Table 3), and that the residuals from the model were normally distributed (Lilliefors test:  $P = 0.47$ ). These results suggested that the higher the mean annual 0+ abundance, the lower was the first-year survival index. Neither mean water temperature nor mean discharge during the period October–March were related to overwinter survival (test of climatic effect,  $P = 0.093$ ), and only 0+ abundance appeared to affect first-year survival. The site-effect, based on residuals from eqn 2, was significant ( $P = 0.027$ ), suggesting that apparent survival differed among sites.

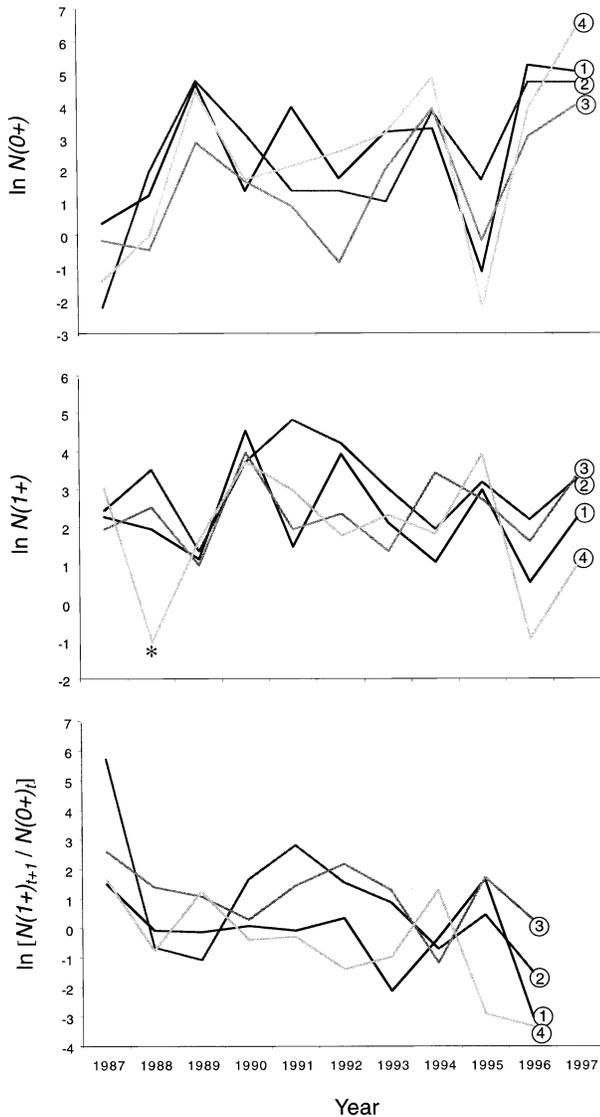
## Discussion

### Synchrony

Using long-term data on roach recruitment dynamics in the Rhône River we have shown, first, that 0+ fish display a high degree of temporal synchrony in their fluctuations. Second, 0+ fluctuate in synchrony over large areas, whereas 1+ fish fluctuate more independently between sites.

