CAN WE USE SINGLE-SPECIES MEASUREMENTS TO ANTICIPATE COMMUNITY CONSEQUENCES OF ENVIRONMENTAL CONTAMINANTS?

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1 INTRODUCTION

Conservation and environmental biologists ultimately seek to understand how humans damage ecosystems, and how this damage can be mitigated or prevented. Unfortunately, it is very difficult to identify the symptoms of a "sick" or "damaged" community or ecosystem. As a result, we use indicators, simple model systems, and focal species to measure damage and/or impact. But while practicality forces us to focus on simple assays, much modern ecological theory raises doubts about the validity of such an approach. Communities and ecosystems are complicated webs of interacting species, with the effects of perturbations often yielding surprises because of the rich web of connections among species and the nonlinear nature of population dynamics (Yodzis 1988). What does this "system" or community view mean for ecotoxicology, which, like so much of environmental and conservation biology, is forced to design pragmatic studies of single species?

2 LESSONS FROM FOOD WEB THEORY AND EXPERIMENTS

There has been a tremendous amount of theoretical and experimental work on food web dynamics (reviewed in Pimm 1982,;Lawton 1989; Pimm et al. 1993; Hall and Raffaelli 1993; Morin and Lawler 1995). The majority of this work has been in three areas: 1) predicting and explaining patterns found in real food webs, 2) understanding the relationship between community dynamics (especially stability) and the structure of food webs, and 3) predicting and describing the effects of perturbations on communities. Work on the latter two areas provides some direct insight into the possible impacts of contaminants on natural communities. Theories and studies on the effect of community structure on community dynamics (area 2) has a long history in the field of Ecology. Up to the early 1970s, ecologists argued that complex systems were more stable and by implication less affected by small perturbations (e.g. Elton 1927; MacArthur 1955; Elton 1958). In 1972, May used dynamic food web models to argue against the traditional view of complexity=stability. In food web models, a complex system is more likely to be unstable (and unable to support all

species) than a simple system. Ecologists quickly pointed out that May's approach was flawed (DeAngelis 1975; Lawler 1978). A randomly chosen complex food web may be less stable than a simple one, but real systems are not random. This spawned an enormous amount of research that continues today asking "what makes real complex webs stable?" given that they are not inherently stable and "what structures or configurations tend to make them unstable?" In theory, answers to the latter question may help in predicting what types of communities will be more susceptible to perturbations from contaminants.

May's original analysis (1972) suggested that there is a relationship between the stability of a community and the product of the number of species (S) in the community and the number of links between species (C). Specifically, a community should be stable if:

$$\alpha(SC)^{1/2} < 1 \tag{1}$$

where α is the average interaction strength between species. This suggests that in real communities we should see a negative relationship between size of the community and connectance (C) (Pimm 1982). However the field evidence has been equivocal. Some studies have found a strong negative and even the predicted hyperbolic relationship (Briand 1983; Schoenly et al. 1991) but other studies have found no relationship or a positive relationship (Warren 1990; Winemiller 1989). However even if the field evidence were not equivocal, equation 1 has little value as a practical metric for ascertaining whether a given community will be susceptible to perturbations from contaminants. First, many authors have pointed out that there exist enormous practical difficulties in cataloguing all the species and connections within a large community and that aggregating species (e.g. lumping all the detritovores together) gives one a spurious (S C) value (Paine 1988; Warren 1990; Martinez 1991). Second, it would take enormous effort and years of experiments to estimate α, the mean interaction strength, for even a medium-sized community.

