Fig. 2   Isotherms plotted with potential density (in kg m^{-3}) as the vertical coordinate. Internal wave distortions are removed from the contour. The remaining structure is an intrusion of cool, low salinity water that slopes downward from left to right.

problem, the slope should have reversed in the up casts. This is not the case and the maps are nearly identical to Fig. 2.

A section made at a 60° angle to that shown in the figures showed that the intrusion was also sloping downwards across isopycnal surfaces in a direction away from the front. Microstructure profiles through similar intrusions[5] have revealed distinctive signatures on the upper and lower boundaries of the minima that have been identified as the appropriate type of double-diffusive convection.

Double-diffusive convection is a consequence of the much lower molecular diffusivity of salt dissolved in water compared to the thermal diffusivity[6]. Consequently, when warm, saline water overlies cool, fresh water in a stratified profile small perturbations lead to a series of centimetre thick rising and descending columns known as salt fingers. When warm, saline water occurs beneath cooler, fresher water (known as the diffusive regime), a sequence of convecting regions separated by their interfaces is formed. Although the observations in Fig. 1 did not have the spatial resolution to detect the signatures of double diffusion, the inference from the microstructure observations is that salt fingering occurred above the minima and the diffusive regime below. Laboratory experiments[7] of diffusively unstable intrusions have shown that the increase in density below a salt fingering region dominates the decrease above the 'diffusive' regime, with the consequence that cool, fresh intrusions tend to sink as they move laterally. The thickening and formation multiple minima are also revealed in the laboratory work.

The cross-isopycnal slope of 100 m-thick intrusions across the Antarctic Front has been inferred[7] by a cross-spectral comparison of horizontally separated profiles. We have obtained the same result directly for much thinner features by mapping against density.

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M. G. GREGG
J. H. McKENZIE

*Applied Physics Laboratory and
Department of Oceanography,
University of Washington,
Seattle 98195*

1. Gregg, M. C. *J. phys. Oceanogr.* **7**, 436 (1977).
2. Pederson, A. M. *Trans. Mar. Technol. Soc. Mar. Temp. Measurements Symp.* 135 (1969).
3. Pederson, A. M. & Gregg, M. C. *I.E.E.E. J. of Oceanic Engng.* (in the press).
4. Dantzler, H. L. *Deep Sea Res.* **21**, 675 (1974).
5. Gregg, M. C. & Cox, C. S. *Deep Sea Res.* **19**, 355 (1972).
6. Turner, J. S. *Buoyancy Effects in Fluids* (Cambridge University Press, 1973).
7. Turner, J. S. & Chen, C. F. *J. Fluid Mech.* **63**, 577 (1974).
8. Joyce, T. M., Zenk, W. & Toole, J. M. *J. geophys. Res.* **83**, 6093 (1978).

Connectance in real biotic communities and critical values for stability of model ecosystems

BIOLOGICAL communities differ in the number of species that they contain; in the number of interactions between species (primarily feeding and competitive relationships); and in the intensity of their interactions. We present here the first extensive empirical data on the relationship between connectance (defined as the fraction of the pairs of species which directly interact[1,2]) and species richness in biological communities. Our results show that connectance may decline considerably as the number of species increases.

A decade ago, most ecologists firmly believed that increased ecosystem complexity (both the number of species and the number of interactions) would lead to greater ecosystem stability. For example, Odum[3] suggested that "Higher diversity, then, means longer food chains and more cases of symbiosis (mutualism, parasitism, commensalism, and so forth), and greater possibilities for negative feedback control, which reduces oscillations and hence increases stability". This attractive and widespread statement has been shaken dramatically by May[1,2,4,5] and his followers[6-13]. May examined the complexity-stability question in model ecosystems by constructing interaction matrices with each off-diagonal element (interaction coefficient) assigned from a distribution of random numbers, where distribution itself has mean value zero, and standard deviation value (interaction strength) s; the stability of the matrices was then evaluated in terms of their eigenvalues[14]. The central feature of May's results for model ecosystems is the sharp transition from stable to unstable behaviour as soon as either the species number m, or the connectance C, or the interaction strength s, exceeds a critical value. If the equation $s\sqrt{mC} > 1$ holds, the system will almost certainly be unstable. In general, by becoming more complex a system becomes less likely to be stable. Selected empirical evidence supports such a conclusion. According to May[4], "this inverts the naive, if well-intentioned, view that 'complexity begets stability', and its accompanying moral that we should preserve, or even create, complex systems as buffers against man's importunities". May's corollaries are useful for sharpening discussion but their application to natural resource management and optimum land use is not without danger.

