

# Qualitative mathematical models to support ecosystem-based management of Australia's Northern Prawn Fishery

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**Abstract.** A major decline in the catch of the banana prawn [shrimp], *Penaeus (Fenneropenaeus) merguensis*, occurred over a six-year period in the Weipa region of the northeastern Gulf of Carpentaria, Australia. Three main hypotheses have been developed to explain this decline: (1) prawn recruitment collapsed due to overfishing; (2) recruitment collapsed due to a change in the prawn's environment; and (3) adult banana prawns were still present, but fishers could no longer effectively find or catch them. Qualitative mathematical models were used to link population biology, environmental factors, and fishery dynamics to evaluate the alternative hypotheses. This modeling approach provides the means to rapidly integrate knowledge across disciplines and consider alternative hypotheses about how the structure and function of an ecosystem affects its dynamics. Alternative models were constructed to address the different hypotheses and also to encompass a diversity of opinion about the underlying dynamics of the system. Key findings from these analyses are that: instability in the system can arise when discarded fishery bycatch supports relatively high predation pressure; system stability can be enhanced by management of fishing effort or stock catchability; catch per unit effort is not necessarily a reliable indicator of stock abundance; a change in early-season rainfall should affect all stages in the banana prawn's life cycle; and a reduced catch in the Weipa region can create and reinforce a shift in fishing effort away from Weipa. Results from the models informed an approach to test the hypotheses (i.e., an experimental fishing program), and promoted understanding of the system among researchers, management agencies, and industry. The analytical tools developed in this work to address stages of a prawn life cycle and fishery dynamics are generally applicable to any exploited natural resource.

**Key words:** banana prawn; fleet dynamics; Gulf of Carpentaria, Australia; Northern Prawn Fishery; opportunity cost; *Penaeus (Fenneropenaeus) merguensis*; prawn recruitment; press perturbation; stability.

## INTRODUCTION

### *Modeling for ecosystem-based management*

Managing an exploited natural resource requires integration across multiple disciplines to gain an understanding of its dynamics. The integrated management of a fishery requires population dynamics, stock assessment, an understanding of fisher behavior, the effects of fishing on the ecosystem, and the ecosystem's effects on all life cycle stages of the stock. For effective decision making, assessments and advice must focus on the specific problems facing industry and resource managers, and must be delivered to meet the time frames of decision makers. Walters and Holling (1990:2066) maintain that "It is a trivial task to define testable hypotheses, but it is not easy to generate

hypotheses that are relevant to changes in the external context and internal structure of managed ecosystems." Hence, a pressing challenge for modeling that supports ecosystem-based management is to integrate knowledge across multiple disciplines, to quickly incorporate knowledge of ecological and human interactions, and to "screen the credible hypotheses, and identify where to concentrate scarce resources" (Walters and Holling 1990).

Modeling efforts to support ecosystem-based management have typically relied on statistical analyses of key components or factors in the system (e.g., Link et al. 2002, Nicholson and Jennings 2004, Jennings 2005, Toscas et al. 2009, McClanahan et al. 2011), or numerical simulation of its trophodynamics (e.g., Yodzis 1998, Christensen and Walters 2004, Fulton et al. 2011, Plagányi et al. 2014). In contrast to these quantitative approaches, qualitative mathematical models (Levins 1998) are based on a general understanding of the relationships that connect ecosystem variables (Puccia and Levins 1985, Dambacher et al. 2009, Ortiz and Levins 2011, Carey et al. 2013). These models contain only the sign (+, −, 0) of species interactions,

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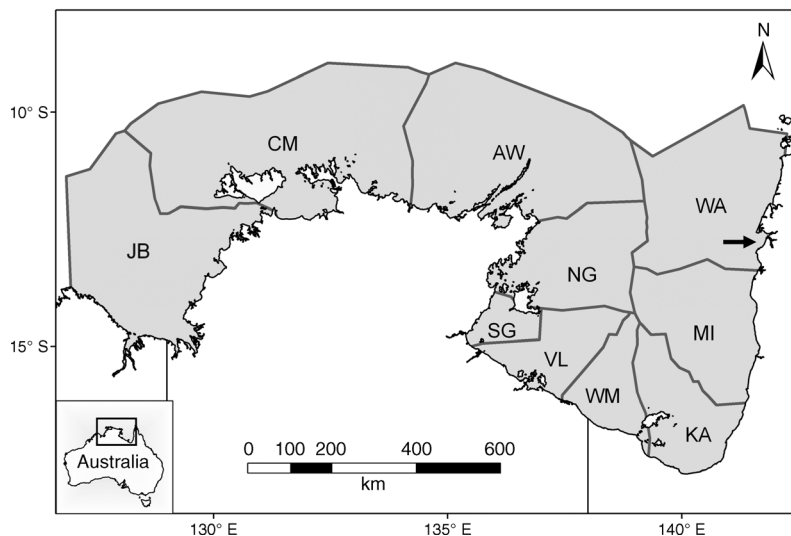


FIG. 1. Stock regions of Australia's Northern Prawn Fishery: AW, Arnhem-Wessels; CM, Coburg-Melville; JB, Joseph Bonaparte Gulf; KA, Karumba; MI, Mitchell; NG, North Groote; SG, South Groote; VL, Vanderlins; WA, Weipa; WM, West Mornington. The arrow in the Weipa region indicates the location of Albatross Bay.

and not their precise magnitude or strength. In this approach, one sacrifices precision in a model for generality and realism (Levins 1966). Qualitative mathematical models can incorporate components and processes of an ecosystem that are important yet difficult to measure, and can be constructed and analyzed relatively rapidly, thus allowing for comparison of alternative models based on different understandings or beliefs about how the system works. The principal goal of this approach is to understand how the structure of a system (i.e., the variables and the signs of their connecting links) affects its dynamics. This is achieved through analysis of a system's feedback properties in predicting how it will respond to a perturbation.

This study applied qualitative mathematical modeling as a means to better understand and predict ecosystem and fishing-fleet dynamics associated with the Weipa region of Australia's Northern Prawn Fishery (NPF). It was part of a larger research project that included stock assessment modeling, statistical modeling of environmental correlates, and trophodynamic ecosystem models (Rothlisberg and Okey 2006).

#### Study area and problem

The NPF in tropical northern Australia (Fig. 1) is one of Australia's most valuable commercial fisheries (Dichmont et al. 2007). The fishery targets two main species-groups of prawns [shrimp], banana prawns (*Penaeus (Fenneropenaeus) merguensis*) and tiger prawns (*P. esculentus* and *P. semisulcatus*). [Note: The subgenera of *Penaeus* were elevated to genus status by Pérez-Farfante and Kensley (1997), although there has been considerable controversy over the revised nomenclature. Recently, Ma et al. (2011), using mitochondrial and nuclear genes, found no correspondence with the

morphological characters used by Pérez-Farfante and Kensley (1997) and recommended the restoration of the old *Penaeus* genus. Therefore, in this work we have used the penaeid binomials according to Holthuis (1980), as suggested by Flegel (2007).] Banana prawn catches can vary greatly between years, although catch levels have generally fluctuated within bounds since the 1980s (Fig. 2). In some areas of the Gulf of Carpentaria, banana prawns form large, free-swimming aggregations (boils) that commercial fishermen target with trawl nets (Die and Ellis 1999; see Plate 1). In some regions of the NPF (e.g., the Karumba region), these aggregations are found by using echo-sounders detecting acoustic marks, and also from light aircraft, because the boils are associated with visibly discolored water. In the Weipa region, the water is more turbid and therefore aerial surveillance is ineffective, so the fishers are restricted to searching only with echo-sounders. In these circumstances, fishers also rely heavily on communications with each other: a collective searching by the fleet (see Plate 1).

Until the late 1990s, the Weipa and Karumba regions were the most important areas for banana prawn fishing in the NPF; the long-term average (i.e., mean) annual catch for Weipa has been 640 metric tons (=Mg) and for Karumba 930 metric tons, with a combined value of over AUD\$12 million (Australian dollars). Catches of banana prawns and fishing effort in the Weipa region of the northeastern Gulf of Carpentaria declined markedly in a six-year period beginning in 2000 (Fig. 2); catches dropped from a pre-2000 average of 643 to 2.8 metric tons in 2003, and effort dropped from a pre-2000 average of 728 boat days to 33 boat days in 2003. In this six-year period (i.e., 2000–2005), catch and effort were well below any previously recorded minimum (Fig. 2). Both catch and effort in the Weipa region remained low

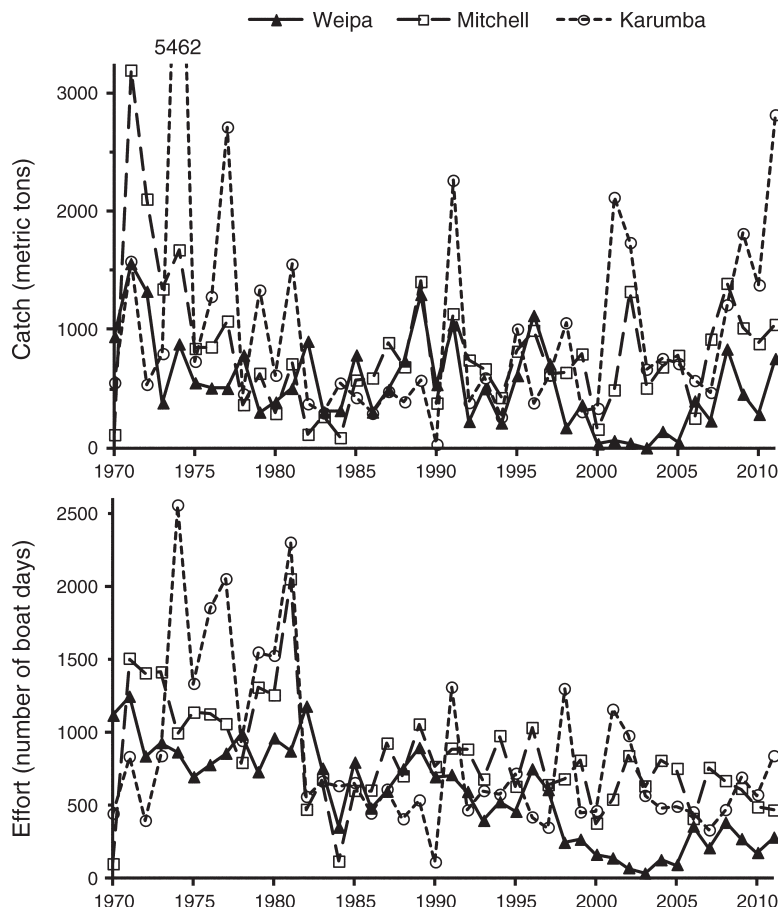


FIG. 2. Annual levels of catch and trawling effort for banana prawns (*Penaeus (Fenneropenaeus) merguensis*) in the Weipa, Mitchell, and Karumba regions of Australia's Northern Prawn Fishery, 1970–2011; see Fig. 1 for region boundaries. Catch is in metric tons (1 metric ton = 1 Mg).

until 2006, when they increased to 399 metric tons and 355 boat days, respectively. In contrast to the Weipa region, catches in other regions of the NPF did not decline. Prince et al. (2008) examined the spatial patterns in the commercial fisheries data for Weipa and other regions and concluded that the Weipa stock had contracted and declined in abundance. They could not dismiss, however, an alternative hypothesis that the low catches were due to low fishing effort.