Another potential source of guidance is work on the types of food web structures which tend to be more stable (Pimm and Lawton 1977, 1978). This work suggested that model food

webs, even when parameterized for real communities, tend to be unstable if they have high omnivory. Although, conversely for the subset of stable food webs, omnivory tends to reduce the return time to equilibrium after a community is perturbed. Overall, however, it was argued that omnivory should be rare in natural systems because it is destabilizing (Pimm and Lawton 1978; Pimm 1982; Pimm et al. 1993). This argument stimulated much research on whether omnivory is indeed rare. Some studies support this supposition and others contradict it (reviewed by Hall and Raffaelli 1993), but more pertinent to our discussion is whether omnivory is indeed destabilizing. With alternate conceptual frameworks for food webs, omnivory is stabilizing (Polis and Strong 1996). Furthermore, an experimental test of the effect of omnivory on a community's response to perturbation (Fagan 1997) found that omnivory was in fact a stabilizing factor. The consistent pattern seems to be that even if some structures (such as omnivory) tend to be more unstable than others, all food web configurations can be stable depending on what the particular strengths and functions of interactions are within a community. It is hard to make general predictions - from theory at least - as to what web structures will be stable, and experimental work is too limited to provide much ground truthing of the theory.

Despite the limitations of food web theory in terms of giving us specific metrics, foods web models can give enormous insight into the general responses of communities to perturbations. Two papers which have looked at responses of communities to specific perturbations suggest that community response is non-intuitive. Yodzis (1988) used dynamic food web models to study the effect of increased mortality of a single species on its abundance or the abundances of its predators, prey, or competitors. Yodzis's theoretical study has direct implications for ecotoxicology because it addresses the question of whether – if released into a community – a contaminant that is lethal to a single species would actually cause a change in the abundance of that species or a species with which it directly interacts. It may seem trivially obvious that if one increases the death rate of a species then the species should decline in abundance. But in nature species exist in a complex web of interacting species, and such

dynamic systems do not behave in simple fashions. In fact Yodzis found that one is likely to observe no effect or an effect opposite to that expected. For example, when the death rate of a target species was increased, the abundance of the target species decreased as expected in only 73% of the cases. In terms of the response of the predators, prey and competitors of the targeted species, the response was very variable. For example, in half the cases no change was seen in prey abundances and in 11% of cases the prey actually decreased even though one would expect prey to increase if its predator suffered a higher death rate. Yodzis found similar counterintuitive community responses in a study of the effect of seal harvesting on a commercial fishery in the Benguela ecosystem (Yodzis 1998).

The reason behind these counterintuitive behavior is simply the ubiquity of indirect effects within communities (Wootton 1994a). A change in the death rate of one species propagates to all the other species in the community, and these changes in turn lead to further changes in all the species and so on. Thus the ultimate change in population numbers may be quite contrary to what one would expect from considering only one or two species together. The main message for ecotoxicology is that when a species is within a community as opposed to isolated in a beaker, knowing that a contaminant is lethal to that particular species does not give an indication of whether the population numbers of that species or its prey will increase or decrease when exposed to that contaminant in nature.

3 THE UTILITY OF FOCAL SPECIES AND LETHALITY MEASURES

Laboratory and field measurements of a contaminant's impact on the survival of selected focal species (*e.g.*, Daphnia, honey bees, or aphids) often are used as indicators of how detrimental a particular contaminant will be to a whole community. In recent years, this emphasis on LD_{50}s and mortality rates has been criticized and instead better use of population and behavioral ecology has been advocated, such as measurements of rates of population growth (as opposed to simply mortality), subtle changes in fecundity, and sublethal changes in behavior (Clements 1997; Cohn and Macphail 1996). Although population and behavioral

ecology clearly offers a broader vision to ecotoxicology than has been traditional, even this vision is limited in its view of assessing effects of contaminants since the premise of much of environmental toxicology remains that impacts can be captured by quantifying changes in 1 or 2 species. This single species is weakened by the food web research (reviewed above) indicating that small changes in species can cascade through networks of interacting species to produce major community-wide changes and that impacts on single species in a community often lead to counterintuitive changes in abundances.

Yodzis (1988) explored whether an increase in the mortality rate of a species is reflected in a change in the abundance of the directly impacted species or of the species with which it directly interacts. In this paper, we use similar multi-species community models to examine how well can we expect monitoring of mortality effects on a single species to capture impacts measured at the community level. Our intention is to examine to what extent the dynamic nature of multi-species interactions can thwart attempts to make predictions concerning community responses based on single-species information. We examine first whether lethality is expected to be a good predictor of the overall changes in abundances in the entire community. Second, we examine the relative sensitivity of communities to changes in death rates versus other changes that a contaminant might cause, such as changes in prey-capture rates, changes in susceptibility to predation or disease, and changes in producer fecundity.

