

Appendix A: Qualitative analysis of model stability and predictions of press perturbation response.

1. MODEL STABILITY

Qualitative stability is determined by the sign and balance of a system's feedback cycles. For n variables in a system, there are n levels of feedback (F_k), where each level has cycles of length k . For example, our simplest system for banana prawns in Weipa (Fig. 3a) has three variables and three levels of feedback

$$\begin{aligned} F_3 &= -a_{1,2}a_{2,1}a_{3,3} - a_{2,3}a_{3,2}a_{1,1} \\ F_2 &= -a_{1,1}a_{3,3} - a_{1,2}a_{2,1} - a_{2,3}a_{3,2} \\ F_1 &= -a_{1,1} - a_{3,3} . \end{aligned} \tag{A.1}$$

Feedback at level one is a sum of cycles of length one, which are the system's self-effects. Feedbacks at higher levels involve products of conjunct and disjunct links. At level two, there is one feedback cycle formed by the product of disjunct self-effects ($-a_{1,1}a_{3,3}$) and two cycles that are the product of pairwise conjunct links ($-a_{1,2}a_{2,1}$, $-a_{2,3}a_{3,2}$). The overall feedback is defined at the highest level of the system and can be calculated by the system's determinant.

The stability of a system can be formally assessed by the Routh–Hurwitz criteria (Levins 1975, Puccia and Levins 1985, Dambacher *et al.* 2003a), which require that: (i) net feedback at each level of the system is negative, and (ii) feedback at higher levels of the system cannot be too strong compared to feedback at lower levels. Systems that fail criterion (i) are dominated by positive feedback, which can be characterized as a self-enhancing series of interactions (*e.g.*, in Fig. 4a, c and d, the interaction of catch and effort has positive feedback at level two, and an increase in effort leads to increased catch, which can lead to a further increase in effort). A system that is unstable due to positive feedback will diverge from, and never return to, the levels of population abundance that characterized its former equilibrium state. Criterion (ii) is determined by a sequence of n inequalities; the one relevant to a three-variable system is

$$F_1F_2 + F_3 > 0. \tag{A.2}$$

This inequality requires that higher-level feedback must not be greater than the product of lower-level feedbacks. Systems failing criterion (ii) do so by over-correcting in response to a perturbation. This over-correction is caused by the system being controlled more by long

feedback cycles than by shorter feedback cycles, which leads to undamped oscillations of steady or increasing amplitude.

The feedbacks detailed in Eq. A.1 unconditionally meet stability criteria (i) and (ii), and thus the simple system (Fig. 3a) is sign stable, meaning that given the sign structure of the community matrix \mathbf{A} in Eq. 3, the system will be stable for all possible values of interaction strengths. Model A (Table 1) is also sign stable with only negative feedback at levels one and two. Conversely, the positive self-effect of the stock in model B (Table 1b) creates, from criterion (i), conditions for stability at both the first and second feedback levels of the system (*i.e.*, stability requires that $a_{SS} < a_{FF}$ and $a_{SS}a_{FF} < a_{SFAFS}$).

In a fixed-quota fishery (Table 1d), the transition between model C and D is determined by a precarious balance of positive and negative terms in the stock's self-effect. In Eq. 9, a value of $\theta = -1$ places S^{-2} in the second term of the stock's self-effect and gives it a positive value. The strength of this positive term is regulated by the inverse square of the stock's abundance, and thus any decline in stock abundance can become self-enhancing by a squared power, making the population prone to sudden collapse.

In models C and D (Table 1d), the lack of reciprocal links or feedback between variables S and F permits these models to be decomposed, with each variable treated as a separate subsystem. Model C is thus sign stable as each variable has a negative self-effect and there are no other conditions to consider; conversely, the positive self-effect on the stock variable in model D imparts instability to the stock subsystem.