Collectively, managers, fishers, and scientists considered various possible explanations for the decline in banana prawn catch in the Weipa region in relation to three broad categories of factors: fishing, environment, and biology, which can be described by three main hypotheses:

- 1) Prawn recruitment collapsed due to overfishing ( $H_1$ ).
- 2) Recruitment collapsed due to a change in the prawn's environment ( $H_2$ ).
- 3) Adult banana prawns were still present, but fishers could not find or catch them ( $H_3$ ) because:
  - (a) the searching power of the fishing fleet had declined;

- (b) adult banana prawns were staying inshore away from fishing grounds; or
- (c) adult banana prawns stopped forming dense aggregations that allowed them to be targeted by the trawl fishery.

The plausibility of each hypothesis was explored through multidisciplinary workshops and working groups tasked with stock assessment, statistical modeling, numerical simulation modeling, and qualitative mathematical modeling. The goal of this latter working group was to provide a conceptual framework that integrated the knowledge of the various disciplines. Here, qualitative mathematical modeling was used to investigate various impacts, and their interactions, on the banana prawn population and to provide insights into the interactions and dynamics of the banana prawn fishery and ecosystem. To do this, a number of analytical frameworks were developed that pertain to model construction and resolution. In this work we present these frameworks as a general approach to any exploited ecosystem, and then apply them to the Weipa banana prawn fishery and ecosystem.

METHODS

Hypotheses  $H_1$ – $H_3$  were critically examined during three workshops (2004 to 2005) with participation of biologists, members and managers of the fishing industry, statisticians, and stock assessment and ecosystem modelers (Rothlisberg and Okey 2006). Workshop participants were interviewed to describe the different facets of the banana prawn fishery, ecosystem, and management measures in the Weipa region. Where possible, these descriptions were validated and augmented by published literature; from this information, multiple models were developed.

In the presentation of these models, we first demonstrate the equivalency of a system of differential equations, a matrix of interactions, and their graphical representation, all of which can be used to describe the structure of an ecosystem based on the sign of the interactions between its populations. Next we establish the means to distinguish, as separate variables, the life cycle stages of a population within specific habitats, and examine how the behavior of both the stock and the fishing fleet can affect the structure and feedback properties of the system. We then expand the fishing-fleet variable into a subsystem that includes catch, effort, and market price, and show how these variables interact with the stock under different economic contexts and spatial scales. Finally, having introduced the basic components required to represent the banana prawn fishery and ecosystem, we provide a brief introduction to the qualitative analysis of system stability and predictions of perturbation response, which is further augmented by the Appendix.

*Model construction and structure*

*From growth equations to community matrices and signed digraphs.*—Relationships between variables can be represented by equations, matrices, or graphs. The simplest model of the Weipa banana prawn ecosystem could be portrayed by three population variables in a system of generalized Lotka–Volterra growth equations

$$\begin{aligned}
 \text{Predators} \quad & \frac{dN_1}{dt} = N_1(\alpha_{1,2}N_2 - \delta_1) + R \\
 \text{Prawns} \quad & \frac{dN_2}{dt} = N_2(-\alpha_{2,1}N_1 + \alpha_{2,3}N_3 - \delta_2 - \iota_2) \\
 \text{Prawn food} \quad & \frac{dN_3}{dt} = N_3(-\alpha_{3,3}N_3 - \alpha_{3,2}N_2 + \beta_3)
 \end{aligned} \tag{1}$$

where variable  $N_1$  is a guild of predators,  $N_2$  is the banana prawn population, and  $N_3$  represents food resources of prawns. The  $\alpha_{ij}$  parameters are interaction coefficients that describe the direct effect of species  $j$  on species  $i$  (interspecific effects such as predation, competition, mutualism), or the effect of a species on itself (intraspecific or self-effects such as competition for a

resource or critical habitat, cannibalism, and so forth). The parameters  $\beta$ ,  $\delta$ , and  $\iota$  denote rates of birth, death, and migration, respectively, and  $R$  is a birth rate of the top predator supported by consumption of a food resource external to the model system, such that it is supplied at a rate that is constant and independent of any model variable.

Direct effects between species can be formally defined by the first partials of the per capita form of the growth equations (i.e.,  $dN/Ndt$ ):

$$a_{ij} = \frac{\partial \left( \frac{dN_i}{N_i dt} \right)}{\partial N_j} \tag{2}$$

These effects are organized in the community matrix  $\mathbf{A}$ , which for the system described by Eq. 1 is:

$$\mathbf{A} = \begin{bmatrix} -R/N_1^2 & \alpha_{1,2} & 0 \\ -\alpha_{2,1} & 0 & \alpha_{2,3} \\ 0 & -\alpha_{3,2} & -\alpha_{3,3} \end{bmatrix} \tag{3}$$

The sign structure of this matrix corresponds to a sign-directed graph, or signed digraph (Fig. 3a), where the  $i$ th and  $j$ th entries of  $\mathbf{A}$  (denoted as  $a_{ij}$ ) are represented as links between variables, and the sign of an interaction term corresponds to the sign value of its graph link. For instance, a predator imparts a rate of death to its prey, which corresponds to a negative link, ending in a circle (—○) that leads from the predator to its prey. The nutritional benefit of prey consumption contributes a positive effect to the predator’s rate of birth, and is depicted as a link ending in an arrow (←) that leads back to the predator. Links originating and ending in the same variable portrays self-effects. For example, density-dependent growth in a population is represented as a negative self-effect (⦿), and self-enhancing growth by a positive self-effect (⊕).

Often the elements of the community matrix are derived simply from the system’s  $\alpha_{ij}$  interaction coefficients, but they can also include terms that are less obvious. For instance, the reproductive capacity  $R$  that the top predator derives from consumption of a food resource that is not a variable, but is instead from outside the modeled system, imparts a negative self-effect to the predator in the form of  $-R/N_1^2$  (i.e., here the food resource can represent a wide range of unspecified benthic species consumed by the top predator). Within the context of the model then, a resource that is not explicitly included as a variable will be represented as though it is intrinsic to, and regulating, the variable through which it enters the system.

*Life stage model.*—Because banana prawns live in different habitats at different stages in their life cycle (i.e., estuary, inshore, and offshore), where they are subjected to different environmental factors and sources of food and mortality, the prawn’s single population variable  $N_2$  (Fig. 3a) can be divided into multiple life

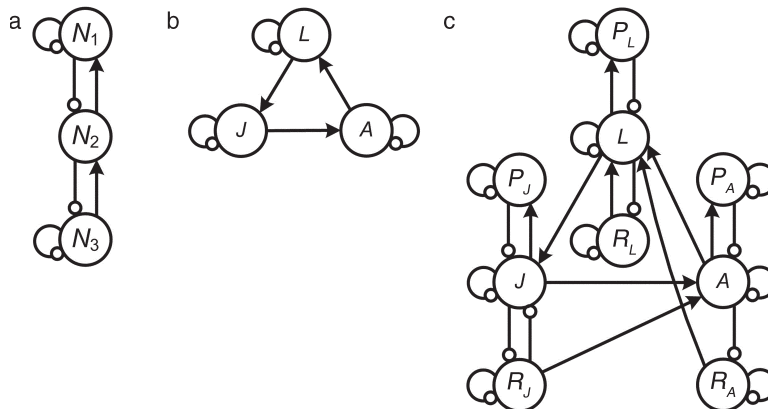


FIG. 3. Signed digraph models. (a) Minimum complexity for the Weipa banana prawn ecosystem corresponding to Eq. 1, where banana prawns ( $N_2$ ) are sustained by a food resource ( $N_3$ ) and are consumed by a guild of generalist predators ( $N_1$ ). (b) Here, the banana prawn variable is split into larval ( $L$ ), juvenile ( $J$ ), and adult ( $A$ ) life stages with links corresponding to matrix  $\mathbf{A}$  of Eq. 5. (c) Links to and from predators ( $P$ ), and alternative ways to apportion benefits of food resources ( $R$ ) to each life stage variable. Links between variables denote direct effects as described by the matrix  $\mathbf{A}$  in Eq. 3; links ending in an arrow denote a positive direct effect, those ending in a circle denote a negative direct effect, and links connecting a variable to itself denote self-effects (see text following Eq. 3 for further explanation).

stages (Fig. 3b). Corresponding growth equations can take the following form:

$$\begin{aligned} \text{Larvae} \quad & \frac{dL}{dt} = f_A \frac{A}{L} - f_L - \delta_L \\ \text{Juvenile} \quad & \frac{dJ}{dt} = f_L \frac{L}{J} - f_J - \delta_J \\ \text{Adult} \quad & \frac{dA}{dt} = f_J \frac{J}{A} - \delta_A. \end{aligned} \quad (4)$$

Here, larval prawns ( $L$ ) develop in offshore waters and settle in the estuary as juveniles ( $J$ ); adults ( $A$ ) then emigrate through the inshore and farther offshore to reproduce. The term  $f_A$  is the rate of reproduction,  $f_L$  is the rate of larval development and transport into the estuary,  $f_J$  is the rate of development and migration of juveniles from the estuary, and  $\delta$  represents rates of mortality. Although there are no interaction coefficients that specifically represent self-effects in these equations, negative self-effects do emerge for each life stage in the system's community matrix

$$\mathbf{A} = \begin{bmatrix} -f_A \frac{A}{L^2} & 0 & \frac{f_A}{L} \\ \frac{f_L}{J} & -f_L \frac{L}{J^2} & 0 \\ 0 & \frac{f_J}{A} & -f_J \frac{J}{A^2} \end{bmatrix}. \quad (5)$$

For instance, the self-effect for larvae  $a_{1,1} = -f_A(A/L^2)$ .

As a rule, a single variable can be divided into any number of life stage variables, as long as the overall feedback, or matrix determinant, of the expanded subsystem equals the single variable's self-effect. In Eq. 3, the single variable for prawns is not self-regulated

(i.e.,  $a_{2,2} = 0$ ), and the overall feedback of the life stage subsystem in Fig. 3b is also zero, as calculated by the determinant ( $\det$ ) of  $\mathbf{A}$  in Eq. 5, the terms of which cancel:

$$\begin{aligned} \det \mathbf{A} &= (f_A/L)(f_L/J)(f_J/A) - (f_A A/L^2)(f_L L/J^2)(f_J J/A^2) \\ &= 0. \end{aligned} \quad (6)$$

Additional, or fewer, life cycle stages can be incorporated within this formulation and the rule for equivalent overall feedback will always be met.

The model can also include variables representing predators and food resources of the individual life stages (Fig. 3c). The links associated with the predator variables are straightforward, as each predator receives the benefit of consumption while inflicting a rate of mortality on a specific life stage. Negative links leading from a life stage to a food resource are also uncomplicated. However, it is incorrect to attribute a birth rate directly back to the prawn life stage that is consuming the resource, because individually each life stage is not self-reproducing (i.e., the benefit of food resources to juveniles cannot directly result in more juveniles via juveniles, but can do so indirectly via the juvenile–adult–larvae–juvenile life stage cycle). Here we need to consider how the benefits of consumption variously affect rates of development, fecundity, and survival throughout the entire life cycle. The nature of the benefit of resources consumed by larvae, juveniles, and adults differs by each life stage (Fig. 3c). The benefit of adult food resources is ascribed to increased growth leading to increased fecundity (Dall et al. 1990), which creates a positive link leading from the adult food resource to prawn larvae. Larval food resources can act to increase larval survival (D'Souza and Loneragan 1999; T. van der Velde, CSIRO Marine and Atmospheric Research, unpublished data), which creates a positive link to larvae.