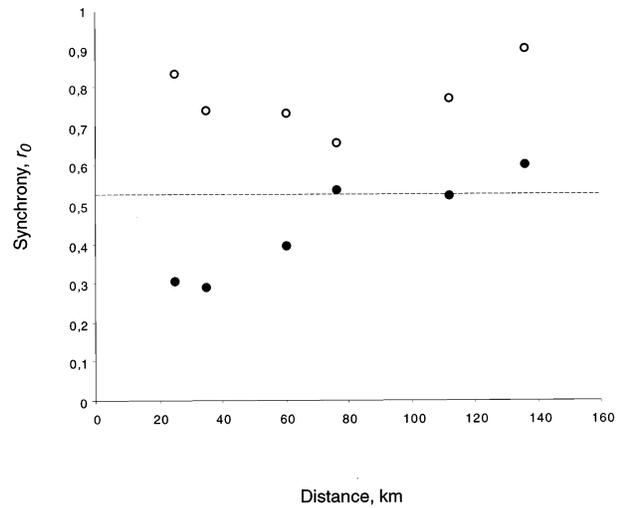
Large-scale synchrony has been investigated in a wide variety of organisms including insects (Pollard, 1991), birds (Ranta *et al.*, 1995a) and mammals (Ims & Steen, 1990; Ranta, Kaitala & Lindström, 1997). Migration (dispersal) and region-wide stochasticity are the two factors most likely to influence spatial synchrony (Hanski & Woiwod, 1993). As fish dispersal is generally highly constrained over large areas, we could expect fish to show less synchrony than other groups (e.g. birds or insects). However, fish are poikilotherms and water temperature is mainly driven by region-wide climatic factors. Therefore, we can expect the synchronizing effect of climatic factors to be more important for fish than for homeotherms. Because of the obstacles created by dams along the Rhône River, migration of juvenile fish between study sites, if it exists, is not likely to be important. This hypothesis is supported by the absence of a negative relationship between the level of synchrony in 0+ dynamics and the distance between each pair of sites, as theoretically expected if dispersal is the driving factor (Ranta *et al.*, 1995b). Weather-related regional stochasticity seems the most likely cause of large-scale 0+ synchrony.

In fish ecology, large-scale weather variations have been shown to synchronize variations of perch year-class strength over large geographic areas, despite highly variable habitats (Koonce *et al.*, 1977; Böhling *et al.*, 1991). In an investigation of spatial scales of



**Fig. 3** Annual variation in 0+ abundance ( $N(0+)$ ), 1+ abundance ( $N(1+)$ ) and apparent survival index ( $N(1+)_{t+1}/N(0+)_{t+1}$ ) for the four study sites during the 1987–97 study period. An asterisk (\*) indicates that a zero has been replaced by the lowest observed value before log-transformation of the data.

inter-annual variations in recruitment, Myers *et al.* (1997) concluded that the correlation scale for recruitment in freshwater species is less than 50 km. Our study shows that for a given river system, coherent recruitment fluctuations can occur on a larger scale (here around 150 km). This discrepancy with Myers *et al.* (1997) reflects the dependence of environmental conditions in a given stretch of river with upstream



**Fig. 4** Spatial synchrony in the dynamics of 0+ (○) and 1+ (●) fish against distance between sites. The dotted line is the limit below which  $r_0$  has  $P > 0.05$ .

systems. Spatial autocorrelation in physical processes along large rivers supports the concept of unity and continuity of the ecological functioning of whole river systems. Therefore, synchrony is liable to occur on larger scale within than between basins. However, more investigations are needed on variations in recruitment within and between basins to support this hypothesis.

The abundance of 0+ fish may also be affected by the stock–recruitment relationship. For instance, the 0+ population may fluctuate in synchrony with adult abundance. Unfortunately, due to a lack of reliable estimates of adult abundance, we cannot test this hypothesis further. In their study, Myers *et al.* (1997) observed that taking account of spawner abundance did not change spatial synchrony in the recruitment of 11 fish species, suggesting that the stock–recruitment relationship is not a major determinant. Moreover, if spatial synchrony was mainly driven by a stock–recruitment relationship, we would expect a low correlation between 0+ abundance and climatic conditions during larval growth, and the presence of temporal autocorrelation of residuals due to autocorrelation in stock abundance, but such results were not observed.

#### Determinants of recruitment variability

*0+ variability.* Previous studies in small lakes have revealed a 2-year cycles in roach recruitment

**Table 2** Results of the multiple regressions (performed for each month from April to September) of mean annual 0+ abundance against sites, mean monthly environmental variables (water temperature and discharge), and mean annual 1+ abundance<sup>†</sup>

