

models in testing plate-tectonic hypotheses with seismic data. Although we cannot test the mechanism for slab flattening<sup>29,30</sup>, the computer simulations indicate that an uncertainty of 1,500 km in locating ancient plate-boundaries can be detected in the current generation of geodynamic and seismic mantle models. Comparable uncertainty exists in locating other ancient plate-boundaries. For example, the position of the ancient Izanagi subduction zone in the northwest Pacific is largely unknown<sup>13</sup>, and results in small but significant differences in geodynamic and seismic heterogeneity structure under northeastern Asia<sup>4</sup>.

Our simulations still have a long way to go towards realism, including the need for treatment of subduction zones as one-sided downwellings rather than simple fluid drips at convergence zones<sup>31</sup>. Other than lacking plates, the main shortcoming of our models is the absence of horizontal viscosity variations resulting from thermal (or stress) variations. Apart from the piecewise rigidity of the upper boundary layer itself, it is not clear how strongly lateral viscosity variations in the deep mantle affect convection<sup>32</sup>, and whether our main conclusions would be changed by modelling them. This question needs to be addressed in future studies. □

Received 20 December 1999; accepted 15 March 2000.

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## Acknowledgements

We thank P. Bird and E. Humphreys for helpful comments on the manuscript.

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# Functional diversity governs ecosystem response to nutrient enrichment

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The relationship between species diversity and ecosystem functioning is a central topic in ecology today<sup>1,2</sup>. Classical approaches to studying ecosystem responses to nutrient enrichment have considered linear food chains<sup>3,4</sup>. To what extent ecosystem structure, that is, the network of species interactions, affects such responses is currently unknown. This severely limits our ability to predict which species or functional groups will benefit or suffer from nutrient enrichment and to understand the underlying mechanisms<sup>5–8</sup>. Here our approach takes ecosystem complexity into account<sup>6,9,10</sup> by considering functional diversity at each trophic level<sup>11–14</sup>. We conducted a mesocosm experiment to test the effects of nutrient enrichment in a lake ecosystem. We developed a model of intermediate complexity, which separates trophic levels into functional groups according to size and diet. This model successfully predicted the experimental results, whereas linear food-chain models did not. Our model shows the importance of functional diversity and indirect interactions in the response of ecosystems to perturbations, and indicates that new approaches are needed for the management of freshwater ecosystems subject to eutrophication.

We designed our experiment to test the effects of nutrient enrichment on the population density of phytoplankton and zooplankton in the absence and presence of zooplanktivorous fish. The classical approach has been to test qualitative predictions obtained from linear food-chain models. In these models, trophic

**Table 1** Qualitative effects of nutrient enrichment as predicted by two linear food-chain models and corresponding experimental results in mesocosms

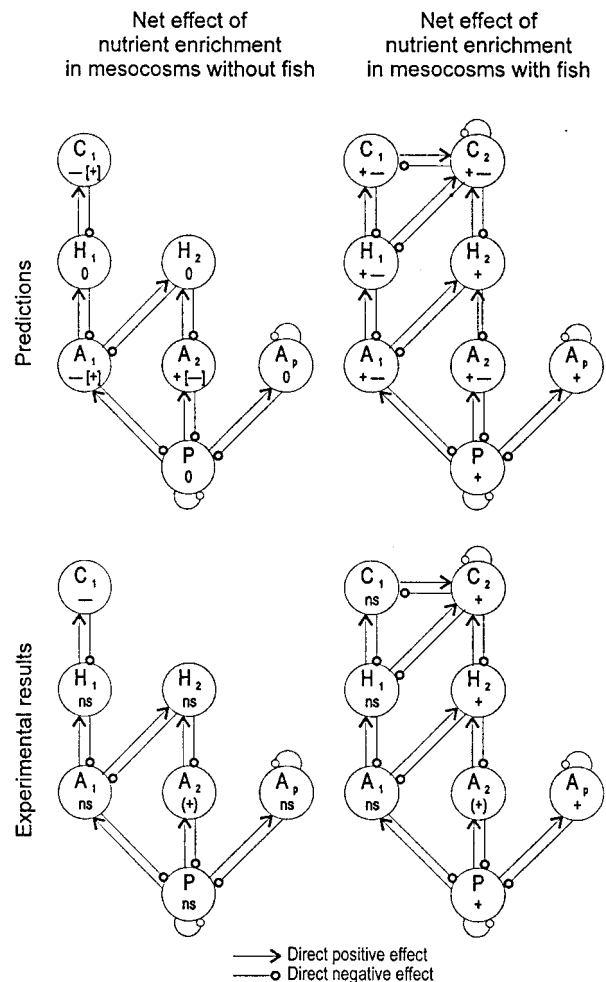
	Model predictions		Experimental results	
	Prey dependence	Ratio dependence	Without fish	With fish
Carnivores	+	+	–	§
Herbivores	0	+	ns	ns
Autotrophs	+	+	ns	ns
Phosphorus	0	+	ns	+