Finally, juvenile food resources regulate the rate at which juvenile prawns grow and mature (Dall et al. 1990); an increase in resources acts to more quickly remove individuals from the juvenile stage and transfer them to the adult stage. This increased rate of development creates a negative link leading from the food resource to juvenile prawns, and a positive link leading to adults.

*Fish stock and fishery interactions.*—To understand the qualitative dynamics of a fishery, we examine the possible ways in which the stock and fishing fleet interact. Starting with the simple case of a linear relationship between stock abundance and catch, we consider the harvest of a stock that follows logistic growth:

$$\frac{dS}{dt} = rS \left( 1 - \frac{S}{K} \right) - qES \tag{7}$$

where  $r$  is the stock’s intrinsic growth rate and  $K$  its carrying capacity or unfished biomass. Here fishing mortality, or catch, is simply the product of catchability  $q$ , fishing effort  $E$ , and stock abundance  $S$  (i.e., catch =  $qES$ ). In constructing a signed digraph of these relationships, the fishing fleet has a negative self-effect from economic processes that regulate levels of revenue, costs, and profits, and management processes that limit the fishing effort of the fleet. These processes could be said to characterize modern, or industrialized, fisheries, but where these processes are absent, as in some artisanal fisheries, the size of the fishery is determined exclusively by levels of catch, and the fishing-fleet variable would not be self-regulated. Either type of fishery (i.e., industrial or artisanal) will have a negative effect on the stock through catchability (i.e.,  $a_{SF} = -q$ ). A positive effect to the fishing fleet from stock represents catch revenues that support the maintenance and growth of the fishing fleet. Finally, from Eq. 7, logistic growth confers a negative self-effect to the stock (i.e.,  $a_{SS} = -r/K$ ). These interactions essentially define a predator–prey type relationship between the fish stock ( $S$ ) and fishing-fleet ( $F$ ) variables (as in model A of Fig. 4).

The basic form of Eq. 7 has a proportional relationship between catch per unit effort (CPUE) and stock abundance, which implies that the fish stock and the fisher encounter each other randomly in space (Fig. 4a). But it is often the case that such encounters are not distributed randomly, and depending on the behavior of the fish stock or the fisher, it is possible for a stock’s catchability to either increase or decrease as its abundance is reduced by fishing. For instance, a population that consistently forms aggregations that can be located is easily targeted by a fishing fleet. Fishers that encounter and focus their effort on aggregations can maintain relatively high levels of catch even as total stock abundance declines, leading to what Hilborn and Walters (1992) term hyper-

stability (Fig. 4b) in the relationship between CPUE and stock abundance. Conversely, hyperdepletion (Fig. 4c) can occur when vulnerability to a given fishing method or gear varies across a population (Hilborn and Walters [1992]; e.g., exposed vs. cryptic fraction of invertebrate population; phenotypic-based gear avoidance by fish). Removal of the most susceptible members of a population leaves a surviving fraction that is more difficult to catch. Either situation represents a modification of catchability by stock abundance that can be generally described by the nonlinear function

$$q = q' \left[ \frac{S}{K} \right]^\theta \tag{8}$$

where  $q'$  is an intrinsic catch rate and the parameter  $\theta$  determines the form of the CPUE–stock and catchability–stock relationships (Fig. 4). Values of  $\theta$  between  $-1$  and  $0$  describe hyperstability (Fig. 4b), whereas those greater than zero describe hyperdepletion (Fig. 4c).

In substituting Eq. 8 into 7

$$a_{SS} = -\frac{r}{K} - \frac{\theta q'E}{S} \left( \frac{S}{K} \right)^\theta \tag{9}$$

the self-effect of the stock  $a_{SS}$  gains a second term that can be either positive or negative depending on the value of  $\theta$ . The sign of this additional term conforms to the sign of the slope for the catchability–stock relationship (Fig. 4). When this term is negative and fishing pressure ( $q'E$ ) is sufficiently high, such that the second term is greater than the first, then the stock’s self-effect will be positive, as in signed digraph models B and D (Fig. 4b, d).

The sign of the link from  $S$  to  $F$  is determined by the slope of the CPUE–stock relationship and is generally positive, except for models C and D, where the slope is 0 (Fig. 4d). See Dambacher and Ramos-Jiliberto (2007: Fig. 6b) for a general treatment of other possible model structures. This zero slope is caused by a value of  $\theta$  equal to  $-1$  in Eq. 8, which essentially describes the imposition of a fixed or constant rate of harvest. Here the level of catch is independent of stock abundance and is equal to  $q'EK$ , which effectively severs the link from stock abundance to the fishing-fleet variable. In practice,  $q'$  and  $E$  are adjusted, or regulated, to produce a targeted level of catch, or to fall within a given catch limit, as in a fixed-quota or input-control fishery.

*Fishery subsystem.*—To include the effects of a fishery in an ecosystem model, one could merely represent the fishing fleet as a predator of the stock, as in variable  $N_1$  of Fig. 3a. And whereas this might be sufficient for many purposes, this single-variable depiction can mask important dynamics concerning the interaction of catch, effort, and market price. In considering these economic components of a fishery, the fishing-fleet

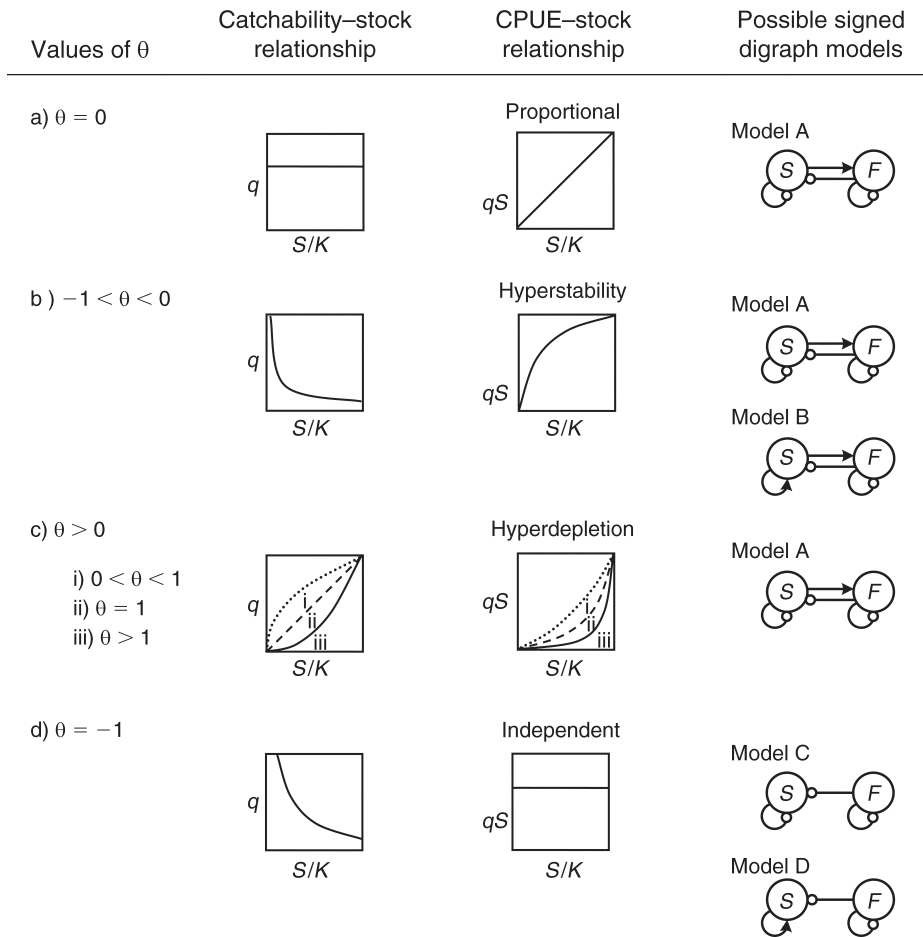


FIG. 4. General relationship of catchability  $q$  and catch per unit effort (CPUE)  $qS$  with a stock's abundance  $S$ , as a proportion of its carrying capacity or unfished biomass  $K$ , for different values of  $\theta$ , where  $q = q'(S/K)^\theta$ , and  $q'$  is an intrinsic catch rate (see explanations of Eqs. 8 and 9);  $x$ -axes are scaled from 0 to 1;  $y$ -axes are scaled to show relative differences. Different values of  $\theta$  lead to (a) proportional, (b) hyperstability, (c) hyperdepletion, or (d) independent CPUE–stock relationship. In (c), curves i–iii describe the relative distribution of vulnerability to capture in a stock's pre-harvested or unfished population, where in (i), individuals that are the least vulnerable, or most difficult, to capture represent a relatively small fraction of the population, whereas in (iii) they represent a majority. Signed digraphs models A–D depict possible interactions between a fish stock and fishing fleet  $F$  for each relationship.

variable can be expanded into a fishery subsystem (Fig. 5) that includes catch ( $C$ ), fishing effort ( $E$ ), and market price ( $M$ ), as distinct model variables (Dambacher et al. 2009). In the expanded fleet–stock model (Fig. 5a), catch levels are determined by both fishing effort and stock abundance, and catch suppresses market price via a supply–demand relationship. The influence of economic forces other than the supply of catch, say through consumer demand or competition with aquaculture production, imparts self-damping to the market price variable. Fishing effort is regulated by the amount of revenue flowing from the processing and sale of the catch, the magnitude of which is controlled by the market through price. This control of revenue flow by the market constitutes a modified interaction (Dambacher and Ramos-Jiliberto 2007), which influences the magnitude of the catch-to-effort link (depict-

ed as a dashed-line link in Fig. 5b), thus creating a positive direct effect leading from the market to effort in the expanded fleet–stock model (Fig. 5a).

In a global market, the price paid for prawns is insensitive to regional levels of catch; thus the link from catch to market price is severed (Fig. 5c). Where the local allocation of effort within a region is determined by levels of local catch (Fig. 5d), the positive link from catch to effort is not based on economic returns, but rather on fisher behavior, and is controlled by the degree of attraction, or avoidance, of fishers to a location based on previous experience or reported levels of catch. Where this behavior is strong, there will be a positive feedback between catch and effort that can dominate local fleet dynamics; an equivalent two-variable system (Fig. 5e) would have a positive self-effect on the local fishing-fleet variable.