In addition to questions of stability, the analyses of system feedback provides insight into the processes that control a system's dynamics. For instance, the determinant, or overall feedback, of the expanded fleet-stock model (Fig. 4a) has five feedback cycles that characterize the main drivers (*i.e.*, positive feedbacks) and regulators (*i.e.*, negative feedbacks) of the fishery (Dambacher *et al.* 2009)¹:

$$\det(\mathbf{A}) = \underbrace{a_{EC}a_{CE}a_{SS}a_{MM}}_{\text{capitalization}} + \underbrace{a_{MC}a_{CS}a_{SE}a_{EM}}_{\text{scarcity driven effort}} - \underbrace{a_{MC}a_{CE}a_{EM}a_{SS}}_{\text{market regulation}} - \underbrace{a_{EC}a_{CS}a_{SE}a_{MM}}_{\text{stock regulation}} - \underbrace{a_{CC}a_{EE}a_{SS}a_{MM}}_{\text{self regulation}}. \quad (\text{A.3})$$

¹ Capitalization describes the process of investing income obtained from catch back into fishing effort which leads to more catch; scarcity driven effort describes a process whereby low levels of a stock supports low levels of catch, which leads to an increase in market price and fishing effort, and thus a further reduction in stock abundance; market regulation is the process of a drop in market price from a high level of catch causing a reduction in investment back into fishing effort and thus a corrective reduction in catch; stock regulation describes the process of a high level of fishing effort causing a reduction in stock abundance, which leads to a reduced level of catch and thus a reduced investment in fishing effort.

For this system to be stable, and also to be an equivalent representation of the two-variable model A (Table 1), the combined strength of the three negative feedback cycles in Eq. A.3 must be greater than that of the two positive cycles. The positive cycles, if too strong, can lead to over-capitalization and over-exploitation in a fishery; the former involves reinvestment of profits into fishing effort whereas the latter describes effort being driven by an ever increasing price for an ever decreasing stock. Negative, stabilizing feedback arises from effort being regulated both by the market and the stock's abundance, and also from the product of self-regulation of each variable. For the global market model (Fig. 4c), conditions for stability and equivalence with model A (Table 1) are the same as a negative value for Eq. A.3, with the exception that the absence of the a_{MC} link eliminates the scarcity-driven-effort and market-regulation feedback cycles.

Whereas analysis of system stability can proceed by consideration of the conditions that underpin stability criteria (i) and (ii), in large complex systems the algebraic arguments behind these criteria can become too complicated to reasonably interpret. Dambacher *et al.* (2003a) developed qualitative metrics that scale the relative balance of positive and negative terms in the conditions for each stability criterion. These metrics have been tested against numeric simulations that randomly specified interaction strengths to the matrix \mathbf{A} , and they emerged as a general means to determine which criterion a model is most vulnerable to failing, and its general potential for stability.

2. PERTURBATION RESPONSE

a. PREDICTIONS FROM THE ADJOINT MATRIX

Press perturbations arise from a sustained change to a system parameter that affects a population's rate of birth, death, or migration. In general, we want to predict the direction of change in equilibrium abundance for each of the N_i populations due to the sustained change of a specific parameter (p_h). These predictions are obtained through the inverse of the negative community matrix (Dambacher *et al.* 2005)

$$\frac{d\mathbf{N}^*}{dp_h} = -\mathbf{A}^{-1} \frac{\partial \left(\frac{d\mathbf{N}}{\mathbf{N}dt} \right)}{\partial p_h}. \quad (\text{A.4})$$

From the matrix equality

$$-\mathbf{A}^{-1} = \frac{1}{\det(-\mathbf{A})} \text{adj}(-\mathbf{A}), \quad (\text{A.5})$$

where 'adj' is the adjoint matrix, Eq. A.4 can be expressed as

$$d\mathbf{N}^* = \underbrace{\frac{1}{\det(-\mathbf{A})}}_{\text{overall feedback}} \underbrace{\text{adj}(-\mathbf{A})}_{\text{relative response}} \underbrace{\frac{\partial\left(\frac{d\mathbf{N}}{\mathbf{N}dt}\right)}{\partial p_h}}_{\text{strength of input or press perturbation}} dp_h. \quad (\text{A.6})$$