Recently, Lawlor[15] has shown that severe constraints must be introduced on the structure of an interaction matrix if it is to represent a biologically acceptable system. He has suggested, *inter alia*, the hyperbolic reduction of the connectance C as the number of species m increases: $Cm = 10$. This relationship ensures stability if the standard deviation s of the interaction coefficients (not variance; this is the mistake of Lawlor), is less than about one-third. Lawlor's comments induce the urgent question: What is the true connectance of real communities?

The question seems to be unanswerable on the basis of very rough, speculative or fragmentary data in most of the literature, even if such data are sometimes used in theoretical considerations. The extensive data collected by one of us[16,17] have allowed reconstitution of the food webs in a great number of plant-aphid-parasitoid communities. The parasitoids belong to three families: Aphidiidae, Aphelinidae and Encyrtidae (Hymenoptera). All host-parasitoid relationships have been tested in the laboratory. The results for one representative community are demonstrated in Fig. 1. In the cannopy of an oak-pine-birch forest (the order Pino-Quercetalia Soó 1962 in the sense of the Zürich-Montpellier phytosociological school) 37 species have been recorded of vascular plants, aphids and their parasitoids; a trophic connectance of 0.059 has been calculated for this community. Some chains have been confirmed by numerous field assessments, for example, 23 geographically distinct observations for that of *Pinus silvestris-Schizolachnus pineti-Pauesia*
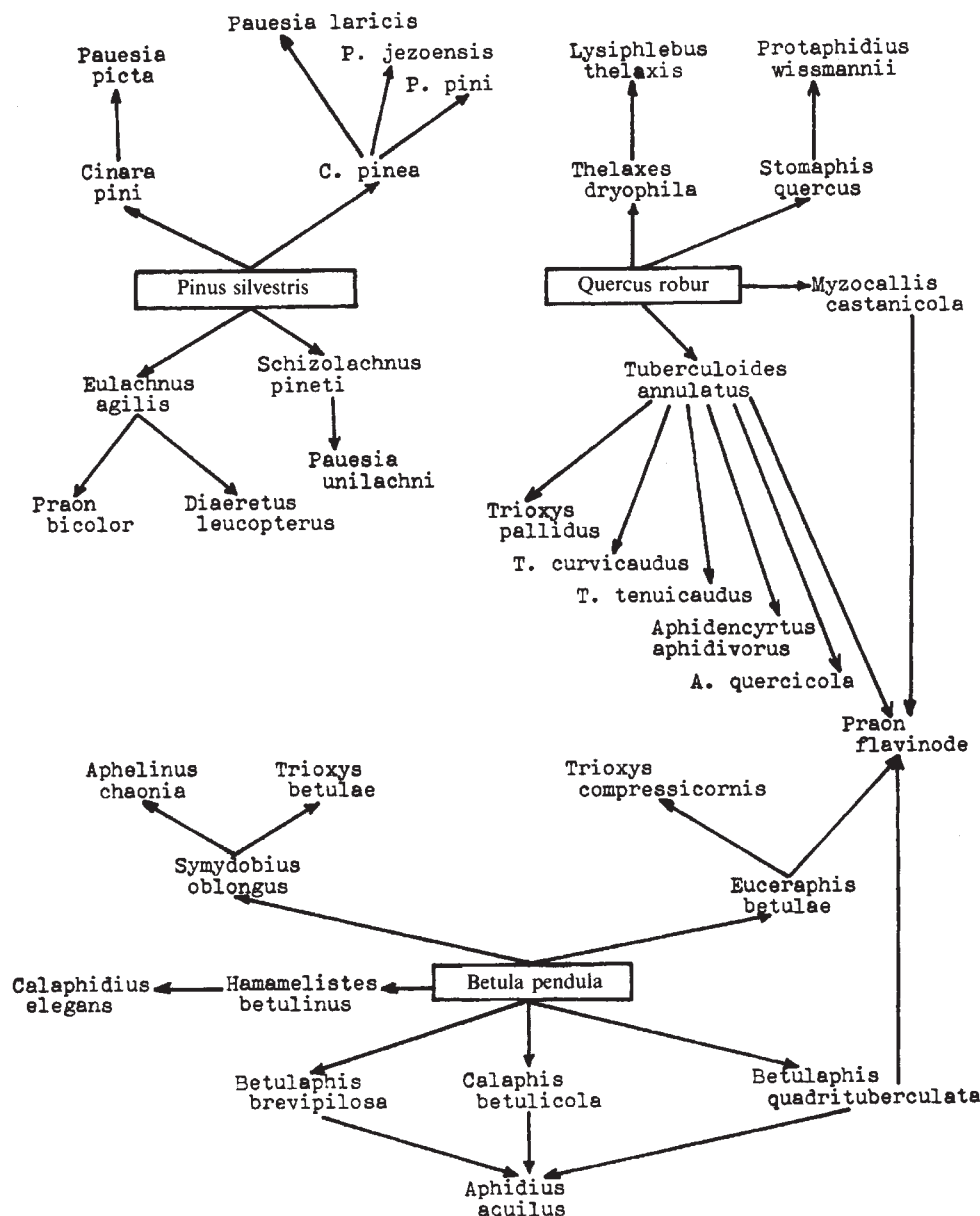
Fig. 1 An example of the plant–aphid–parasitoid food web: a cannopy of oak–pine–birch forest in Central Europe (number of species = 37, trophic connectance = 0.059, potential total connectance = 0.137).