3.1 Are changes in mortality rates correlated with community impact?

There are many ways to pose this question and these will differ depending on how a contaminant affects the milieu of species in the community of concern. In this analysis, we explore one specific scenario. We suppose that we do not know the actual food web or the strengths of interactions between species in our community of concern. However, we do know that there is 1 and only 1 highly sensitive species in the community and we have been lucky enough to choose this species as our focal species. We examine only changes in the death rate of the focal species and assume that there are not direct impacts on other species

or on the focal species's predation rates or consumption rates. Although contaminants can certainly impact multiple species, we assume here that it affects only 1 species and that we know which species is affected and to what degree the mortality is increased. In this setting, is a measurement of contaminant's lethality a reasonable metric for the cascade of changes in species abundances that will occur when the death rate of the target species changes? This would be the case if, in our analysis, high lethality generally causes large community impacts and low lethality causes low impacts regardless of the identity of the focal species (the species whose death rate changes) or the community in which the species resides.

3.2 The communities

In order to contrast the single-species versus community perspective on toxicological impacts, we constructed a series of Lotka-Volterra community models (May 1974; Pimm 1982) for a variety of communities with 3 to 16 component species. In this framework, the interactions between species are rates that are a linear function of density. For example, the rate of predation of a herbivore on a producer is $a_{p,h}h$. With this framework, a 3-species community model is (Fig. 1):

$$dc/dt = c(-d_c + a_{c,h}h)$$
$$dh/dt = h(-d_h + a_{h,p}p - a_{h,c}c) \tag{2}$$
$$dp/dt = p(b_p - a_{p,p}p - a_{p,h}h)$$

where dc/dt is the rate of change of the density of the top carnivore, dh/dt is the rate of change of the herbivore, and dp/dt is the rate of change of the producer. The 'a' parameters are measures of the interaction rates between species. The 'd' parameters are the death rates of consumers and the 'b' parameter is the fecundity of the producer. In this framework, deaths of producers are due exclusively to consumption. Thus their death rate is encapsulated in the $a_{i,j}SiSj$ terms. Similarly, the reproduction rate of consumers is governed by their consumption of prey. Consumers' fecundity is also encapsulated in the $a_{i,j}SiSj$ terms. Notice that species on the bottom trophic level (the producers) experience a self-damping

intraspecific competitive effect (through the $a_{p,p}p$ term), but that all other species are controlled by what they eat or what eats them.

This type of model is a first order approximation of real community dynamics. In real communities, the interactions between species are nonlinear; also higher order interactions may be present (Wootton 1994). It is well known that nonlinear effects can dramatically change the response of a community to perturbations (McCann et al. 1998). For example, in a linear model, there is 1 globally stable equilibrium (May 1974), whereas a nonlinear model can display multiple stable equilibria. When multiple stable equilibria exist, the community may jump to a completely new equilibrium in response to a relatively small perturbation (e.g., Spencer 1997). With a highly nonlinear model, we could expect much more dramatic changes in communities out of proportion to small changes in mortality. Thus, our linear modeling approach is likely to underestimate the actual changes in abundances.

We compared 2 archetypal food webs (Figs. 1 and 2) and three community food webs drawn from actual ecosystems (Figs. 3, 4 and 5). These food webs provide a small sample of the webs of interactions that might be found between 'types of organisms' in a real community. In the Mono Lake, California salt marsh and Shoals food webs, the species in the community are lumped into functionally related species which may include a guild of species or simply a single species. In our discussion, we will refer to these functionally similar groups (the nodes in the food web diagrams) simply with the term 'species'.