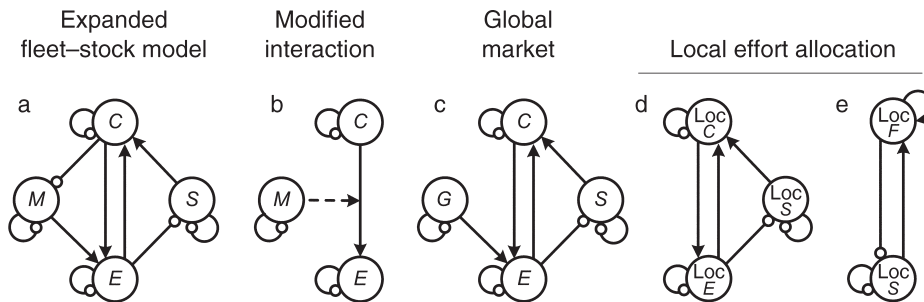


FIG. 5. Signed digraph model of (a) stock ( $S$ ), and a commercial fishing fleet depicted as an expanded subsystem including catch ( $C$ ), effort ( $E$ ), and market price ( $M$ ), which is equivalent to the two-variable model A (Fig. 4). Market price is regulated by a supply–demand relationship with catch, and controls the level of catch-derived revenue supporting effort. Such control constitutes a modified interaction (Dambacher and Ramos-Jiliberto 2007), shown in (b) as a dashed-line link. This modified interaction creates a direct effect in the signed digraph in (a) that leads from the market to fishing effort, the sign and direction of which is determined by multiplying the sign of the dashed-line link with sign of the link leading from catch to effort. Because both are positive, the direct effect of the market on effort is also positive. In (c), market price is determined by a global market ( $G$ ) whose demand is insensitive to regional supply of catch. In (d), the allocation of local effort ( $Loc E$ ) is driven not by economic returns, but by reported or previously experienced levels of local catch ( $Loc C$ ). Where the positive feedback between local catch and effort is strong, then there can be a net positive feedback in the catch–effort subsystem. Thus, when collapsed to a two-variable system (e), the local fishing fleet ( $Loc F$ ) variable will have a positive self-effect.

*Stability and press perturbation analysis*

The question of stability arises from a concern about whether or not a model is a feasible representation of a real system. Here it is asked if the model possesses the twin virtues of persisting despite a perturbation, and whether it can exhibit familiar dynamics. Perturbations can be considered in two general forms, a pulse or a press perturbation (Bender et al. 1984). Assessments of system stability pertain to a system’s response to a pulse perturbation, which is an instantaneous increase or decrease in the level of one or more variables. In stable systems, variables have the ability to return to a former equilibrium, but if the system is unstable then the variables will not return to their former levels. Alternatively, a press perturbation involves an input to the system via a sustained change in a parameter, which causes a permanent shift to a new equilibrium. Here we provide only a general overview of stability and press perturbation analyses; a more detailed treatment is provided in the Appendix.

Assessment of model stability is based on the analysis of a system’s feedback cycles, both in terms of the balance of positive and negative cycles, and the balance of short vs. long feedback cycles (Puccia and Levins 1985, Dambacher et al. 2003b). Here we must introduce the notion of levels of feedback, with the link-length of cycles defining  $n$  levels of feedback. The lowest level of feedback has cycles of length one, which are simply the variable’s self-effects. Feedback at level two can involve the product of pairwise interactions, such as predator–prey, mutualism, and competition. The highest level of feedback has cycles with  $n$  number of links, and is defined by the system’s overall feedback. Negative feedback acts to dampen the effects of a perturbation, whereas positive feedback acts to amplify them; accordingly, the first criterion for stability, criterion

(i), is that the system is not dominated by positive feedback. A second criterion for stability, criterion (ii), is that a system is not dominated by higher-level feedback, or cycles with long path lengths. A system dominated by feedback cycles with long path lengths tends to respond to a pulse perturbation by overcorrecting, which leads to sustained oscillations with constant or increasing amplitude.

Predictions for change in equilibria resulting from a press perturbation require an analysis of all of the direct and indirect effects, or pathways, leading from the input variable to the response variable. Generally, where all such pathways are of the same sign, then one can unambiguously predict the sign of a variable’s response (i.e., +, increase; –, decrease; or where there are no pathways, 0, no change). But where there are both positive and negative effects, then the response prediction is qualitatively ambiguous. Resolution of this ambiguity can be conditioned on knowledge of the relative strength of key interactions, or by considering the relative balance of positive vs. negative effects in a response.

Through this latter approach, one can assign a probability for sign determinacy to a prediction based on the results of numerical simulations (Dambacher et al. 2003a, Hosack et al. 2008). For example, a response variable receiving three positive effects and one negative effect will have a probability of a positive response >90%. In this work we distinguish response predictions with a relatively high or low probability of sign determinacy based on a cutoff of  $\geq 85\%$ . Similarly, a relative potential for stability can be assigned to a model based on a weighting of the positive and negative feedbacks, or terms, used to assess stability criterion (i) and (ii) (Dambacher et al. 2003b); see the Appendix for further detail.



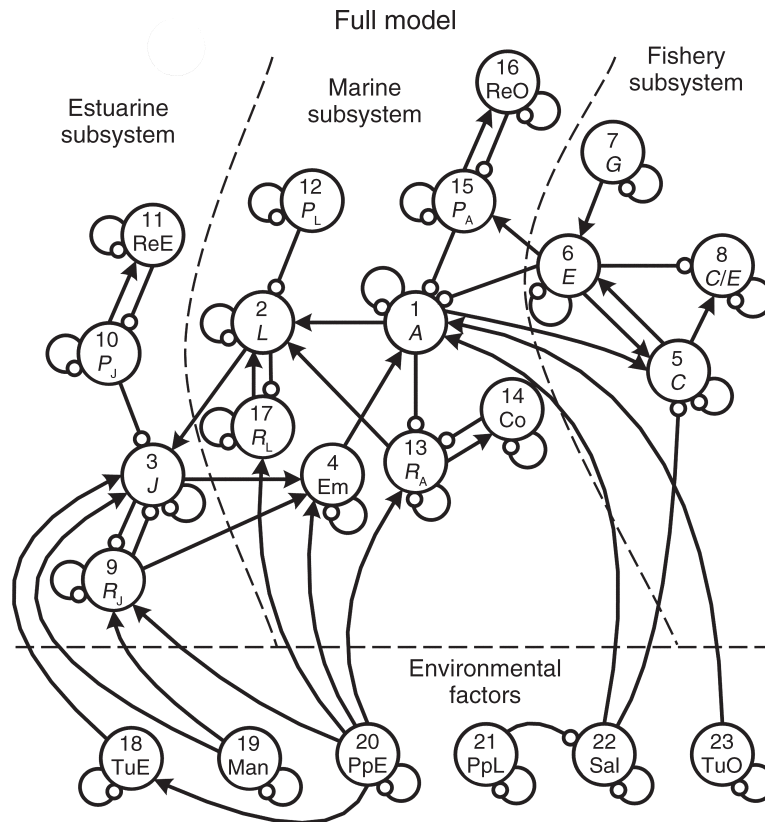


FIG. 6. Full signed digraph model of Weipa banana prawn fishery and ecosystem. Numbers 1–17 represent biological and fishery variables, and numbers 18–23 are environmental factors: 1, adult prawns ( $A$ ); 2, larval prawns ( $L$ ); 3, juvenile prawns ( $J$ ); 4, emigrant prawns ( $Em$ ); 5, catch ( $C$ ); 6, fishing effort ( $E$ ); 7, global market price ( $G$ ); 8, catch per unit effort ( $C/E$ ); 9, juvenile prawn food resource ( $R_J$ ); 10, estuarine predators of juvenile prawns ( $P_J$ ); 11, recreational estuarine fishing ( $ReE$ ); 12, marine predators of larval prawns ( $P_L$ ); 13, adult prawn food resource ( $R_A$ ); 14, competitors for food resources ( $Co$ ); 15, marine predators of adult prawns ( $P_A$ ); 16, recreational ocean fishing ( $ReO$ ); 17, larval prawn food resource ( $R_L$ ); 18, estuarine turbidity ( $TuE$ ); 19, mangrove habitat ( $Man$ ); 20, early wet-season or summer rainfall ( $PpE$ ); 21, late wet-season or autumn rainfall ( $PpL$ ); 22, nearshore salinity ( $Sal$ ); and 23, ocean turbidity ( $TuO$ ).

## RESULTS

### *Weipa banana prawn fishery and ecosystem*

Having developed the theoretical tools to describe various components of the Weipa banana prawn fishery and ecosystem, we next assemble a relatively detailed signed digraph model (i.e., full model) to incorporate and synthesize the diverse perspectives, knowledge, and understanding of workshop participants. From this detailed model we develop a core model of reduced complexity, but with equivalent dynamics, to assess system stability and more easily consider alternative hypotheses regarding system structure.

*Construction of full model.*—The full model depicts banana prawns with four life cycle stages (Fig. 6), and conforms to Dall et al.'s (1990) classification of a Type II prawn life cycle: spawning takes place, and larvae are found, in offshore waters, post-larvae immigrate and settle in mangrove-lined estuaries, and juveniles are euryhaline and can tolerate low salinities (down to 5‰) in the upper reaches of the estuary (Vance et al. 1990, 1998). Near the end of their juvenile stage, banana

prawns emigrate to coastal demersal habitats, and as adults move to deeper offshore areas. The emigration of juveniles is influenced by prawn size, but can be triggered, or accelerated, by rainfall through its associated effects on river flow and salinity, i.e., low salinity stimulates the emigration of smaller prawns (Staples and Vance 1986, Vance et al. 1998, Loneragan and Bunn 1999). Late wet-season (January to April) rains can reduce inshore salinities, causing adult prawns to move offshore where they become available to the prawn fishery (Vance et al. 2003).

The full model includes specific food resources and predators for individual life cycle stages, and recreational fisheries for banana prawn predators in both the estuary and marine subsystems (Fig. 6). Similar to Fig. 3c, the benefits of food resources for adults contribute to fecundity, for juveniles they result in accelerated development, and for larvae they result in increased survival. Because banana prawns constitute a relatively minor portion of the ecosystem's biomass and an equally minor portion of the total annual food resource

TABLE 1. Sign of direct effects between environmental factors and biological variables in qualitative mathematical model of Weipa banana prawn fishery and ecosystem (Fig. 6).

Direct effect			Mechanism
Sign	To	From	
0	15	1	Prawn life cycle stages (1, adults; 2, larvae; 3, juveniles) are minor component in the diet of their predators; positive effect to predators (10, 12, 15) is negligible and thus omitted.†
0	12	2	
0	10	3	
+	15	6	Shark (15) consumption of discards increases local predation pressure on banana prawns (6 is fishing effort).‡
+	3	18	
+	9	19	Mangroves (19) trap and retain nutrients that enrich juveniles' food supply (9).#
+	3	19	
+	2	20	Early wet-season rainfall (20) increases larval food supply in marine waters (2).§
+	4	20	
+	9	20	Early wet-season rainfall (20) increases juvenile emigration (4) from estuary.§, ¶
+	13	20	
+	18	20	Early wet-season rainfall (20) increases juvenile food supply (9).§
+	13	20	
+	18	20	Early wet-season rainfall (20) increases adult food supply (13).§
+	18	20	
−	22	21	Late wet-season rainfall (21) decreases nearshore salinity (22).§
−	5	22	
+	1	22	Decreased nearshore salinity (22) increases movement of prawns to fishing grounds, increasing prawn catchability and catch (5), and hence mortality of adults (1).§
+	1	23	
+	1	23	Turbidity (23) suppresses predation of adults in marine waters (1).§, ¶

Notes: Numbers correspond to variables defined in Fig. 6. Early wet season is August to November, and late wet season is January to April.

† Salini et al. (1990).

‡ Hill and Wassenberg (1990), Hill (1992, 2000).

§ Vance et al. (2003).

¶ Dall et al. (1990).