Here $d\mathbf{N}^*$ gives the predicted shifts in equilibrium abundance of each population, and $(\partial(d\mathbf{N}/\mathbf{N}dt)/\partial p_h)dp_h$ is the strength of the input or press perturbation. Showing the inverse matrix in the form of the adjoint matrix and system determinant is useful because elements of the adjoint matrix detail the relative variation of the system's response in terms of both the direct and indirect effects of a perturbation (Dambacher *et al.* 2002).

In Eq. A.6, the system's determinant, or overall feedback, scales the magnitude of the response of each variable. In systems that are stable, feedback cycles that are positive in sign act to diminish the magnitude of the determinant, thereby increasing the relative effect of the input or press perturbation. Hence, systems that are strongly influenced by positive feedback, such that their determinant or overall feedback is diminished, will have a relatively high sensitivity to press perturbations.

Since the sign of $\det(-\mathbf{A})$ will always be positive in stable systems, the adjoint matrix gives the sign and qualitative conditions for each predicted response. And as we are only concerned with the sign of the input, and not its magnitude, we omit from Eq. A.6 the last term $(\partial(d\mathbf{N}/\mathbf{N}dt)/\partial p_h)dp_h$, but presume, or require, that the input is sufficiently large to cause observable responses. Thus the sign (sgn) or direction of change in equilibrium abundances due to a (sufficiently large) positive input to any variable can be expressed as a matrix

$$\text{sgn } \Delta\mathbf{N}^* = \text{sgn}[\text{adj}(-\mathbf{A})]. \quad (\text{A.7})$$

In interpreting the adjoint matrix, the responses of a system's variables to a change in a parameter are read down the column of the variable that is directly controlled by that parameter. In the simple system described by Eq. 1 and Fig. 3a,

$$\text{sgn } \Delta\mathbf{N}^*_{\text{Fig. 3a}} = \begin{bmatrix} + & + & + \\ - & + & + \\ + & - & + \end{bmatrix}, \quad (\text{A.8})$$

a sustained enhancement of the productivity of the system can, in the growth equation for N_3 (food resources for prawns), be considered as an increase in the parameter β_3 . Here a sustained increase in β_3 constitutes a positive press perturbation to N_3 and, from the third column of the adjoint matrix in Eq. A.8, all variables are predicted to increase.

For a negative press perturbation, the signs of the adjoint matrix elements are simply reversed. For example, an increase in the rate of prawn migration, via an increase in the magnitude of ι_2 , constitutes a negative input to N_2 (the prawn population). The responses for this perturbation are read down the second column of Eq. A.8, but with a change in signs. Thus, the abundance of prawn food N_3 is predicted to increase, whereas prawns and their predators are both predicted to decline in abundance.

Predictions from the adjoint matrix also provide information about the likely correlation of changes among variables. In Eq. A.8, an input to variable N_3 results in a predicted increase in all three variables, thus giving a positive correlation in the direction of change for all variables in the system. An input to N_2 gives a prediction for positive correlation between N_1 and N_2 , whereas N_3 is predicted to be negatively correlated with N_1 and N_2 .