The relative values of the interaction parameters (i.e., the $a_{i,j}$'s) allow us to describe different types of communities with the same basic food web structure. For example, in a plant-grazing mammal interaction, individual herbivores typically have a heavy impact on individual plants while individual plants have a low impact on individual mammals. The reverse is typical in a plant/phytophagus insect interaction (e.g., individual insects have a low per capita impact on individual plants). For the simple 3-species food web (Fig. 1), we used 6 different sets of $a_{i,j}$ parameters representing 4 different types of communities: plant-mammal herbivore-mammal predator (2 different sets of parameters), plant-phytophagus

insect-parasitoid (2 different sets of parameters), plant-phytophagus insect-insect predator, plant-phytophagus insect-disease. For the 6-species food web (Fig. 2) with 3 plant species, 2 herbivores, and 1 carnivore, we selected different a_{ij}'s to represent a plant-mammal herbivore-mammal carnivore and a plant-phytophagus insect-insect predator community. The real-world food webs, shown in Figs. 3, 4, and 5, were based on the Mono Lake community (Wiens et al. 1993), the terrestrial community of a California salt marsh (Briand 1983) and the French Frigate Shoals (Polovina 1984). For the Mono Lake and salt marsh food webs, we had no estimates for the parameters, and thus we selected relative sizes of parameters which reflected the actual species in the community (Appendix). For the Shoals food web, Polovina (1984) estimated parameters from data on the component species using the ECO-PATH framework (see also Christensen and Pauly 1992). Following the method suggested by Walters et al. (1997), we prepared a Lotka-Volterra community model using Polovina's parameters.

3.3 Community Impact Following Changes in Death Rate

Communities with linear interaction rates have a single stable equilibrium with a particular density for each species of the community (May 1974). If the community is perturbed (such as by release of a contaminant that changes death rates), the equilibrium shifts, the densities of the species change, and some species may be lost altogether. To quantify the level of community impact, we look at the change in the equilibrium abundances of the species in the community caused by the increase in the death rate of the focal species. We define the community impact as the average percent change in the equilibrium species densities. For example, in a community with 3 species, if species 1 experiences an 80% decline; species 2, a 20% increase; and species 3, a 200% increase, then the community impact would be $(80 + 20 + 200)/3 = 100$. A community impact over 100 is quite severe, since this means that the average species either disappeared or more than doubled in density.

We took each species above the lowest trophic level and simulated chronic increases in its

mortality rate. For a community with 6 species, this translated into 6 simulations in which a different species was treated as the focal and therefore the species which experienced an increase in its mortality rate. We varied mortality enhancement from 0% to 300% in increments of 0.1% . It is worth noting that a 300% increase in instantaneous death rates (the d_i's in our model) corresponds to a 75% reduction in the life expectancy, and a 100% increase in instantaneous death rate halves the life expectancy. Thus the range of 0% to 300% increase in death rate corresponds to a reasonable range of a 0% to 75% decrease in life expectancy.

Each line in Fig. 6 represents the community impact observed with different focal/sensitive species. We did not simulate enhanced mortality of primary producers. We also did not include the Shoals food web for this analysis. Two points are immediately apparent from Fig. 6. First, death rate alone was not a good predictor of the change in the model communities due to increases in mortality rates. In some communities, a large change in a species death rate led to a large change in the densities of the component species of the community whereas in other communities, a large change in the death rate led to little change. In general, changes in the death rate of top predators caused a greater community impact than changes in the death rate of species at lower trophic levels, but this is not always the case. Note in Fig. 6 that some of the dashed lines (for species at the second trophic level) are very high. The second, related, point is that the food web structure of the community and the strengths of interactions between species must be known in order to estimate the impact of the change in death rate on the community.

It may seem obvious that in real world assessments, the focal species must be chosen carefully and should not be chosen randomly (as we did). However, in many cases, estimates of the potential impacts of a contaminant must be given with little information on the community or communities in which it will be released. In many cases, if not most, a detailed food web and estimates of the strengths of interaction between species will not be known. With this in mind, it is worth asking whether certain categorizations of species

might help us predict when mortality changes of a species will lead to large community impacts. For example, does enhanced mortality of generalists tend to cascade through webs of interacting species with greater impact than the same amount of extra mortality imposed on specialists? In order to ask these sorts of questions we divided the species in our food webs according to the following characteristics: abundance relative to other non-producers in the community, number of links to other species, and trophic level.