# Manson et al. (2005).

of their predators (Salini et al. 1990), changes in their abundance are assumed to have a negligible effect on the consumption rate of their predators. The model therefore omits a positive link between stages in the banana prawn life cycle and their predator variables (Fig. 6, Table 1). Other prawn species (e.g., tiger prawns, *P. semisulcatus*, *P. esculentus*, and Endeavour prawns, *Metapenaeus* spp.) are included as potential competitors for food resources.

Market price in the NPF is set at a global scale and is not sensitive to regional levels of catch. Thus the full model incorporates the expanded depiction of the fleet with a global market (i.e., *G* in Fig. 5c), with the added effect from fishing effort (*E*) of discarded bycatch increasing local predation pressure on adult prawns (*P<sub>A</sub>*), primarily through attraction of sharks, but also other predators (Hill and Wassenberg 1990, Hill 1992, 2000); catch per unit effort *C/E* is included as a response variable.

Variables 18–23 represent environmental factors that can directly affect the growth rate of specific variables or act to modify (i.e., enhance or suppress) the intensity of interactions between other variables (Fig. 6, Table1). Links that are a result of modified interactions (Dambacher and Ramos-Jiliberto 2007) include suppression of predation by turbidity ( $a_{3,18}$ ,  $a_{1,23}$ ) or prey refugia ( $a_{3,19}$ ), and increase vulnerability to fishing; e.g., decreasing salinity in the nearshore leading to increased prawn movement to the fishing grounds ( $a_{5,22}$ ,  $a_{1,22}$ ). The environmental factors do not receive feedback from any of the biological or fishery variables, and their inclusion in the full model allows consideration of how they interact with each other and affect the whole

system. For example, early wet-season (August to November) rainfall (PpE) directly affects emigrating prawns (Em), and the food resources of all banana prawn life stages ( $R_L$ ,  $R_J$ ,  $R_A$ ), but also indirectly suppresses predation of juveniles through estuarine turbidity (TuE).

*Stability properties of full model and derivation of core model.*—Because the environmental factors in the full model (i.e., factors 18–23; Fig. 6) do not receive feedback from the rest of the system, they do not contribute to, or affect, its inherent stability. Omitting these six environmental factors from the full model leaves a reduced model with 17 interacting variables. The stability of this 17-variable system depends, in part, on non-positive overall feedback for the expanded life stage and fishery subsystems. The overall feedback of the prawn subsystem is zero, based on the equality established in Eq. 6. Negative overall feedback is presumed for the fishery subsystem based on the condition, or assumption, that the fishery is not overcapitalized, such that  $a_{EC}a_{CE} < a_{CC}a_{EE}$  (see text associated with Eq. A.3 in the Appendix for additional discussion). Although we can analyze the stability of the 17-variable system, we can more easily consider an equivalent model of reduced dimension by decomposing it into independent subsystems, as we did for models C and D (Fig. 4d). Because we have chosen to omit the positive link to predators from larval and juvenile prawns, there is no feedback between them, and we can assess the stability of the subsystems associated with these predators independently (see Appendix for further discussion). Marine predators of larvae (variable 12) can thus be treated as a separate subsystem, as can estuarine

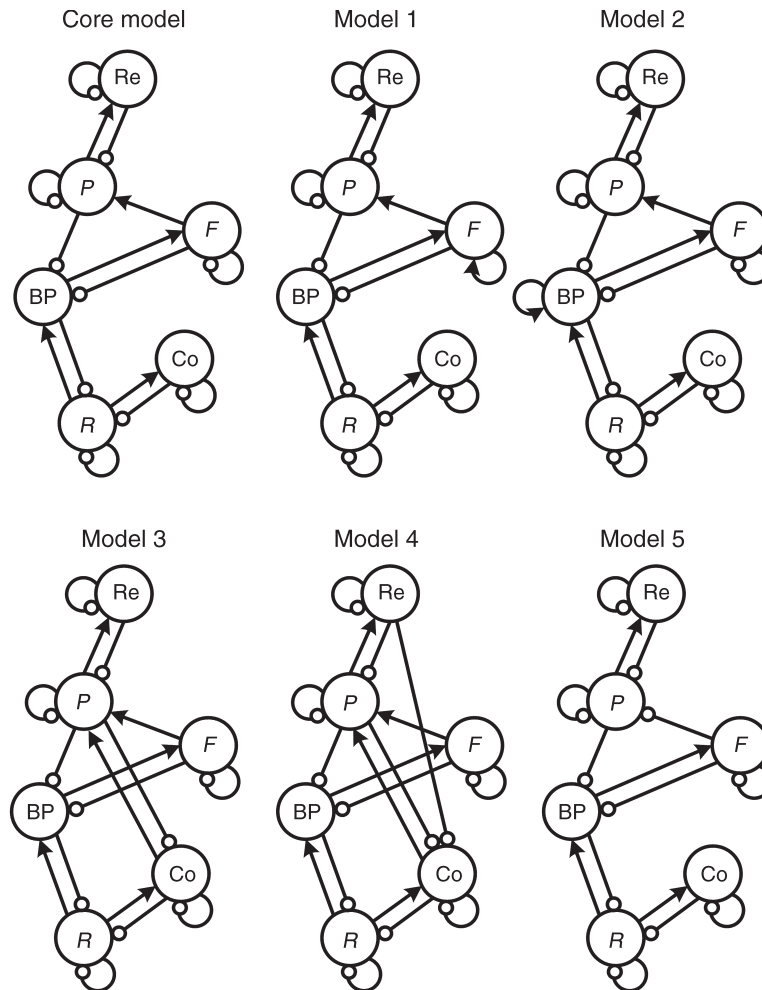


FIG. 7. Core and alternative signed digraph models of the Weipa banana prawn fishery and ecosystem: BP, banana prawns; Co, competitors for food resources; F, fishing fleet; P, predators of banana prawns; R, food resource; Re, recreational fishing.

predators of juveniles (variable 10) and recreational fishing (variable 11), and both subsystems are sign stable (i.e., given the sign structure of the associated matrix  $\mathbf{A}$  of the subsystem, it will be stable for all possible parameter magnitudes in  $\mathbf{A}$ ). The same cannot be done for predators of adult prawns (variable 15), however, because they receive feedback from the fishery subsystem through discarded bycatch. A six-variable core model (Fig. 7) can be created by reducing the prawn life stage subsystem to its single-variable equivalent by aggregating larval, juvenile, and adult food sources. Similarly, the subsystem of fishery catch, effort, and CPUE can be reduced to a single fishing-fleet variable ( $F$ ) with a negative self-effect.

The six-variable core model (Fig. 7) has stability properties that are equivalent to the 17-variable reduced model (i.e., variables 1–17; Fig. 6). Each level of feedback in the core model has only negative cycles, and thus there can never be excessive positive feedback and failure of criterion (i). For criterion (ii), however,

the feedback cycle of banana prawns, their fishery, and predators ( $BP \rightarrow F \rightarrow P \rightarrow BP$ ) is of potential concern. Stability criterion (ii) requires that this feedback cycle not be too strong. Based on the results of simulation studies (Dambacher et al. 2003b), this model has a relatively high potential for stability.

*Response predictions of full model.*—Although there are 23 possible variables in the full model to consider for response predictions, far fewer are relevant to our investigations. Of particular interest are response predictions associated with change in the level of rainfall in either the early or late wet season. An increase in early wet-season rainfall (Fig. 8a) is predicted to increase prawn catch ( $C$ ) and fishing effort ( $E$ ), and increase the abundance of all life stages of banana prawns, but the predicted change in fishery catch per unit effort ( $C/E$ ) is ambiguous. An increase in late wet-season rainfall (Fig. 8b) is predicted to suppress the abundance of adult banana prawns, but gives an ambiguous prediction for change in the other banana prawn life stages, as well as

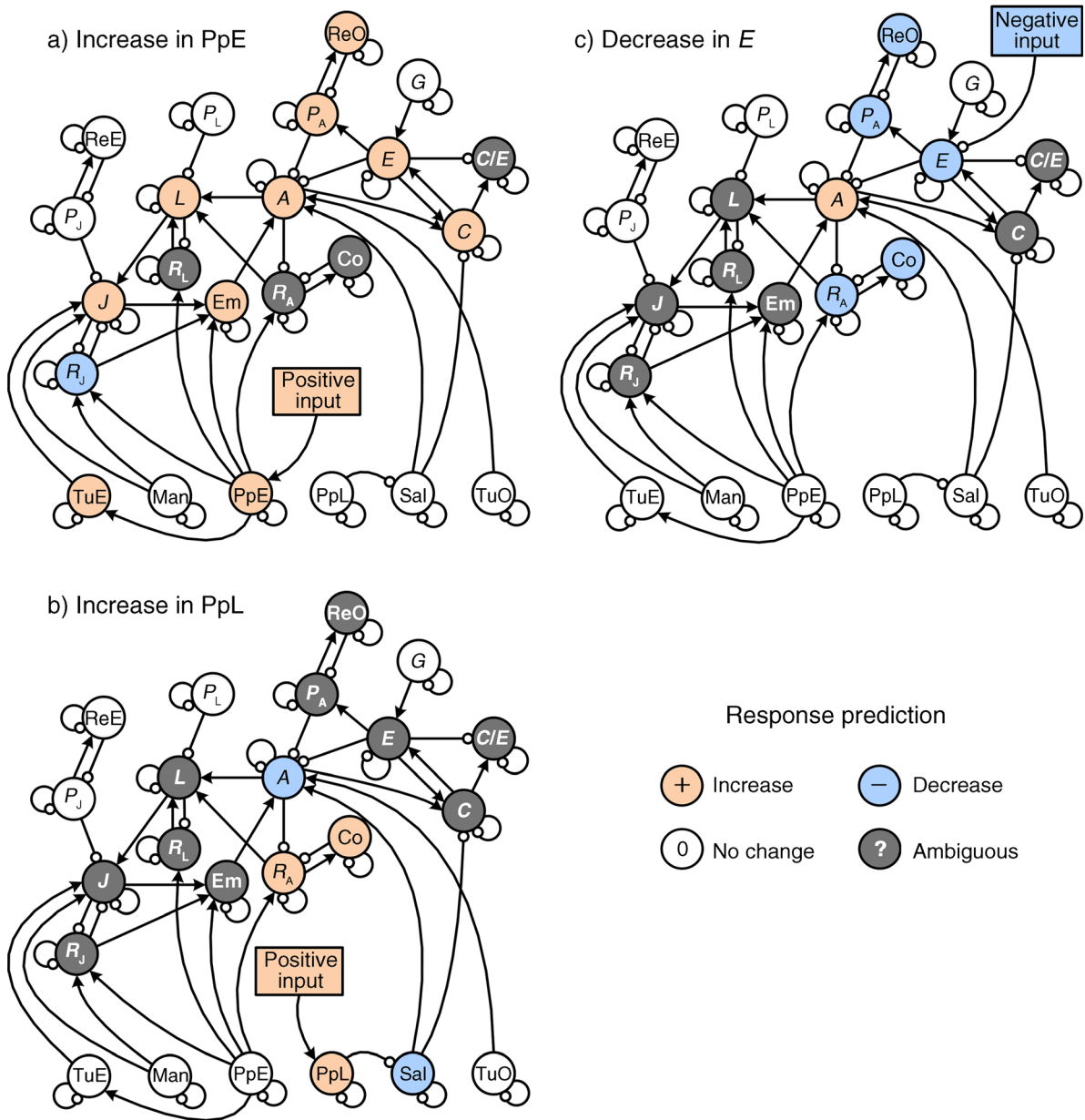


FIG. 8. Qualitative response predictions for (a), an increase in early wet-season or summer rainfall, (b) an increase in late wet-season or autumn rainfall, and (c) a decrease in fishing effort for full signed digraph model of Weipa banana prawn fishery and ecosystem (Fig. 6). Response predictions are from the adjoint matrix of Eq. A.10 in the Appendix; model variables are as defined in Fig. 6.

for changes in catch, effort, and catch per unit effort. A decrease in fishing effort (Fig. 8c), is predicted to benefit adult banana prawns, but predictions for the other life stages, as well as catch, are ambiguous; identical predictions would be obtained for a decrease in the market price of prawns.