Qualitative effects are indicated by their sign: +, 0 and – denote a positive effect, no effect and a negative effect, respectively, of nutrient enrichment on density. Experimental results: + and – denote a significant positive effect and a significant negative effect, respectively ( $P \leq 0.05$ ); brackets, marginally significant effect ( $0.05 < P \leq 0.10$ ); ns, nonsignificant effect ( $P > 0.10$ ); §, no test possible because the sum of invertebrate carnivores density and fish biomass is senseless.

levels are homogeneous, that is, autotrophs, herbivores and carnivores are described as single compartments. According to the classical prey-dependent model, only the top trophic level and even-numbered trophic levels below the top level should benefit from nutrient enrichment<sup>3</sup>. Thus, in a three-trophic-level food chain, carnivores control herbivore abundance, and autotrophs, which are released from control by herbivores, control nutrients. Consequently, nutrient enrichment should affect only carnivores and autotrophs (Table 1). In contrast, according to the ratio-dependent model<sup>4</sup>, all trophic levels should benefit from nutrient enrichment (Table 1). Alternative models with either donor control<sup>15</sup> or density-dependent regulation in the top trophic level<sup>16</sup> lead to the same predictions as the ratio-dependent model.

To assess the importance of the internal structure of the pelagic food web<sup>11–14</sup>, we developed a model of intermediate complexity with several trophic groups per trophic level (Fig. 1, Box 1). As trophic groups are groups of species that share similar prey and similar predators<sup>7,17</sup>, they represent functional groups from a food-web perspective. Primary producers were divided into edible planktonic algae ( $A_1$ ), protected planktonic algae ( $A_2$ ) and periphyton ( $A_p$ ). We assumed exploitation competition for mineral phosphorus (P) among these groups because of the high nitrogen to phosphorus ratio (20:1). Moreover, periphyton species experienced interference competition, included in the model in the form of a density-dependent loss, because periphyton entirely covered the euphotic zone of the mesocosm walls at the end of the experiment. The second trophic level was divided into small herbivores ( $H_1$ ), which feed mainly on small edible algae ( $A_1$ ), and large herbivores ( $H_2$ ), which feed on both groups of algae ( $A_1$  and  $A_2$ ). Invertebrate ( $C_1$ ) and vertebrate ( $C_2$ ) carnivores are the third trophic level. Invertebrate carnivores ( $C_1$ ) feed mainly on small herbivores ( $H_1$ ). Vertebrate carnivores ( $C_2$ ) are generalist zooplanktivorous fish, which eat small and large herbivores ( $H_1, H_2$ ) as well as invertebrate carnivores ( $C_1$ ). As they feed on more than one trophic level, they are actually omnivorous<sup>7</sup>. Although the density of fish was controlled, their biomass showed large changes depending on treatment because of their strong phenotypic variability. The ratio between final and initial fish biomass varied between 5.9 in the low-nutrient, high-fish treatment to 24.0 in the high-nutrient, low-fish treatment. This requires inclusion of fish biomass as a dynamic variable in the model. We incorporated mutual interference among fish in the form of a density-dependent biomass loss because of the relatively high fish densities in mesocosms.

