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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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*