unilachni. Other chains are not so remarkable, for example, that of *Betula pendula–Betulaphis brevipilosa–Aphidius aquilus*. The potential total connectance is highly overestimated because it has been calculated on the basis of both the discovered trophic connections and all potential competitive interactions derived from the structure of the food webs regardless of the biological reality. The aggregation of the populations[18] and the differentiation of the food niches considerably reduce the number of competitive interactions. For example, *Cinara pinea* can never directly compete with *Eulachnus agilis* or *Schizolachnus pineti* despite the common plant host.

Food webs have been reconstructed for 31 plant–aphid–parasitoid communities; the summary of the connectance analysis is presented in Fig. 2. The analysed communities cover a broad variety of Central European biotopes and successional stages. With regard to the previous comments, we may conclude that the decrease in total connectance with increased species richness fits very closely the relationship $Cm = 3$. This reduced connectance ensures the stability of model ecosystems if the standard deviation s of the interaction coefficients is less than 0.577, that is, the variance is less than one-third. It means that with this modest value of s, an increasing number of species does not cause a decrease of model stability: a conclusion which, at
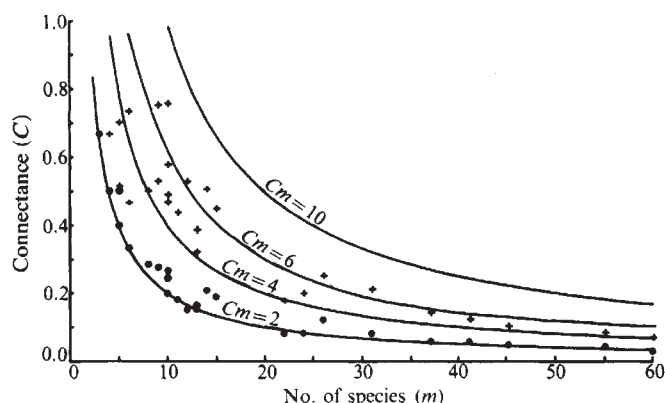

Fig. 2 Four hyperbolic approximations and the empirical relationships between connectance (c) and species number (m) in real plant–aphid–parasitoid communities. Potential total C (+) was calculated on the basis of both the discovered trophic connectance (●) ions and all potential competitive interactions derived from the structure of the food webs (see, for example, Fig. 1) regardless of the biological reality.

least, does not contradict the traditional ecological hypothesis. Connectance values for pure competition communities have recently been estimated by McNaughton[19]. His data for communities consisting of up to 20 plant species follow roughly the product $Cm = 4.7$.