We used loop analysis<sup>18</sup> to make qualitative predictions about the effects of nutrient enrichment on the equilibrium values of the various functional groups. We then compared these predictions with corresponding experimental results in which trophic groups



**Figure 1** Food-web model describing direct interactions among functional groups in the lake ecosystem, predicted net effects of nutrient enrichment on the equilibrium values of functional groups, and corresponding experimental results in mesocosms. P, mineral phosphorus;  $A_1$ , edible algae;  $A_2$ , protected algae;  $A_p$ , periphyton;  $H_1$ , small herbivores;  $H_2$ , large herbivores;  $C_1$ , invertebrate carnivores;  $C_2$ , fish. Model predictions are indicated by their sign: +, 0, - and +- denote a positive effect, no effect, a negative effect and an indetermined effect, respectively, of nutrient enrichment on equilibrium values. Signs in square brackets correspond to possible but unlikely predicted effects (Box 1).

Experimental results: + and - denote a significant positive effect and a significant negative effect, respectively ( $P \leq 0.05$ ). Brackets denote a marginally significant effect ( $0.05 < P \leq 0.10$ ); ns denotes a nonsignificant effect ( $P > 0.10$ ).

**Table 2** Experimental and statistical results

Group	Without fish		P value	With fish		P value	N	P value	N*F
	N <sub>1</sub>	N <sub>2</sub>		N <sub>1</sub>	N <sub>2</sub>				
P	15.1 ± 5.2	20.4 ± 6.8	0.521	7.02 ± 1.02	27.75 ± 3.10	0.0001	0.481	0.09	
$A_p$	2.5	2.5	0.817	1.1	1.6	0.01	0.5	0.9	
Phytoplankton — mean ± s.e.m. (number of individuals ml <sup>-1</sup> )									
$A_1$	353900 ± 155844	231017 ± 77294	0.536	501120 ± 170503	219633 ± 182364	0.211	0.135	0.275	
$A_2$	19317 ± 4633	35717 ± 4801	0.067	178625 ± 63167	2057458 ± 1700197	0.098	0.213	0.181	
A	373217 ± 160464	266733 ± 73566	0.650	679745 ± 150701	2377092 ± 1656390	0.401	0.673	0.333	
Zooplankton — mean ± s.e.m. (number of individuals l <sup>-1</sup> )									
$H_1$	1090 ± 277	759 ± 41	0.427	4150 ± 944	3528 ± 814	0.628	0.266	0.417	
$H_2$	140 ± 31	131 ± 19	0.873	71.8 ± 15.8	178.8 ± 8.8	0.005	0.522	0.373	
H	1230 ± 293	890 ± 43	0.430	4222 ± 957	3707 ± 820	0.717	0.285	0.429	
$C_1$	51.6 ± 33.3	3.1 ± 1.1	0.024	32.7 ± 17.0	160.5 ± 119.1	0.139	0.293	0.741	
Fish — mean ± s.e.m. (g m <sup>-2</sup> )									
$C_2$				11.48 ± 0.64	33.05 ± 2.00	0.0001	0.0036	0.068	

N<sub>1</sub>, low nutrient level; N<sub>2</sub>, high nutrient level. In mesocosms with fish, means for the two levels of fish are displayed. N, nutrient enrichment effect; F, fish stock effect; N\*F, nutrient enrichment\*fish stock interaction effect. P values for F and N\*F effects are given for information. For all but periphyton ( $A_p$ ) analyses, some logarithmic transformations were performed to correct for heteroscedasticity.

were distinguished (Fig. 1). As phosphorus and nitrogen were continuously added in mesocosms filled with lake water, our manipulations are press perturbations that should reveal both direct and indirect interactions<sup>19</sup>. The duration of the experiment (two months) allowed tens of generations of phytoplankton and few generations of zooplankton, which should be enough to detect effects of direct and indirect interactions<sup>20,21</sup>. Moreover, the final biomass of zooplanktivorous fish varied between 98 and 390 kg Ha<sup>-1</sup>, which is comparable to typical fish biomass of mesotrophic to eutrophic lakes<sup>22</sup>.

Linear food-chain models failed to explain our experimental results. Nutrient enrichment significantly decreased invertebrate carnivore density ( $C_1$ ) in mesocosms without fish ( $P = 0.024$ ), contradicting the predictions of both the prey-dependent and the ratio-dependent three-level food-chain models (Tables 1 and 2). The effects of nutrient enrichment in mesocosms with fish matched the predictions of the prey-dependent model only for the herbivore level (no significant effect) and the predictions of the ratio-dependent model only for the nutrient level ( $P = 0.0001$ ).