In Fig. 7, we look at the community impact versus relative abundance. We quantify relative abundance for species i as the ratio of species i's abundance divided by the mean abundance of all non-producer species. The relative abundance seems to have low predictive value. Species whose relative abundance varies 10-fold show no clear pattern of community impact. In Fig. 8, we decompose the relative abundance results into separate trend lines for the 10 different communities. For some communities, abundance and impact are positively related; in others it is negatively related. The trophic level and the number of links (Figs. 9 and 10) show a more consistent trend with community impact, and in both cases, a higher trophic level or higher number of links is correlated with a higher impact. However, there is wide variance and the best assessment is that a community is more likely to be sensitive to mortality increases that affects species with many links. But this is by no means certain.

Furthermore, when we examined the influence of trophic level and number of links within individual communities, we found no predictable patterns. For example, in the 3-species communities, high trophic level was associated with reduced impacts and a greater number of links was associated with higher impacts. However, the 6-species communities showed the exact opposite trend (i.e., increased impacts with high trophic level and reduced impact with more links). The 2 other communities showed other combinations of effects. In the California salt marsh community, mortality changes applied to higher trophic levels yielded higher impacts, but there was no close association between number of links and impacts. In the Mono Lake community, mortality changes applied to higher trophic level yielded reduced impacts, while a higher number of links correlated with higher impacts. Thus, for

these model communities, knowledge of a single species was not sufficient to give even a qualitative estimate of the impact on the community caused by an increase in mortality of a single focal species. Instead the specific food web and strengths of interactions within the community had to be known.

4 LETHAL VERSUS SUBLETHAL EFFECTS

Our analyses thus far have assumed that the perturbation from the contaminant alters only mortality rates. However a great deal of recent research indicates that contaminants can have many sublethal effects which alter fecundity, behavior, and immune system function. For example, the widely publicized decline in human sperm count is often attributed to combinations of environmental pollutants, with enormous geographic variation, but estimated annual rates of decline of 1.5% in the United States and 3% in Europe (Swan et al. 1997). Animal foraging rates are often reduced by chemical contaminants (e.g., Peakall 1982; Donkin et al. 1995; Gopal and Ram 1995; Roper et al. 1995), with possible cascading effects through communities (Schmitz et al. 1997). Intraspecific interactions are also likely to change with exposure to certain compounds. For example, deer mice exposed to extremely low concentrations of pesticide combinations dramatically alter their levels of aggression, with implications for spacing behavior and population dynamics (Porter et al. 1998). Probably the best documented evidence of toxicant-induced changes in species interactions comes from studies of chemical impacts on immune systems. It has been repeatedly shown that low dosages of toxicants can suppress immune systems in mice and rats (Porter et al. 1984; Olson et al. 1987; Porter et al. 1998). Such changes have obvious implications for the interactions between diseases and their hosts. In short, there is compelling evidence of changes in predator-prey, host-pathogen, and within-species interaction coefficients due to chemical exposure. There is also evidence of changes in fecundity due to chemical exposures. In terms of human health and risk analysis, many of these subtle effects are clearly important. But, when it comes to community dynamics, it is important to ask how the impact of these sub-

lethal effects compares to the impact of direct alterations of death rates. Perhaps sublethal effects are dwarfed in importance by mortality changes, which would imply that our ecotoxicology could continue to focus on death rates as the key parameter that defines ecosystem impact.