The low connectance assessed by us in plant–aphid–parasitoid communities, arises undoubtedly from their organisation in guilds of species interacting within each guild, whereas their interactions with species in other guilds are only loose. Such an organisation may reduce the destabilising effect of greater system complexity[1,2]. It seems likely that the majority of the plant–aphid–parasitoid communities possesses structures which correspond to the boundary conditions of model stability. This is, of course, a rather speculative conclusion as we are unable to estimate the *s* values. On the other hand, there is no evidence for the existence of any plant–aphid–parasitoid communities outside the region $2 < Cm < 6$. Destabilising effects can be expected, through increased connectance caused by hyperparasitoids and predators, both with broader food spectra[20,21]; further study is required on this point.

M. REJMÁNEK
P. STARÝ

Institute of Entomology,
Czechoslovak Academy of Sciences,
Viničná 7, 128 00 Praha, 2,
Czechoslovakia

1. May, R. M. *Nature* **238**, 413–414 (1972).
2. May, R. M. *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, 1973).
3. Odum, E. P. *Fundamentals of Ecology* (Saunders, Philadelphia, 1971).
4. May, R. M. in *Theoretical Ecology: Principles and Applications* (ed. May, R. M.) 142–162 (Blackwell, Oxford, 1976).
5. May, R. M. in *The Breakdown and Restoration of Ecosystems* (ed. Holgate, M. W. & Woodman, M. J.) 11–25 (Plenum, New York, 1978).
6. Gilpin, M. E. *Nature* **254**, 137–139 (1975).
7. Goodman, D. *Q. Rev. Biol.* **50**, 237–266 (1975).
8. Pielou, E. C. *Ecological Diversity* (Wiley, New York, 1975).
9. Turk, J., Wittes, J. L., Wittes, R. & Turk, A. *Ecosystems, Energy, Population* (Saunders, Philadelphia, 1975).
10. Whittaker, R. H. *Communities and Ecosystems* 2nd edn (Macmillan, New York, 1975).
11. Goh, B. S. & Jenkins, L. S. *Ecol. Model.* **3**, 63–71 (1977).
12. Logofet, D. O. & Svirežev, Ju. M. *Problemy Kibernetiki* **32**, 187–202 (1977).
13. McLean, J. M., Shepherd, P. & Curnow, R. C. in *New Trends in Mathematical Modelling* (ed. Straszak, A. & Owsiński J. W.) 257–296 (Ossolineum, Wroclaw, 1978).
14. Barnett, S. & Storey, C. *Matrix Methods in Stability Theory* (Nelson, London, 1970).
15. Lawlor, L. R. *Am. Nat.* **112**, 445–447 (1978).
16. Starý, P. *Biology of Aphid Parasites (Hymenoptera: Aphidiidae) with Respect to Integrated Control* (Junk, The Hague, 1970).
17. Starý, P. *Acta Ent. Bohemoslov,* 75, 164–177 (1978).
18. Way, M. J. & Cammel, M. E. in *Animal Populations in Relation to Their Food Resources* (ed. Watson, A.) 229–247 (Blackwell, Oxford, 1970).
19. McNaughton, S. J. *Nature* **274**, 251–253 (1978).
20. Stary, P. *Acta Ent. Bohemoslov.* **74**, 1–9 (1977).
21. Hodek, I. *Biology of Coccinelidae* (Junk, The Hague, 1973).