In contrast, the predictions of our intermediate complexity model were consistent with the experimental results. In mesocosms without fish, the experimental results showed a marginally significant increase in the density of protected algae ( $P = 0.067$ ) and a decrease in the density of invertebrate carnivores ( $P = 0.024$ ) with nutrient enrichment in agreement with the model (Table 2). The outcome of a press perturbation such as nutrient enrichment is

determined by the relative strengths of the various propagation paths for the perturbation in the system<sup>18,23</sup>, and counterintuitive results are common in complex food webs<sup>23</sup>. The lower invertebrate carnivore density with nutrient enrichment is counterintuitive but is in agreement with our model predictions (Fig. 1, Box 1). A positive indirect effect of nutrient enrichment is transmitted along the left food chain (P–A<sub>1</sub>–H<sub>1</sub>–C<sub>1</sub>) from mineral phosphorus to invertebrate carnivores. But a negative indirect effect is transmitted through consumption of edible algae by large herbivores (P–A<sub>2</sub>–H<sub>2</sub>–A<sub>1</sub>–H<sub>1</sub>–C<sub>1</sub>). This effect is predicted to be stronger because of the greater conversion efficiency of edible algae compared with protected algae (Box 1), leading to a net negative effect. The lack of response of mineral phosphorus concentration, periphyton abundance and densities of small and large herbivores agrees with model predictions.

In mesocosms with fish, nutrient enrichment had positive effects on all levels of the right trophic chain (A<sub>2</sub>:  $P = 0.098$ ; H<sub>2</sub>:  $P = 0.005$ ; C<sub>2</sub>:  $P = 0.0001$ ), as well as on periphyton ( $P = 0.01$ ) and mineral phosphorus ( $P = 0.0001$ ) (Table 2). Note that all the determined model predictions are in agreement with the corresponding experimental results (that is, increases in mineral phosphorus concentration, periphyton abundance and large herbivore density). According to the qualitative analysis of our model, the positive effects of nutrient enrichment on mineral phosphorus, periphyton, large herbivores and fish in mesocosms with fish cannot be explained without incorporating fish predation on invertebrate

## Box 1

### Mathematical model

The dynamic model corresponding to the graphical model of Fig. 1 is:

$$\frac{dP}{dt} = I - qP - (I_1A_1 + I_2A_2 + I_pA_p)P$$

$$\frac{dA_1}{dt} = A_1(k_1I_1P - m_1 - a_{11}H_1 - a_{12}H_2)$$

$$\frac{dA_2}{dt} = A_2(k_2I_2P - m_2 - a_{22}H_2)$$

$$\frac{dA_p}{dt} = A_p(k_pI_pP - m_p - m'_pA_p)$$

$$\frac{dH_1}{dt} = H_1(b_{11}a_{11}A_1 - d_1 - e_{11}C_1 - e_{11}C_2)$$

$$\frac{dH_2}{dt} = H_2(b_{12}a_{12}A_1 + b_{22}a_{22}A_2 - d_2 - e_{22}C_2)$$

$$\frac{dC_1}{dt} = C_1(f_{11}e_{11}H_1 - \mu_1 - u_{12}C_2)$$

$$\frac{dC_2}{dt} = C_2(f_{12}e_{12}H_1 + f_{22}e_{22}H_2 + v_{12}u_{12}C_1 - \mu_2 - \mu'_2C_2)$$

where  $I$  is the external nutrient input;  $q$  is the nutrient loss rate;  $l_j$ ,  $a_{ij}$ ,  $e_{ij}$  and  $u_{ij}$  are the consumption rates of  $P$ ,  $A_i$ ,  $H_j$  and  $C_j$ , respectively, by consumer  $j$ ;  $k_j$ ,  $b_{ij}$ ,  $f_{ij}$  and  $v_{ij}$  are the conversion efficiencies of consumed food type  $i$  into new biomass of consumer  $j$ ;  $m_j$ ,  $d_j$  and  $\mu_j$  are the per capita death rates of  $A_i$ ,  $H_j$  and  $C_j$ , respectively;  $m'_p$  and  $\mu'_2$  are density-dependent interference rates of periphyton and vertebrate carnivores, respectively. The model for mesocosms without fish has  $C_2 = 0$ .