Month	Independent variables	df	MS	F-ratio	P	Multiple R <sup>2</sup>	D
April	Site	3	3.38	0.96	1	0.34	2.29
	Water temperature	1	0.15	0.04	1		
	Discharge	1	31.10	8.86	0.03*		
	1+ abundance	1	15.63	4.45	0.264		
May	Site	3	5.74	1.78	1	0.40	2.25
	Water temperature	1	41.07	12.76	0.006**		
	Discharge	1	0.06	0.02	1		
	1+ abundance	1	14.24	4.43	0.27		
June	Site	3	1.61	1.62	1	0.60	2.08
	Water temperature	1	6.50	6.50	0.09		
	Discharge	1	0.35	0.35	1		
	1+ abundance	1	0.49	0.23	1		
July	Site	3	3.33	0.82	1	0.24	1.95
	Water temperature	1	0.18	0.05	1		
	Discharge	1	8.06	1.98	0.846		
	1+ abundance	1	13.03	3.21	0.498		
August	Site	3	7.88	2.35	0.588	0.37	2.24
	Water temperature	1	32.32	9.65	0.024*		
	Discharge	1	0.19	0.06	1		
	1+ abundance	1	20.30	6.06	0.12		
September	Site	3	2.52	0.57	1	0.17	2.05
	Water temperature	1	0.06	0.01	1		
	Discharge	1	4.39	0.99	1		
	1+ abundance	1	14.02	3.16	0.528		

<sup>†</sup> Given are degrees of freedom (df), mean squares (MS), F-ratio, Bonferroni probabilities (P), multiple R<sup>2</sup> and Durbin-Watson statistic (D) calculated for residuals.

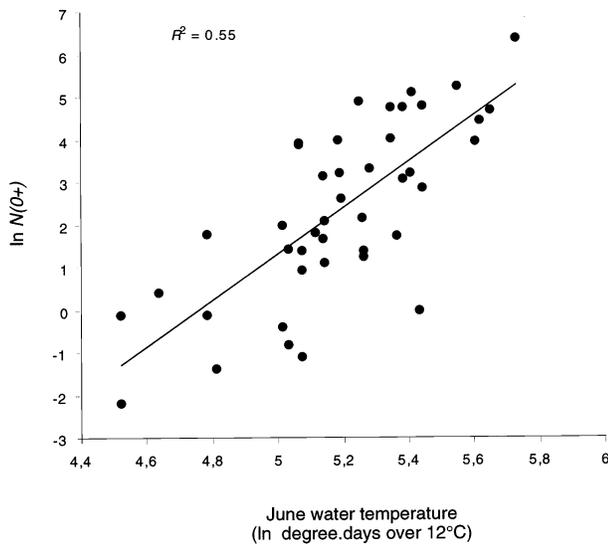
\*  $P < 0.05$ ; \*\*  $P < 0.01$

(Townsend, Sutherland & Perrow, 1990), but these results came from lake populations and resulted from particularly low survival and a low density of adult roach. Such a situation is unusual in freshwater fish populations (Mills & Mann, 1985), and hitherto there is no evidence for cycles in roach recruitment in river populations.

Our results indicate that only weather-related parameters are involved in the determination of inter-annual 0+ variability. Despite the absence of larval abundance data, because of the sampling procedures used, this study clearly underscores the larval stage as a critical period in the recruitment dynamics. The correlation between June water temperature and the mean annual 0+ abundance illustrates the importance of environmental factors during early life. Climatic conditions during the larval period determine

the survival rate of the first life-stage, and hence year-class strength, suggesting that year-class strength is principally determined during the first few months of life.

The importance of climatic conditions during the larval period for year-class strength has already been shown for species such as lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) (Nilo, Dumont & Fortin, 1997) and bass (*Dicentrarchus labrax* (L., 1758)) (Henderson & Corps, 1997). In many cyprinid fish, year-class strength is largely determined by the growth in the first few weeks after hatching (Mann, 1979, 1991; Mills & Mann, 1985), and year-class strength can be predicted from mean length at the end of the first growing season (Mann, 1997). However, larval growth alone is not sufficient to explain recruitment variability (Houde, 1997b) and frequently high and



**Fig. 5** Relationship between mean annual 0+ abundance and June water temperature (degree-days over 12 °C). Fitted using the log-transformed data.

variable early larval mortality could explain the great differences in year-class abundance (Houde, 1987). Mortality is growth-dependent and these two rates are both important in the determination of year-class strength. Factors acting on these two rates during first life-stages therefore underlie recruitment variability.