Response predictions from the full model are conditional on the presumed stability of the fishery (i.e.,  $C$ ,  $E$ ,  $G$ ) and life stage (i.e.,  $L$ ,  $J$ ,  $Em$ ,  $A$ ) subsystems. In general, where the response predictions are interpretable, the responses of catch and effort are of the same

sign, as are the predicted responses of all banana prawn life stages (see Appendix: Eq. A.10 for all response predictions of the full model). This uniformity of response within each subsystem indicates that practically no information has been gained from this expanded depiction of the system. In fact, the added resolution afforded by each of the banana prawn life stages and the detailed components of the fishery subsystem comes at the cost of considerable ambiguity in model predictions. These ambiguities can only be resolved by precisely ascribing magnitudes to the model's interaction

strengths, which is beyond the current state of knowledge.

Apart from the benefits the detailed full model provides as a communication tool and an aid for conceptualizing the system, a model with fewer variables and life stages, like the six-variable core model (Fig. 7), can provide the same level of understanding and increase the predictability of the system's qualitative dynamics. Predictions from the core model (Table 2) are generally equivalent to predictions from the full model (Appendix: Eq. A.10). Prediction signs of the core model, however, are completely determined; this reduction in ambiguity is a result of collapsing the banana prawn life stages and the fishery subsystem back into single variables.

#### *Alternative hypotheses and models*

Compared to the simplest three-variable model (Fig. 3a) and the full model (Fig. 6), the core model (Fig. 7) represents an intermediate level of complexity, yet preserves the essential dynamics and feedback properties of the full model. Hence, it can be used as a basis to more simply and easily investigate the consequences of different hypotheses on system structure and dynamics. Five alternative models were developed that incorporate different hypotheses about the effects of the banana prawn fishery and trophic interactions in the system (Fig. 7). Model 1, patterned after Fig. 5e, closely couples fishing effort in the Weipa region to local catch levels, thus creating a positive self-effect in the fishing-fleet variable ( $F$ ). Because aggregations of banana prawns can be targeted by the fishing fleet, model 2 considers a hyperstable CPUE with an excessive rate of harvest that gives a positive self-effect to banana prawns, as in model B of Fig. 4b. Model 3 considers the effect of ocean predators ( $P$ ) also consuming species that compete for food with banana prawns ( $Co$ ), i.e., other prawn species such as tiger prawns, but also various fishes. Model 4 has the added link of a negative effect from recreational harvest ( $Re$ ) to fishes that are competitors of banana prawns ( $Co$ ). Model 5 depicts a scenario where the fishery has a net negative effect on predators (i.e., negative link from fishing fleet  $F$  to predator  $P$ ), and presumes that bycatch mortality of predators greatly outweighs the effect of fishery discards in attracting predators.

Model 1 is extremely prone to instability due to criterion (ii). The positive self-effect on the local fishing fleet diminishes lower-level feedback and elevates the relative influence of the long negative feedback cycle involving the prawn, predator, and fishing-fleet variables. This imbalance in system feedback is likely to impart an oscillatory behavior to the fishery, contributing to boom-bust cycles of prawn catch. In model 2, the positive self-effect on banana prawns diminishes lower-level feedback, but it can be countered by the negative self-effect on the fishing-fleet variable. Like model 1, it is prone to failing criterion (ii), and thus can exhibit boom-bust cycles of

catch, but its conditions for stability are less severe due to self-regulation in the fishing-fleet variable, which bolsters lower-level feedback. For model 2 to be stable, the positive feedback caused by harvesting an aggregating stock cannot be too great, and the fishery must be strongly self-regulated (e.g., as in adherence to strict limits to catch or effort). From Eq. 9 we gain the insight that the strength of the positive self-effect in the stock will be high when the abundance of banana prawns is low. When this occurs, then system stability critically depends on a reduction in fishing pressure  $q'E$ , which can be achieved through limitations to fishing effort or the effectiveness of fishing gear.

In models 3–5, lower-level feedback is not diminished by any positive self-effects. Thus they are not prone to oscillations from failing criterion (ii), but rather, instability in these systems most likely will be caused by excessive positive feedback and failure of criterion (i). In model 3, the additional predator-prey interaction between  $P$  and  $Co$  introduces a positive feedback cycle of length four:  $P \rightarrow BP \rightarrow R \rightarrow Co \rightarrow P$ ; stability in this system depends on this cycle not being too strong. Model 4 also has this positive feedback cycle, but the added impact of recreational fishing ( $Re$ ) on  $Co$  introduces both a negative feedback cycle of length three (i.e.,  $Re \rightarrow Co \rightarrow P \rightarrow Re$ ), and a positive feedback cycle of length six (i.e.,  $Re \rightarrow Co \rightarrow R \rightarrow BP \rightarrow F \rightarrow P \rightarrow Re$ ). Finally, the negative effect of bycatch mortality on predators in model 5 introduces positive feedback at the third level of the system:  $P \rightarrow BP \rightarrow F \rightarrow P$ . Overall, the latter three alternative models each have a relatively high potential for stability, with model 4 having the highest, followed by models 3 and 5.

Of interest in the predictions from these alternative models and the core model is the response of the system to a positive input to the fishing-fleet  $F$ , say through increased effort (Table 2a). In the core model, and the first four alternative models, there is a predicted negative response of banana prawns ( $BP$ ), and a positive, if not ambiguous, response in all other variables that arises from the consumption of discarded bycatch by predators ( $P$ ), and reduced consumption of, and competition for, prawn food resources ( $R$ ).

For a positive input to the food resources of banana prawns (Table 2b), there is a predicted positive, if not ambiguous, response in all variables and all models, except for predicted declines in abundance of banana prawns ( $BP$ ) in model 1, and predators ( $P$ ) and recreational fishing ( $Re$ ) in model 5. In model 1, the positive self-effect in the fishing-fleet variable reverses the benefit of increased prawn productivity through a self-enhancing allocation of local effort that overshoots and diminishes the local stock's abundance. In model 5, increased productivity in the system translates into increased bycatch mortality for the predators ( $P$ ), with negative flow-on effects to recreational fishing ( $Re$ ).

A positive input to banana prawns (Table 2c), e.g., through increased turbidity, which reduces predation, is



TABLE 2. Predictions of qualitative response to a positive input to (a) effort of fishing fleet, (b) prawn food resources, and (c) banana prawns, for the core and alternative models (Fig. 7).

Input and response variable	Core	Model 1	Model 2	Model 3	Model 4	Model 5
a) Input to <i>F</i>						
BP	–	–	–	(–)	(–)	?
<i>F</i>	+	+	?	(+)	(+)	+
<i>R</i>	+	+	+	+	+	?
Co	+	+	+	(+)	?	?
<i>P</i>	+	+	?	+	+	–
Re	+	+	?	+	+	–
b) Input to <i>R</i>						
BP	+	–	+	(+)	(+)	+
<i>F</i>	+	+	+	(+)	(+)	+
<i>R</i>	+	+	?	+	+	?
Co	+	+	?	(+)	?	?
<i>P</i>	+	+	+	+	+	–
Re	+	+	+	+	+	–
c) Input to BP						
BP	+	–	+	+	+	+
<i>F</i>	+	+	+	+	+	+
<i>R</i>	–	+	–	(–)	?	–
Co	–	+	–	–	–	–
<i>P</i>	+	+	+	?	?	–
Re	+	+	+	?	?	–

Notes: Model variables are BP, banana prawns; Co, competitors for food resources; *F*, fishing fleet; *P*, predators of banana prawns; *R*, food resources; Re, recreational fishing. Ambiguous predictions with a relatively high probability of sign determinacy ( $\geq 0.85$ ) are enclosed in parentheses, and “?” denotes those with a low probability.

predicted to increase banana prawn abundance in all models, except in model 1, where the fishery is driven by self-enhancing feedback. Prawn abundance (BP) in model 1 is predicted to decline, whereas all other variables are predicted to increase. In the other models, there is generally a predicted decline in the food resources of prawns (*R*) and their competitors (Co).

*Opportunity cost and effort allocation in the Weipa fishery*

Managers of fishing fleets and individual boat operators must often decide how to spread effort across the various regions of the NPF. In the project workshops, managers and operators maintained that because Weipa is the most northerly fished region in the Gulf, relocation to another region exacts a relatively long travel time and high fuel cost. Additionally, offshore turbidity in Weipa is usually too great to permit the use of spotter planes to locate prawn aggregations, a technique commonly used in the Mitchell and Karumba regions of the Gulf of Carpentaria with great advantage to the fishery (Die and Ellis 1999, Prince et al. 2008). Hence, a boat operator deciding to fish in the Weipa region must weigh the benefits of catch in Weipa against the opportunity costs of not fishing elsewhere. This dilemma appears to be reflected in the catch and effort data for the Weipa region and the nearby Mitchell and Karumba regions. In Weipa, there is a significant relationship between the allocation of effort and the level of the previous year’s catch, whereas there appears to be no such relationship

in the other two regions (Fig. 9). This relationship in Weipa suggests that positive feedback can occur in the form of a self-fulfilling prophesy, whereby an experience of low catch in a fishing season, for whatever reason, is subsequently reinforced by withdrawal of effort in the following year, leading to a further diminishment of catch.

We thus sought to account for the spatial dynamics that resulted from the interplay of effort allocation between Weipa and other regions in the NPF, by recasting the dynamics of local effort allocation (Fig. 5d) to also include allocation to adjacent regions. An effort allocation model (Fig. 10) examined the effect of opportunity costs for fishing in two areas of the NPF, here (subscript h) vs. there (subscript t), with here being the Weipa region and there being elsewhere in the NPF. Effort is allocated between the two areas based on the balance of influences on the variable  $BCO_h$ , which represents the ratio of benefits to costs for fishing in the Weipa region. An opportunity cost variable ( $OCO_h$ ) diminishes this ratio as a function of increased levels of catch outside of the Weipa region. This model has two sets of positive feedback cycles between regional catch, effort, and the benefit-to-cost ratio for fishing in Weipa. Stability in this system requires strong negative feedback in the two cycles that involve regional stocks (i.e.,  $S_h \rightarrow C_h \rightarrow BCO_h \rightarrow E_h \rightarrow S_h$ , and  $S_t \rightarrow C_t \rightarrow OCO_h \rightarrow BCO_h \rightarrow E_t \rightarrow S_t$ ).