Loop analysis<sup>18</sup> can be applied directly to the graphical model to predict qualitative changes in equilibrium biomasses following a press perturbation in mineral phosphorus. It was also used to check that the equilibrium is potentially stable, that is, that the first Routh–Hurwitz criteria<sup>18</sup> are met. The system is too complex to check the second Routh–Hurwitz stability criteria analytically, but numerical simulations showed the equilibrium to be stable.

For the model without fish, the sign of the predicted changes is undetermined. However, the sign of these changes can be resolved if additional constraints are taken into account. The equilibrium values for the densities of edible algae, protected algae and invertebrate carnivores can be calculated from the above equations and differentiated with respect to  $I$  to evaluate their changes as function of changes in nutrient supply:

$$\frac{\partial A_2^*}{\partial I} = \frac{b_{12}a_{12}}{P^*\alpha}, \quad \frac{\partial A_1^*}{\partial I} = \frac{-b_{22}a_{22}}{P^*\alpha} \quad \text{and} \quad \frac{\partial C_1^*}{\partial I} = \frac{-b_{11}a_{11}b_{22}a_{22}}{P^*\alpha},$$

where  $\alpha = b_{12}a_{12}l_2 - b_{22}a_{22}l_1$  and equilibrium values are denoted by an asterisk.

Thus, the qualitative effects of nutrient enrichment on these functional groups hinge on the sign of the lumped parameter  $\alpha$ , hence on  $(b_{12}a_{12})/b_{22}a_{22}$ , the ratio of the direct effects of edible and protected algae on large herbivores, and on  $l_1/l_2$ , the ratio of the nutrient uptakes of edible and protected algae. If  $(b_{12}a_{12})/b_{22}a_{22} > l_1/l_2$ , nutrient enrichment increases the density of protected algae at the expense of both edible algae and invertebrate carnivores; if the reverse is true, nutrient enrichment increases the biomass of both edible algae and invertebrate carnivores at the expense of protected algae.

As large herbivores are generalists and protected algae escape predation better, the consumption rate of edible algae is expected to be equal to or higher than that of protected algae; hence  $a_{12} \geq a_{22}$ . The conversion efficiency of protected algae ( $b_{22}$ ) is generally lower than that of edible algae ( $b_{12}$ ) for large herbivores<sup>11</sup> because of structures that are difficult to digest. Therefore the direct effect of edible algae on the growth rate of large herbivores ( $b_{12}a_{12}$ ) is expected to be stronger than that of protected algae ( $b_{22}a_{22}$ ). Phosphorus uptake per unit of carbon by algae does not appear to depend on size or presence of protections<sup>30</sup>; hence  $l_1 \approx l_2$ . Thus we conclude that generally  $(b_{12}a_{12})/b_{22}a_{22} > l_1/l_2$ , which implies that  $\partial A_2^*/\partial I > 0$ ,  $\partial A_1^*/\partial I < 0$  and  $\partial C_1^*/\partial I < 0$ : in mesocosms without fish, nutrient enrichment is expected to benefit protected algae at the expense of both edible algae and invertebrate carnivores.

For the model with fish, a complex array of factors affects nutrient enrichment effects, which prevents the signs of the net effects from being resolved.

carnivores. Although predation within the level of carnivores may be weak in terms of energy and material flows, it has a major impact on the dynamic response of the community to nutrient enrichment.

Contrary to linear food-chain models, our model of intermediate complexity correctly predicts the qualitative responses of most functional groups to experimental nutrient enrichment. We conducted a sign test on the agreement between all determined predictions (seven in mesocosms without fish and three in mesocosms with fish) and the corresponding experimental results. Only one effect differed (the nutrient enrichment effect on edible algae in mesocosms without fish is not significant whereas we expected a negative effect). Thus, the level of agreement cannot be ascribed to chance ( $P \leq 0.025$ ). Our model is the result of a trade-off between complexity and predictive ability, and, therefore, it does not rule out alternative explanations of experimental results. It does show, however, that taking functional diversity within trophic levels into account is critical to understanding the response of lake ecosystems to environmental perturbations. Some counterintuitive results of nutrient enrichment, such as the decreased density of invertebrate carnivores in the absence of fish, cannot be explained without including multiple functional groups and their resulting indirect interactions. In the prey-dependent linear model, the only indirect interaction that can occur is the trophic cascade<sup>17</sup>. In our model, additional indirect interactions, also known in other systems<sup>24</sup>, are important in the dynamic response of the ecosystems, and yet are ignored in the classical linear food-chain approach<sup>25</sup>. We conclude that a functional group approach to ecosystems using careful analysis of major species and assumptions on their interactions may provide a better understanding of ecosystem functioning.