**Table 3** Parametric bootstrap likelihood ratio test of density dependence and climatic effect for roach apparent survival\*

<i>Density dependence</i>	
Maximum likelihood parameter estimates under null hypothesis (density independence)	$a = 0.424$
Maximum likelihood parameter estimates under alternative hypothesis (density dependence)	$a = 0.816,$ $b = -0.518$
Likelihood ratio statistics	$T(b) = -7.167,$ $P < 0.001$
<i>Contribution of climatic variables</i>	
Without environmental variables	RSS = 44.750
With environmental variables	RSS = 32.213, $P = 0.093$

\* The null hypothesis for the test of density dependence is  $b = 0$  (eqn 1), and the alternative hypothesis is  $b < 0$  (eqn 2). Contribution of climatic variables is tested by comparing residual sum of squares (RSS) with (eqn 3) or without (eqn 2) climatic variables (see 'Methods'). Number of bootstrap samples = 1000.

How can abiotic factors affect recruitment dynamics? In temperate fish, the influence of temperature on growth and mortality rate is well established and numerous studies have focused on temperature as a key factor determining year-class strength (e.g. Koonce *et al.*, 1977; Mills & Mann, 1985; Eckmann, Gaedke & Wetzlar, 1988; Henderson & Corps, 1997). Growth of larval roach is temperature-dependent (Broughton & Jones, 1978) and water temperature increases both larval metabolism processes and food supply (Mills & Mann, 1985). Between-year differences in water temperature lead to between-year differences in larval growth rate and in food availability (Mann, 1997). As larval size is related to the capacity to begin exogenous feeding, faster growth reduces the critical period when the larval stage is more vulnerable, and increases swimming performance. Larger fish are then better able to forage and to avoid predation, considered by Mills (1982) as the principal cause of mortality. Temperature thus acts on mortality of first life-stages and can be a major determinant of year-class strength.

Previous studies have revealed that environmental variability and disturbance might influence fish population dynamics (Horwitz, 1978; Schlosser, 1985; Strange, Moyle & Foin, 1992). However, our results suggest that monthly temporal variation in environmental variables does not influence 0+ cohort size. This discrepancy could result from differences in temporal variability between our study sites and previous studied systems. Previous studies that document the influence of flow variability on fish population dynamics were generally conducted in upstream sections. Analysing the variability patterns of discharge as a function of stream position, Horwitz (1978) revealed a general downstream decrease in temporal variability. As a result, we could expect an increase in the influence of intra-annual environmental variability on fish dynamics towards the headwaters.

The absence of any relationship between 0+ and 1+ abundance of the same year suggests that competition between the two age-classes is not important, which is contrary to the negative between-cohorts interaction observed in other studies (e.g. Henderson & Corps, 1997).

*Survival variability.* Our results reveal a density-dependent first-year survival in roach recruitment dy-

namics, and suggest that climatic conditions are not likely to have an influence. Intraspecific competition within age-classes thus influences first-year survival, and regulates recruitment fluctuations. The low level of 1+ fish synchrony, despite high 0+ synchrony, confirms that apparent survival is not principally determined by large-scale climatic factors. More local factors are likely to influence this apparent survival. The importance of local factors is confirmed by a site-effect on apparent survival. However, the apparent observed survival includes both the survival rate and eventual displacement of juveniles during winter (emigration and/or immigration) between sampling reaches (channelized canal) and unsampled (by-passed) reaches. This variable must therefore be interpreted with care.

In freshwater fish, some authors suggested that recruitment variability may depend predominantly on biotic influences (Myers *et al.*, 1997), and trophic interactions are expected to play a key role in determining recruitment dynamics (Schlosser, 1998). Although we cannot clearly determine from this study the modes of action of density dependent mechanisms, examination of other studies provides some suggestions.