From the qualitative predictions of the effort allocation model, for an increase in opportunity cost (Fig. 11a), in the Weipa region, effort ( $E_h$ ) is unambiguously predicted to decrease and stock size

( $S_h$ ) to increase. In the other regions the opposite is predicted, i.e., an increase in effort ( $E_t$ ) and a decrease in stock size ( $S_t$ ). The predicted response of catch in either region is ambiguous, and it depends on the relative magnitude of the direct effect of effort on catch ( $+a_{CEa_{SS}}$ ), which contributes to an increase in catch, vs. the indirect effect of effort on catch via the stock ( $-a_{CSa_{SE}}$ ), which contributes to a decrease in catch. Note that this response dynamic is the same as for the expanded fleet–stock model (Fig. 5a); see expression (a) in Eq. A.9 and associated text in the Appendix for further detail.

For a decrease in rainfall in the Weipa region that diminishes the productive capacity of the stock, fishing effort is predicted to shift out of the Weipa region to other regions in the NPF (Fig. 11b). The predicted change in stock abundance in Weipa is ambiguous, and could even increase despite lowered productivity, because a reduction in harvest mortality has the potential to offset diminished recruitment.

In general, any cause acting to reduce the catch of prawns in Weipa will be reinforced by a shift in fishing effort away from the Weipa region. In terms of a press perturbation, this shift will be especially sensitive to the relative strength of the two positive feedback cycles that drive regional effort allocation:  $C_h \rightarrow BCo_h \rightarrow E_h \rightarrow C_h$  and  $C_t \rightarrow OCo_h \rightarrow BCo_h \rightarrow E_t \rightarrow C_t$ . If these cycles are particularly strong, then the magnitude of the system's overall feedback will be diminished and the responses to the regional shifts in effort allocation will be relatively large (i.e., see Eq. A.6 and associated text in the Appendix for further explanation). Finally, in this system a change in CPUE in a region ( $C_h/E_h$  or  $C_t/E_t$ ) will not necessarily be correlated with a change in the region's stock, because CPUE can either increase or decrease with change in stock size depending on the relative changes in effort, as determined from regional trade-offs of benefits and costs.

#### Application to a decision support framework

The dynamics associated with the various models developed in this work were used to examine how low catch levels might have occurred in the Weipa region. Predictions from the core and alternative models are generally consistent with the three main hypotheses of why the catch of banana prawns declined in the Weipa region. The first hypothesis, that catches were low because of an over-harvest of banana prawns, to the extent that the prawns gained a positive self-effect, is represented in model 2 (Fig. 7), which has a relatively low potential for stability. The second hypothesis, that an environmental effect was responsible for the low catches, can be considered through specific perturbations to the full model e.g., such as through a change in early wet-season rainfall, (Fig. 8a), or more simply through input to the biological variables in the core and alternative models; e.g., an input to prawn resources or predators (Fig. 7). The

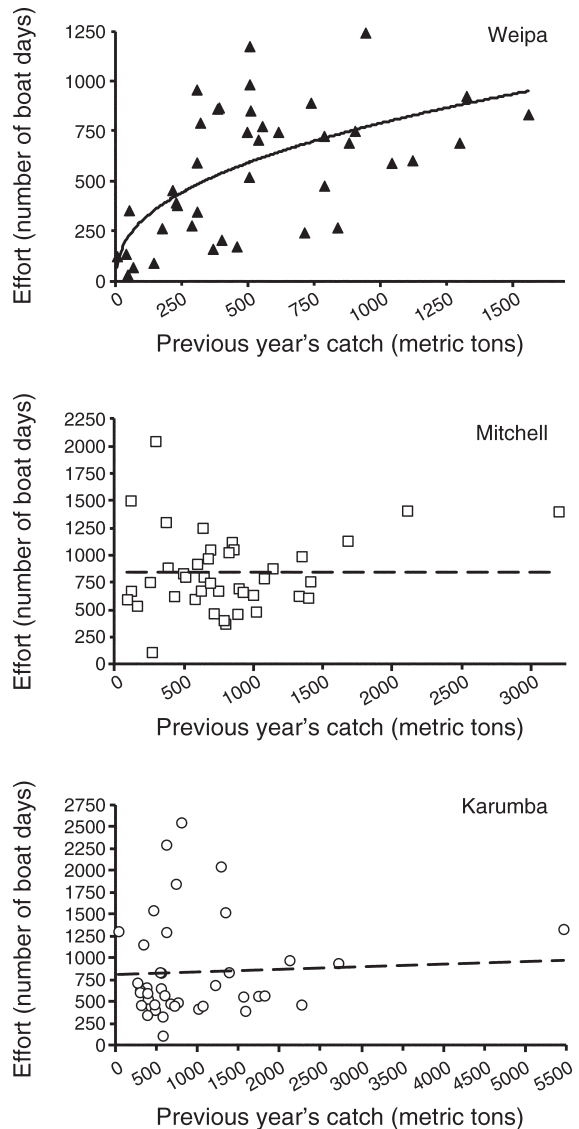


FIG. 9. The relationship between effort (boat days) vs. previous year's catch of banana prawns in three regions (Weipa, Mitchell, and Karumba) of Australia's Northern Prawn Fishery (Fig. 1), 1970–2011. In the Weipa region, the power function  $\text{effort} = 45(\text{previous year's catch})^{0.42}$  describes a significant ( $P < 0.05$ ) nonlinear relationship (solid line), whereas nonsignificant linear relationships (dashed lines) were found in the Mitchell and Karumba regions.

third hypothesis, that catch declined because the fishing fleet could no longer find or catch prawns, is addressed in a number of ways. A decline in the searching power of the fishing fleet is implied in model 1 (Fig. 7) and the effort allocation model (Fig. 10), where a reduced allocation of local effort can be reinforced by a concomitant decrease in catch. The effort allocation model accounts for this phenomenon as a trade-off in opportunity cost and catch levels in the Weipa region vs. other regions in the Gulf. The hypothesis that adult prawns were staying inshore and

Effort allocation model

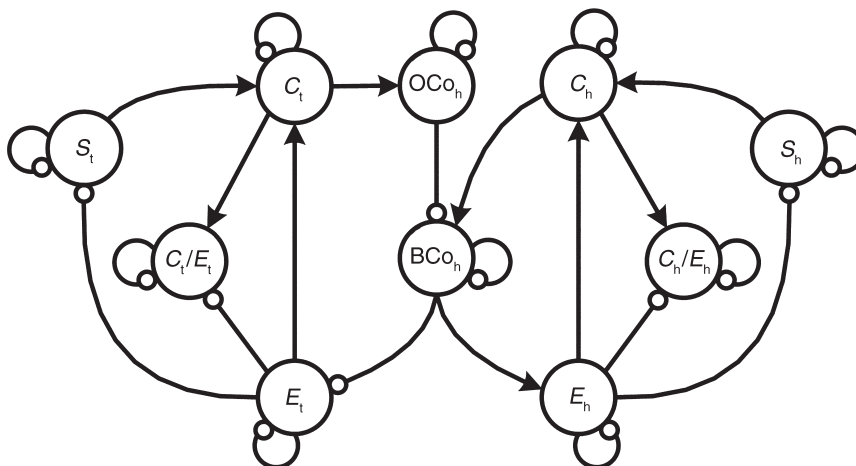


FIG. 10. Signed digraph model of effort allocation and opportunity cost for the Weipa region of Australia's Northern Prawn Fishery. Effort  $E$ , in boat days, is allocated either to the Weipa region (i.e., subscript h, here) or to other regions (i.e., subscript t, there) in the fishery depending on a benefit-to-cost ratio for the Weipa region ( $BCo_h$ ). This ratio is suppressed by an opportunity cost  $OCo_h$  for staying in Weipa region. Banana prawn stocks  $S$  positively affects the level of catch  $C$  in each region, but catch in Weipa, or "here," has a positive effect on the benefit-to-cost ratio, whereas catch from "there" increases the opportunity cost for fishing "here," which then suppresses the benefit-to-cost ratio. Catch per unit effort  $C/E$  is included as a response variable for each region.

were less available to the fishery can be accounted for in the full model through a negative input to late wet-season rainfall (Fig. 8b), and in the core and alternative models simply as a negative input to the fishing-fleet variable and a simultaneous positive input to banana prawns. The hypothesis that banana prawn adults no longer aggregate is equivalent to the hypothesis that prawns are remaining inshore, as both cause reduced catchability.

Conclusions from these analyses supported incorporating the three main hypotheses on declines in banana prawn catch into a decision support framework (Okey and Dichmont 2006) for the Northern Prawn Fishery Management Advisory Committee (NORMAC). To distinguish between hypotheses on the decline of banana prawn catch, it was suggested that an experimental fishing program be conducted in the Weipa region, and no other region in the NPF. Fishing would be opened in Weipa for a week earlier than the normal start of the banana prawn season, typically in early April, thus removing any opportunity cost for fishing in the Weipa region. For the experiment to be successful, it was estimated that at least 40–50 vessels would need to participate to achieve a sufficient level of searching effort. If, given this level of effort, a catch of at least 400 metric tons of banana prawn was not obtained, then it would have been interpreted as a strong indicator of recruitment failure for the Weipa stock, and the Weipa region subsequently would have been closed for a three-year period to allow the stock to recover (Richey 2005). Although this management experiment was endorsed

by the Australian Fisheries Management Authority, it was subsequently rejected by NORMAC, due to its concern about the potential for a deleterious effect on Weipa's banana prawn stock if the entire NPF fleet (up to 76 boats at the time) were to concentrate their effort there (Richey 2006).

In 2003 the NPF started recruitment surveys in selected fishing zones in the Gulf of Carpentaria (Kenyon et al. 2011). These recruitment surveys are used by managers of the NPF fleet to make decisions on where to apportion effort at the start of each season. The survey of early 2006 showed a comparatively high biomass of banana prawns concentrated in, and adjacent to, Albatross Bay, and low biomasses elsewhere in the NPF (Fig. 12). The stark contrast in biomass between regions in the 2006 recruitment survey (a contrast never before seen in previous year's surveys), caused fleet managers to concentrate substantial effort in the Weipa region, which effectively implemented the central objective of the experimental fishing program. A relatively high level of catch in the Weipa region in 2006 was followed by both increased effort and catch in 2007 and in all subsequent years (Fig. 2).

This chain of events gives considerable weight to the hypothesis that the searching power of the fleet had declined, and is consistent with dynamics associated with positive feedback in the effort allocation model of Fig. 10; i.e., the recruitment survey provided a positive input to the benefit-to-cost ratio for the Weipa region, leading to increased effort and increased catch, which



PLATE 1. Fishing fleet searching for dense banana prawn schools (boils) in Gulf of Carpentaria, Australia; fishing nets are held at surface in readiness to “shoot away” on banana-prawn boil when located. Photo credit: P. C. Rothlisberg.

maintains the increased benefit-to-cost ratio for Weipa.

#### DISCUSSION

This work has provided a general representation of the Weipa banana prawn fishery and ecosystem. Through qualitative mathematical models, knowledge from fishers, managers, and biologists was combined to develop a conceptual framework that supported a wider and ongoing investigation. One of the chief benefits of this framework identified during the workshops was that it provided a rapid means for people with different backgrounds and experiences to visualize and understand how their ideas related to those of others, and how they fitted into a larger context that attempted to represent the whole system. In particular, the detailed full model was valued by the workshop participants as a tool to communicate across disciplines.