These results have important implications for ecosystem management. Lake eutrophication is characterized by increased algal abundance, decreased water transparency and a potential deficit of oxygen<sup>26</sup>. The classical prey-dependent linear food-chain model predicts that nutrient enrichment should increase algal biomass in lakes with an odd number of trophic levels. Therefore lake restoration usually seeks to eliminate trophic cascades either by direct suppression of zooplanktivorous fish or by addition of piscivorous fish. The mixed success<sup>27</sup> of these restorations is understandable in the context of our more complex model. Nutrient enrichment should not affect all algae in the same way. Successful ecosystem restoration needs a new theoretical approach that takes into account community structure and functional diversity. □

## Methods

### Characterisation of trophic groups

The first trophic level was divided into three functional groups: edible algae ( $A_1$ ), protected algae ( $A_2$ ) and periphyton ( $A_p$ ). Edible algae ( $A_1$ ) are small (length  $< 35 \mu\text{m}$ ) and unprotected (*Chroomonas* sp., *Coelastrum astroideum*, *C. microporum*, *Colacium* sp., *Cryptomonas* sp., *Cyclotella ocellata*, *Monoraphidium contortum*, *Quadracoccus ellipticus*, *Scenedesmus acuminatus*, *Tetraedron minimum*, *Trachelomonas* sp. and small undetermined unicells). Protected algae ( $A_2$ ) are large (length  $\geq 35 \mu\text{m}$ ) or protected by thick walls or gelatinous sheaths (*Ceratium hirundinella*, *Cosmarium meneghini*, *Cosmarium* sp., *Crucigenia crucifera*, *C. quadrata*, *C. tetrapedia*, *Dictyosphaerium* sp., *Oocystis lacustris*, *Pediastrum boryanum*, *P. duplex*, *Scenedesmus quadricauda*, *Schroederia indica*, *Staurastrum* sp. and *Synedra ulna*). Herbivores were divided into two functional groups. Small herbivores ( $H_1$ ), which are roughly 50 to 200  $\mu\text{m}$  long and feed mainly on small edible algae ( $A_1$ ), include nauplii of cyclopids and calanoids and herbivorous rotifers (*Brachionus angularis*, *B. calyciflorus*, *B. quadridentatus*, *Filinia longiseta*, *Hexarthra mira*, *Keratella cochlearis*, *K. quadrata*, *Lecane* spp., *Polyarthra dolichoptera-vulgaris* and *P. major*). Large herbivores ( $H_2$ ), which are roughly 400  $\mu\text{m}$  to 2 mm long and feed on the two groups of algae ( $A_1$  and  $A_2$ ), include cladocerans (*Bosmina*, *Daphnia*, *Ceriodaphnia* and *Diaphanosoma*) and copepodites and adults of calanoid copepods (*Eudiaptomus gracilis*). Invertebrate carnivores ( $C_1$ ) include carnivorous rotifers (*Asplanchna girodi*, *A. priodonta*) and copepodites and adults of cyclopoid copepods (*Acanthocyclops robustus* and *Thermocyclops crassus*).

### Graphical models and qualitative predictions

The nodes in the graphical models correspond to dynamical variables (P: mineral phosphorus;  $A_1$ : edible algae;  $A_2$ : protected algae;  $A_p$ : periphyton;  $H_1$ : small herbivores;  $H_2$ : large herbivores;  $C_1$ : invertebrate carnivores;  $C_2$ : fish). Links between nodes correspond to direct effects between trophic groups, determined by the coefficients of the Jacobian

matrix for the dynamical system (Box 1) at equilibrium<sup>18</sup>. An arrow or a line ending with a circle from node  $i$  to node  $j$  corresponds to a positive or a negative direct effect, respectively, of trophic group  $i$  on trophic group  $j$ . The principle of loop analysis is to identify all propagation pathways of a perturbation from one variable to another and to study feedbacks of variables excluded from these pathways<sup>18</sup>.