In some cases, climatic conditions during winter have also been suggested as influencing year-class strength (Flath & Diana, 1985), and overwinter mortality has been hypothesized to be one of the mechanisms underlying recruitment variability (Toneys & Coble, 1980). Previous studies suggested that insufficient reserves associated with reduced food intake in winter could explain 0+ overwinter mortality (Schlosser, 1987; Cunjak, 1988, 1996), which has been shown to be density and size-dependent (Schlosser, 1998). Laboratory and field evidence of size-related overwinter mortality of 0+ fish has been demonstrated not only for roach (see Mills & Mann 1985), but also for yellow perch (*Perca flavescens* (Mitchill, 1854)) (Toneys & Coble, 1980; Post & Evans, 1989) and smallmouth bass (*Micropterus dolomieu* Lacepède, 1802) (Oliver, Holeton & Chua, 1979). Post & Evans (1989) showed that overwinter mortality depends upon both first year growth and the winter duration. The combination of variability in first year growth and winter duration could then explain the annual variability in overwinter mortality, and hence recruitment fluctuations. However, results from field studies are in some cases conflict-

ing and size-related overwinter mortality is not a general rule. In this study, no relation was evident between overwinter survival and any measure of winter climatic conditions. Moreover, although growth is temperature-dependent, we failed to demonstrate a positive correlation between overwinter survival and water temperature. Therefore, the hypothesis of a size-related overwinter survival is not confirmed.

However, we are aware that the lack of a relation between overwinter survival and mean environmental variables should be treated cautiously. A more thorough analysis of potential thresholds and intra-annual variation should now be conducted in future studies. These studies should focus more precisely on relationships between temporal variability and fish dynamics.

In cyprinids, density-dependent growth is most often associated with food availability (Mann, 1991), and has been commonly reported in *R. rutilus* (e.g. Burrough & Kennedy, 1979; Linfield, 1980; Townsend & Perrow, 1989). Intra-cohort competition for resources could then be a density-dependent mechanism influencing first-year survival rate. Hamrin & Persson (1986) suggested that strong year-classes in *Coregonus albula* result in small 1+ fish because of greater intraspecific competition within the cohort throughout their first year. Intraspecific competition may result from competition for limited resources, such as space or food (Borgström, Heggenes & Northcote, 1993). This competition for resources could act on the amount of energy stored by 0+ fish, and could therefore affect their first-year survival rate.

For species with complex life histories, current theory on population dynamics hypothesizes that both stochastic forces and density-dependent processes regulate populations. These controlling factors and the proportional influence of each factor vary during different life-history stages (Paulik, 1973; Fogarty & Idoine, 1986; Lipcius & Cobb, 1994). Theory postulates that larvae are primarily influenced by stochastic variations resulting in density-independent survival and dispersal, whereas density-dependent processes such as predation and emigration regulate juveniles and adults (Pile *et al.*, 1996).

In fish, most species have a complex life history characterized by multiple developmental stages with

different ecological requirements. We have shown in this study that 0+ abundance is mainly determined by density-independent factors, whereas density-dependent processes are the most likely underlying mechanism in the determination of first-year survival. Our results support those of numerous studies which have shown that in highly fecund species from the north temperate zone, density-independent factors play a major role during the early life-stages and that density-dependence becomes more important subsequently (Larkin, 1978). Our results suggest that spatial synchrony driven by climatic factors may decrease with age or size as density dependent factors become more important. Thus, studying synchrony for the different life history stages could enhance our understanding of the population dynamics of spatially-structured species. However, in most studies that report synchronous fluctuations in populations of various taxa (from insects to mammals), spatial synchrony is usually analysed for the whole population (that is without distinction between the different life history stages) or by considering only adults. Our analysis showed that spatial synchrony may vary between age classes and we warn against calculating synchrony values for age-structured species without taking this structure into account. Moreover spatial synchrony may be driven by different factors at different stages; for some species dispersal may be the key factor for adults while it is climate for juveniles. According to theoretical models, spatial synchrony increases the risk of regional extinction of metapopulations (Gilpin & Hanski, 1991; Allen, Schaffer & Rosko, 1993; Heino *et al.*, 1997). If spatial synchrony decreases with age or size, as our results suggest, we expect small, short-lived fish species to display more spatial synchrony in the adult stage than large, long-lived species and to be more at risk of regional extinction following climatic perturbations. In conclusion, studying synchrony for different life-history stages could enhance our understanding of the population dynamics of spatially structured species and eventually reveal interesting perspectives in conservation biology.

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