Abnormal visual resolution of cats reared in stroboscopic illumination

REARING animals in a visually restricted environment can lead to marked abnormalities of both the response properties of single visual neurones[1-4] and the visual capacities of the organism[5,6]. These findings have important implications for understanding the development of human vision and have led to many studies of visually deprived humans[7-9]. Although there are similarities between the effects of deprivation in animals and humans there are still major difficulties in extrapolating from experimental deprivation to clinically observed amblyopia. There is, therefore, a need for quantitative psychophysical studies of visually deprived animals using the same tests as those used with human patients. We have quantified the pattern vision of visually deprived cats by measuring their spatial contrast

sensitivity, an approach which has frequently been used to characterise the vision of human amblyopes[7-9]. We report here that the spatial resolution of cats reared in stroboscopic illumination is seriously impaired and that changes in their contrast sensitivity are similar to those seen in certain types of amblyopia.

Stroboscopic illumination prevents the perception of motion while allowing rather restricted pattern vision. Animals reared in this illumination show greatly reduced directional selectivity and binocularity of visual neurones in the superior colliculus and visual cortex[10,11], impaired orientation tuning in cortical neurones[11], and marked difficulties in visually guided behaviour[12,13]. However, there is as yet no quantitative description of their visual capacities.

Six cats were used. Three were reared from birth in a room illuminated by a 3-μs strobe light, flashed at a frequency of 40 min^{-1} for 12 h per day. One control cat was reared in a long duration (750 ms) flash of the same frequency as the strobe light. This 750-ms flash permitted the perception of motion while providing a control for the periodicity and low luminance of the strobe environment. The effective luminance of these two types of illumination was equated using a behavioural test in which luminance thresholds for grating discrimination were determined in normal cats for each of these light sources (T.P. and W.H.M., in preparation). When the deprived cats were at least a year old they were removed from the visually restricted environment. Testing began after at least 2 months of adaptation to normal illumination. Two more cats were obtained from a supplier and presumably had normal visual experience during development.

Our behavioural testing techniques resembled those developed by Berkley[14]. The cats were trained to discriminate between a vertical grating of sinusoidal horizontal luminance profile and a uniform field, each at a mean luminance of 15.9 cd m^{-2}. They responded by pressing with their nose on one of two transparent response panels through which the stimuli were visible. The stimuli were 30 cm behind the response panels, subtended a visual angle of $16° \times 20°$, and were generated on display oscilloscopes by conventional techniques[15].

On each trial the stimulus was present for 2 s before the response panel could be activated. Correct responses were rewarded with beef purée and the next trial began 5 s later. Following incorrect responses, no food reward was delivered and the start of the inter-trial interval was delayed 10 s. The position of the correct stimulus varied randomly.

Once the cats mastered the task (4 consecutive days $\geq$80% correct, 200 trials a day), measurement of contrast thresholds over a range of spatial frequencies began. Performance at a single spatial frequency was tested during each daily session of 200 trials. We used the method of constant stimuli to generate a psychometric function in each session: five contrast levels chosen to bracket the threshold were presented in random order within each block of five trials. Contrast threshold was defined from the resulting psychometric function as the contrast corresponding to 75% correct.

The results are shown in Fig. 1a. At the frequency of peak sensitivity, normal cats and the 750-ms control cat can resolve gratings of ~1.4% contrast. Their sensitivity decreases at lower and higher spatial frequencies. The functions for the three strobe cats show greatly reduced sensitivity at all spatial frequencies and a peak shifted towards lower frequencies. The minimal resolvable contrast for the three cats ranged from 7.6 to 29%. Strobe cats also showed a reduction of about 1.5 octaves in the high-frequency cut-off. Figure 1b shows log sensitivity loss for the three strobe cats, relative to the 750-ms control. This plot clearly demonstrates increasing sensitivity loss with higher spatial frequencies.

The functions in Fig. 1a have shown little change over more than 2 years of testing despite continuing exposure of the cats to a normal laboratory environment. Thus, these deficits are relatively permanent. It is unlikely, moreover, that optical factors can account for these losses. We tested all cats at a distance of 30 cm, which is close to the near point of accommodation for