### Experimental mesocosm study

Experimental methods were described in detail elsewhere<sup>26,28</sup>. Mesocosms were suspended in the lake of Cr eteil (suburbs of Paris, France). Each bag contained about 9.5 m<sup>3</sup> water (1.5 × 1.5 × 4.3 m deep) and was filled randomly and in several steps between 15 and 20 June 1990 with lake water pumped from 1.5 m depth. A two nutrient level × three fish density level balanced factorial design was implemented with three replicates per treatment. (Two additional nutrient treatments without fish are excluded from our analyses to maintain a balanced design. A fourth level of fish density is also excluded because of fish starvation at the end of the experiment.)

Mesocosms were fertilized with soluble phosphorus (KH<sub>2</sub>PO<sub>4</sub>) and nitrogen (NH<sub>4</sub>NO<sub>3</sub>) with a N:P ratio of 20:1 in each treatment three times a week from 27 June to 23 August 1990. The low nutrient treatment was 0.32  $\mu\text{g P l}^{-1} \text{d}^{-1}$  and 6.4  $\mu\text{g N l}^{-1} \text{d}^{-1}$  per enclosure and the high nutrient treatment was 3.16  $\mu\text{g P l}^{-1} \text{d}^{-1}$  and 63.6  $\mu\text{g N l}^{-1} \text{d}^{-1}$  per enclosure.

Two-month-old cyprinids (roach: *Rutilus rutilus*; and common bream: *Abramis brama*) born in the lake were introduced on 29 June 1990. Their mean ( $\pm$  s.e.m.) total length and mean wet weight determined from 30 individuals preserved in 4% formalin were 30.0  $\pm$  0.3 mm and 0.250  $\pm$  0.009 g, respectively. The three levels of fish density were 0, 10 and 20 individuals per enclosure.

Throughout the experiment, 12 water samples were collected in each enclosure between the surface and the bottom with a 2 l Friedinger bottle and mixed. A 300-ml subsample was preserved in 4% formalin for phytoplankton counts<sup>29</sup>. The remaining water was filtered through a nylon mesh with a 50- $\mu\text{m}$  aperture and zooplankton was preserved in 4% formalin.

Phytoplankton and zooplankton counts were made on samples taken on 22 August 1990. Phytoplankton counts used the Uterm ohl inverted microscope technique at ×40 magnification. The zooplanktonic individuals were counted in Dolfuss chambers under a dissecting microscope. The development of periphyton was monitored weekly using a nominal scale (barren walls, low cover and high cover).

At the end of the experiment (23 August 1990), fish were recaptured, preserved in 10% formalin, dried and then weighed to the nearest milligram.

### Statistical analyses

Two separate analyses of variants (ANOVA) tested for effects of nutrient enrichment in mesocosms without fish (one way ANOVA: two levels of nutrient) and effects of nutrient enrichment in mesocosms with fish (two way ANOVA: two levels of nutrient, two levels of fish) on all trophic groups but periphyton. These separate ANOVAs allowed us to compare the experimental results with separate predictions about nutrient effects from our model directly, in the presence or absence of fish. A Mann–Whitney rank test was performed on periphyton abundance. Some logarithmic transformations of density were performed to correct for heteroscedasticity.

Received 7 February; accepted 22 February 2000.

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**Acknowledgements**

We thank A. Bertolo, C. de Mazancourt, A. Gonzalez, M. Hochberg, N. Mouquet, O. Petchev, S. Ponsard, M. van Baalen and S. Yachi for comments on the manuscript. This work was supported by grants from the 'Programme Environnement, Vies et Sociétés'.