In the expanded fleet-stock model (Fig. 4a)

$$\text{sgn } \Delta \mathbf{N}^*_{\text{Expanded fleet-stock model}} = \begin{matrix} & \begin{matrix} 1 & 2 & 3 & 4 \end{matrix} \\ \begin{matrix} 1 \text{ C} \\ 2 \text{ E} \\ 3 \text{ S} \\ 4 \text{ M} \end{matrix} & \begin{bmatrix} + & ?^a & + & ?^a \\ ?^b & + & ?^b & + \\ ?^{-b} & - & ?^c & - \\ - & ?^{-a} & - & ?^d \end{bmatrix} & \begin{matrix} \mathbf{a} : a_{CE}a_{SS} - a_{CS}a_{SE} \\ \mathbf{b} : a_{EC}a_{MM} - a_{EM}a_{MC} \\ \mathbf{c} : a_{CC}a_{EE}a_{MM} - a_{CE}(\mathbf{b}) \\ \mathbf{d} : a_{CC}a_{EE}a_{MM} - a_{EC}(\mathbf{a}), \end{matrix} \end{matrix} \quad (\text{A.9})$$

half of the qualitative predictions are ambiguous (denoted by '?'s) due to the contribution of both positive and negative effects (note that in Eq. A.9 expression (a) is a factor in expression (d), and expression (b) is a factor in expression (c)). The elements of the adjoint matrix detail both the direct and indirect effects in the system, and their analysis provides insights that can differ from analyses that are limited to only direct effects between a fish stock and a fishery. For instance, only direct or instantaneous effects are typically considered in CPUE-stock relationships (see Table 1). Here, CPUE is depicted as monotonically non-decreasing functions of stock size, and for the first three relationships, a change in CPUE infers either a proportionate or directional change in stock abundance. Such an inference, however, is based only on direct effects, and does not account for indirect effects that can arise between a market, a fishery, and a stock. In the expanded fleet-stock model (Fig. 4a, Eq. A.9), for a positive input to either market price (*i.e.*, through increased consumer demand), or fishing effort (*i.e.*, through an influx of venture capital), the abundance of the stock is predicted to decrease. With either source of input, a predicted decrease in stock abundance will unambiguously match a predicted change in CPUE only when catch decreases and effort increases. For catch to decrease requires expression (a) in Eq. A.9 to be negative, which depends on the indirect effect of effort on catch, via the stock, being greater than its instantaneous or direct effect (*i.e.*, $a_{CS}a_{SE} > a_{CE}a_{SS}$).

Otherwise, the predicted change in CPUE can be either positive or negative, and thus is not a reliable qualitative indicator of stock abundance. Similarly, for a change in the productivity of the stock, the predicted change in the stock will unambiguously match the ratio of the predicted change in catch and effort only when expression (b) in Eq. A.9 is negative, such that the market, through supply and consumer demand, strongly moderates the rate of capital reinvestment into the fishery. This condition partially overlaps with conditions for system stability (*i.e.*, a negative value for Eq. A.3), and will be met when the market regulation feedback in Eq. A.3 is relatively strong and capitalization feedback in the fishing fleet is relatively weak.

b. WEIGHTED PREDICTIONS

In Eq. A.9 there are at most only two or three algebraic terms to consider for any given adjoint matrix prediction, but in larger more complex systems, the arguments can become too large to reasonably interpret. In these instances, we can instead take a probabilistic interpretation of ambiguous predictions. Here, a ratio is taken of the net to the total number of terms, creating a weighted prediction. In general, prediction weights greater than 0.5 (*i.e.*, greater than a 1:2 ratio of the net to total number of adjoint matrix terms) have been shown to have a high degree of sign determinacy in both empirical studies (Dambacher *et al.* 2002) and computer simulations (Dambacher *et al.* 2003b). Hosack *et al.* (2008) developed the means to attribute a probability of sign determinacy to each adjoint matrix prediction, and in this work a probability ≥ 0.85 is used to distinguish high from low sign determinacy.