Settling upon the most useful resolution or level of detail in a model is arguably the most important step in modeling a complex system. In building up from small and simple models to larger and more complex ones, we chose a more useful intermediate level of complexity, as well as a suite of alternative models to represent various hypotheses about how the fishery

and the ecosystem interact. Erring on the side of too-simple leads to trivial results, whereas models with extraneous detail can be unwieldy and less informative. Here we sought the *relevant subsystem* that encapsulated the essential dynamics of the system and was tailored to the specifics of the problem at hand (Dambacher et al. 2009). The goal is a parsimonious representation of the feedbacks that encompass the variable(s) of concern and the source of the perturbation. Qualitative mathematical models are especially suited to this task, because they can be used to rapidly investigate the implications of different model structures for a system's dynamics.

In the course of the workshops, we were challenged to develop a theoretical basis to represent and relate the biological, environmental, and socioeconomic components of the system. This challenge necessitated the development of a formal analytical approach to modified interactions, which was subsequently addressed in Dambacher and Ramos-Jiliberto (2007), but also further elaborated in Fig. 4, which presents a general description of the possible relationships between catchability and CPUE with stock abundance. In addition, this work necessitated the examination of a fishing fleet as a subsystem that includes effort, catch, and market price, which was formally



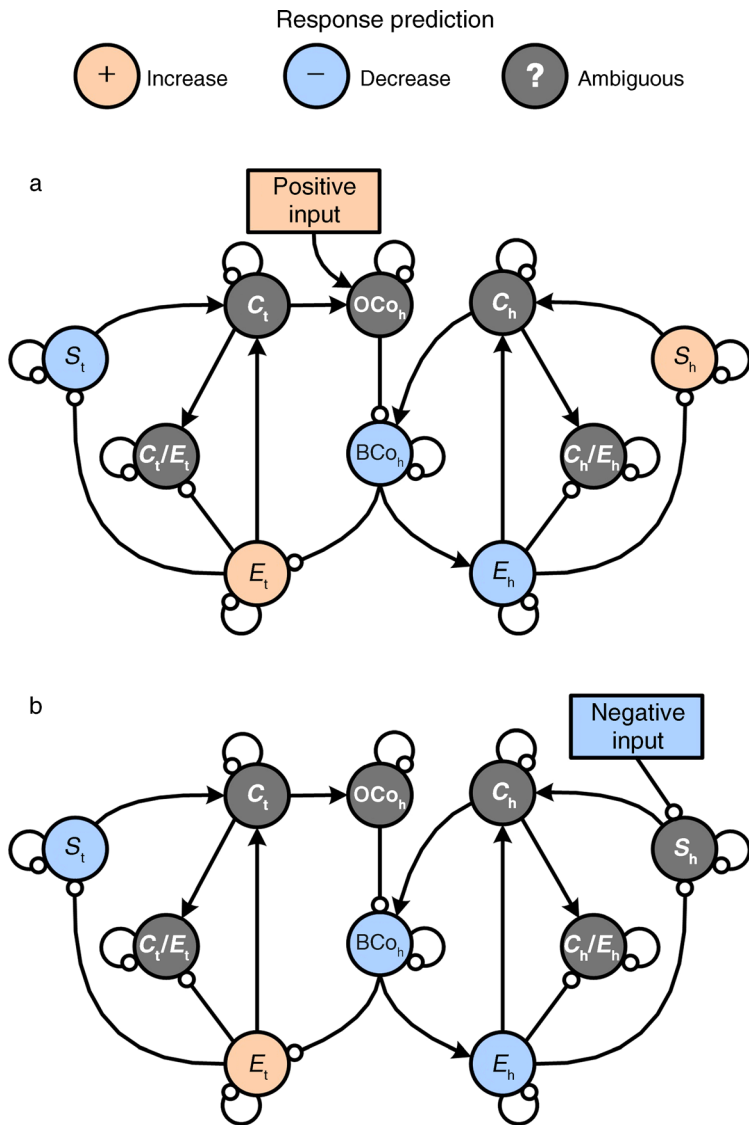


FIG. 11. Qualitative response predictions for (a) an increase in opportunity cost, and (b) a decrease in the productive capacity of the Weipa banana prawn stock for the effort allocation model (Fig. 10); response predictions are from the adjoint matrix of Eq. A.17. Names of model variables correspond to spatial separation of “here” (subscript h) for Weipa region, vs. “there” (subscript t) for another region of Australia’s Northern Prawn Fishery:  $BCo_h$ , benefit-to-cost ratio here;  $C_h/E_h$ , catch per unit effort here;  $C_t/E_t$ , catch per unit effort there;  $C_h$ , prawn catch here;  $C_t$ , prawn catch there;  $E_h$ , fishing effort here;  $E_t$ , fishing effort there;  $OCo_h$ , opportunity cost for expending fishing effort here;  $S_h$ , prawn stock here;  $S_t$ , prawn stock there.

developed in Dambacher et al. (2009). Here we also made a rudimentary attempt to account for spatial dynamics in a fishery by defining the feedbacks associated with fisher behavior and the local allocation of effort.

In comparing the predictions from the full and core models, we found that many predictions from the full model were ambiguous, whereas those for the core model were completely determined (i.e., see Appendix: Eqs. A.10 and A.11). Ambiguity in the more detailed full model arose as a consequence of the feedbacks associated with the expanded resolution of the prawn life stage and fishery subsystems. Determination of all

of these ambiguities would require a nearly complete quantification of the model’s interaction strengths; such quantification, however, would inevitably constrain the model’s generality to the specific context of the data that informed the parameterization. For example, the predicted response of prawn larvae, juveniles, or emigrants to an increase in early wet-season precipitation is sensitive to the magnitude of the rate of development of juveniles across the individual estuaries that adjoin Albatross Bay (Fig. 1). Moreover, the response of juveniles can also be shown to depend on the rate of capitalization in the fishery, which itself is a compound parameter that



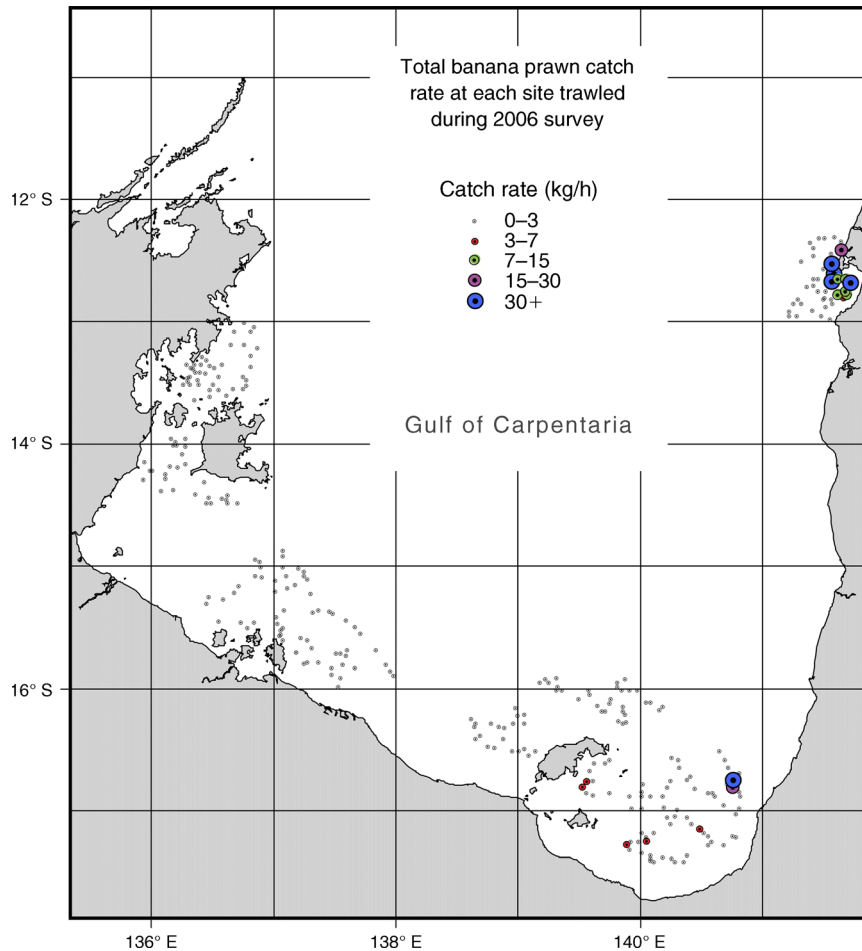


FIG. 12. Catch rates of banana prawns in recruitment surveys for the Northern Prawn Fishery, 21 January to 6 February 2006 (adapted from unpublished 9 February 2006 data analysis, Australian Fisheries and Management Authority, Canberra, Australia).

depends on such disparate factors as the cost of diesel fuel or the global market price of prawns. Here we observe Levins' (1966, 1993) trade-off in model building, such that an increase in the level of detail, or reality, in a model can increase the need for precision in the specification of its parameters, which in turn, can diminish the general applicability of the model. By reducing model resolution, and thus model reality, we reduced the need for precise specification of model parameters and were able to more clearly address the implications of alternative hypotheses to the qualitative dynamics of the system.

Although the events leading to the resumption of relatively normal levels of fishing effort and catch in Weipa give credence to the hypothesis that the six-year period of low catch levels was due to reduced searching power in the fleet, Prince et al. (2008) interpreted the reduced levels of catch, and a reduction in the amount and spatial dispersion of fishing effort, as being more consistent with a reduction in population abundance and hyperstability of catch rates for an aggregating stock (as in model 2 of Fig. 7). Their analysis, however,

was undertaken in the absence of data from the fishery-independent survey. Since the inception of the surveys in 2003, the distribution of banana prawn recruits has been widely dispersed across the fishing grounds within Albatross Bay, although at times their abundance has also been relatively low. Thus, it is not completely certain whether the six-year period of low catches was due to lack of recruits or effort or both. Nonetheless, post-2005 recruits have been sufficiently high, in comparison to other regions, to attract fishing effort and produce catches that have led NORMAC to conclude that the status of the banana prawn stock for the Weipa region is not a concern (Stuart Richey, *personal communication*).

A general result of the models considered here is that system stability requires that fisheries behave in a self-regulated manner, either through limitations in effort or catchability imposed by managers. This requirement is especially important for fisheries targeting an aggregating stock, as in model 2 (Fig. 7), which emphasizes the importance of NORMAC's control of effort in the NPF. Another important

conclusion from this study is that a change in CPUE will not necessarily be correlated with a change in the size of the banana prawn stock. This was observed most clearly from perturbation, or input, to environmental variables in the full model (Fig. 8; Appendix: Eq. A.10), and from input to any variable in the effort-allocation model (Fig. 11; Appendix: Eq. A.17). Thus, interpreting long-term changes in catch and effort data must consider whether the catchability of prawns has changed, and whether effort has fallen in the Weipa fishery as a result of change in opportunity costs for fishing in the Weipa region compared to the rest of the fishery.

The qualitative mathematical models developed in this study are an initial attempt to provide a framework for understanding and predicting the dynamics of the Weipa banana prawn fishery and ecosystem, although the approach is generally applicable to any exploited natural resource. The models provided a first means to compare predictions from the different hypotheses and a basis for future work. As more information is collected, additional models based on more refined hypotheses could be considered, or the current models recast to address aspects of the problem not considered thus far.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/13-2030.1.sm>