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**Adaptive plasticity in mate preference linked to differences in reproductive effort**

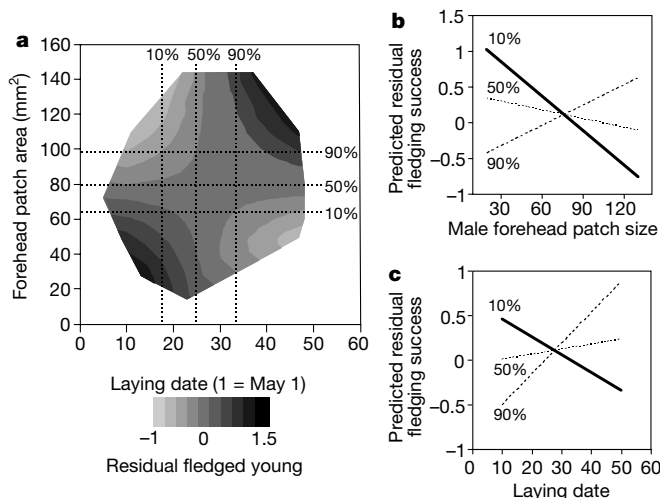
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There is abundant evidence for the existence of marked mate preferences in natural populations, but the occurrence of within-population variation in mate preferences has received little attention<sup>1–3</sup> and is often regarded as nonadaptive deviation from the optimal norm<sup>2,3</sup>. Here we show experimentally that the preference of female collared flycatchers *Ficedula albicollis* for male forehead patch size, a sexually selected trait<sup>4–6</sup>, varies with the time of breeding, an environmental factor with strong effects on reproductive success. Contrary to expectations based on time-constrained choice models<sup>7,8</sup>, only late-breeding females prefer males with a large patch size. The variation in mate preference matches a seasonal change in female reproductive success: long-term data reveal a positive relationship between female reproductive success and male patch size exclusively in late breeders. In addition, female reproductive effort, as assessed by clutch size, appears to be adjusted relative to both timing of breeding and male phenotype. We conclude that not only can mate preferences display adaptive plasticity within populations, but this plasticity can also be linked to differences in reproductive investment.

During the breeding season male collared flycatchers display a conspicuous white forehead patch which is subject to sexual selection through male–male competition over territories<sup>4</sup> and sperm competition<sup>6</sup>. Females choose mates in mid-May, soon after their migration back from the African winter quarters to our study area, on Gotland, Sweden. Males assist their females with caring for nestlings, and male parental care is an important determinant of breeding success for females<sup>9</sup>. Breeding success is also strongly seasonally dependent, declining for later breeding birds<sup>10</sup>, indicating that females are time-constrained in their choice of mate. Experiments have shown the existence of a trade-off between male investment in mating competition and male investment in parental care<sup>11</sup> and suggest that males trade-off these two components of reproductive effort differently depending on their arrival date at the breeding grounds<sup>12</sup>. Among males arriving early, large-patched ones (which are more likely to become polygynous<sup>5</sup> and obtain extra-pair copulations<sup>6</sup>) have a higher premating reproductive effort and are consequently in poorer condition at the time of feeding offspring, as compared with small-patched males; no such pattern is found among late breeders<sup>12</sup>.

We investigated how the seasonal increase in large-patched males' allocation of effort to postmating activities affects female reproductive success by analysing a long-term data set collected from the same collared flycatcher population between 1981–1995. The analysis showed that a female's reproductive success is related to both her timing of breeding and the forehead patch size of her mate. The number of offspring fledged from a breeding attempt (when controlling for age and clutch size) was dependent on the interaction between laying date and male forehead patch size (Table 1 and Fig. 1a). Relatively more young were fledged from late breeding attempts when the male had a large forehead patch size as compared with a small forehead patch size, whereas the reverse pattern was found in early breeders (Fig. 1b, c). Thus, the relationship of a female's reproductive success to the patch size of her mate depends on her breeding date. These findings are consistent with a model of



**Figure 1** Interaction between time of breeding and male appearance (forehead patch size) on reproductive success of female collared flycatchers. **a**, Contour plot of interaction between laying date and male forehead patch size on residual number of fledged young (controlling for year, parental age effects and clutch size); darker contours represent higher values of reproductive success. Dotted lines with percentages indicate the position of the 10th, 50th and 90th percentiles for the variable whose axis they intersect. **b**, Predicted dependence of residual fledged young on male forehead patch size for three different values of laying date, corresponding to the percentiles marked in **a**. **c**, Predicted dependence of residual fledged young on laying date for three different values of male forehead patch size, corresponding to the percentiles marked in **a**.

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