3. PREDICTIONS FOR WEIPA MODELS

Below are adjoint matrix predictions for all models developed for the Weipa banana prawn fishery and ecosystem. Ambiguous predictions with a relatively high probability of sign determinacy (≥ 0.85) are enclosed in parentheses; “?” denotes those with a low probability. See figures in main text for associated signed digraph models and definition of variable names, specifically, Fig. 5 for full model, Fig. 6 for core and alternative models 1–5, and Fig. 9 for effort allocation model.

$$\text{sgn } \Delta \mathbf{N}_{\text{Model1}}^* = \begin{array}{c} \begin{array}{cccccc} & 1 & 2 & 3 & 4 & 5 & 6 \end{array} \\ \begin{array}{l} 1 \text{ BP} \\ 2 \text{ F} \\ 3 \text{ R} \\ 4 \text{ Co} \\ 5 \text{ P} \\ 6 \text{ Re} \end{array} \end{array} \begin{bmatrix} - & - & - & + & + & - \\ + & + & + & - & - & + \\ + & + & + & - & - & + \\ + & + & + & ? & - & + \\ + & + & + & - & ? & ? \\ + & + & + & - & ? & (+) \end{bmatrix} \quad (\text{A.12})$$

$$\text{sgn } \Delta \mathbf{N}_{\text{Model2}}^* = \begin{array}{c} \begin{array}{cccccc} & 1 & 2 & 3 & 4 & 5 & 6 \end{array} \\ \begin{array}{l} 1 \text{ BP} \\ 2 \text{ F} \\ 3 \text{ R} \\ 4 \text{ Co} \\ 5 \text{ P} \\ 6 \text{ Re} \end{array} \end{array} \begin{bmatrix} + & - & + & - & - & + \\ + & ? & + & - & - & + \\ - & + & ? & ? & + & - \\ - & + & ? & ? & + & - \\ + & ? & + & - & ? & ? \\ + & ? & + & - & ? & ? \end{bmatrix} \quad (\text{A.13})$$

$$\text{sgn } \Delta \mathbf{N}_{\text{Model3}}^* = \begin{array}{c} \begin{array}{cccccc} & 1 & 2 & 3 & 4 & 5 & 6 \end{array} \\ \begin{array}{l} 1 \text{ BP} \\ 2 \text{ F} \\ 3 \text{ R} \\ 4 \text{ Co} \\ 5 \text{ P} \\ 6 \text{ Re} \end{array} \end{array} \begin{bmatrix} + & (-) & (+) & - & ? & ? \\ + & (+) & (+) & - & ? & ? \\ (-) & + & + & (-) & + & - \\ - & (+) & (+) & + & ? & ? \\ ? & + & + & ? & + & - \\ ? & + & + & ? & + & (+) \end{bmatrix} \quad (\text{A.14})$$

$$\text{sgn } \Delta \mathbf{N}_{\text{Model4}}^* = \begin{array}{c} \begin{array}{cccccc} & 1 & 2 & 3 & 4 & 5 & 6 \end{array} \\ \begin{array}{l} 1 \text{ BP} \\ 2 \text{ F} \\ 3 \text{ R} \\ 4 \text{ Co} \\ 5 \text{ P} \\ 6 \text{ Re} \end{array} \end{array} \begin{bmatrix} + & (-) & (+) & - & ? & (+) \\ + & (+) & (+) & - & ? & (+) \\ ? & + & + & (-) & + & ? \\ - & ? & ? & + & (-) & ? \\ ? & + & + & ? & + & (-) \\ ? & + & + & ? & + & (+) \end{bmatrix} \quad (\text{A.15})$$

$$\text{sgn } \Delta \mathbf{N}_{\text{Model5}}^* = \begin{array}{c} \begin{array}{cccccc} & 1 & 2 & 3 & 4 & 5 & 6 \end{array} \\ \begin{array}{l} 1 \text{ BP} \\ 2 \text{ F} \\ 3 \text{ R} \\ 4 \text{ Co} \\ 5 \text{ P} \\ 6 \text{ Re} \end{array} \end{array} \begin{bmatrix} + & ? & + & - & - & + \\ + & + & + & - & - & + \\ - & ? & ? & ? & + & - \\ - & ? & ? & (+) & + & - \\ - & - & - & + & + & - \\ - & - & - & + & + & ? \end{bmatrix} \quad (\text{A.16})$$