4.1 Modeling the Relative Importance of Sublethal Effects

At first glance, it might seem that any toxicant's impact on mortality would always have a greater community-level impact than a proportionate change in predator-prey, competition, or fedundity rates; death is so final compared to a modest change in prey consumption. To address this formally, we used our community models to contrast small perturbations of fecundity (b_i's in equations) or interaction coefficients (a_{ij}'s) versus death rates (d_i's). In this case, the interaction coefficients encompass rates that predators (including herbivores) capture prey, rates that prey (including plants) are captured by predators, and the rate of within-species competition. Specifically, we changed each parameter (Fig. 11) singly by .1% and recorded the resultant community impact (as defined in the previous section). The impact was then normalized by dividing by the highest community impact observed. Note that the actual amount that we changed the parameters was not critical, and we would have the same results if we had perturbed the parameters by .05% or .001%. This is because a) we were looking at the response of the community to changes in mortality relative to changes in predation, competition or fecundity and b) these models behave linearly to small perturbations from equilibrium. However, it is important to note that we are comparing the effects of equal percent changes in mortality rates versus interaction rates. This roughly translates to comparing equal percent changes in mean lifespan versus mean number of prey eaten in some time period. There has been abundant work documenting decreased prey capture rates in response to low levels of contaminants. However, we do not have information on actual relative impacts of different levels contaminants on mean life span versus number of prey captured per time period, or number of individuals captured as prey

per time period, or number of offspring produced.

In Figs. 11, 12, 13, 14, and 15 , we show the relative impacts caused by the small changes in individual parameters in each of these 5 communities. On the right are shown the parameters of the model. Note, a_{ij} is the impact of species j on species i. On the left, the size of the circle indicates relative sensitivity of the community to each parameter. The locations of the circles on the left and the parameters on the right correspond. The color of the circles, dark grey circles with black perimeters, light grey, and solid black, indicate the relative impacts due to changes in death rates, fecundities and predator-prey rates respectively. Note that each producer has only a fecundity circle since their death rate is encapsulated in the $a_{i,j}$ terms in which 'i' is the producer and 'j' is a consumer, and that each consumer has only a death rate circle since their fecundity is encapsulated in the $a_{i,j}$ terms in which 'i' is the consumer and 'j' is a producer.

In general, the solid black circles (sensitivity to death rates) are not appreciably larger than the dark grey circles (sensitivity to predator-prey interaction rates). This indicates that overall the communities were equally sensitive to changes in the interaction rates as to changes in the death rates. In the 6-species food webs (Figs. 11 and 12) and the Shoals food web (Fig. 15), the community was actually more sensitive to changes in the interaction rates than to changes in death rates. Clearly in these model food webs, a proportional change in interaction rates (for example, prey captured per hour) had as much of an impact on the community as equal proportional changes in death rates (Fig. 16). In our comparison of 5 food webs, we discerned no simple pattern in terms of which interaction terms were important. Neither predation terms, intraspecific competition terms, nor fecundity terms of a specific trophic level were uniformly important in all webs. Instead, in each community a different set of interaction terms was important.

5 DISCUSSION

In this paper, we used dynamic food web models to explore whether a measurement of the lethality of a contaminant to a target species is a good predictor of the total change of species abundances in the community. If the lethality is a good predictor, then one would expect a tight relationship between lethality and community impact. That is, high lethality leads to large impacts on communities, and low lethality leads to low impacts on communities. Instead, our analysis suggests that without knowing the organization of the affected community, it was not possible to predict whether the contaminant (whether extremely lethal or only slightly lethal) would cause a large or small change in the community. A contaminant that causes only minor mortality in a target species might cause large impacts in one community but small impacts in another. Similarly, a highly lethal contaminant might cause small or large impacts depending on the community into which it is released. This implies, perhaps not surprisingly, that we will need detailed information on the species in the community and the strengths of interactions between them. Unfortunately, measuring the strengths of species interactions is not trivial. However, there has been much recent progress on practical methods for measuring these directly using experiments (Wootton 1994a) and indirectly using population-level measures (Yodzis 1998).

Our results on the link (or lack thereof) between mortality of focal species and community-wide changes echo many of the general results found in studies of trophic cascades in which changes in one species cascade through the community (see reviews in Fretwell 1987; Power 1992; Wootton 1994a). This body of work has been concerned with the propagation of impacts down from top-level predators or up from producers. Our analysis differed in that we considered all species as potential target species; thus, we were not concentrating specifically on changes that propagate from upper or lower levels of a food web. Despite numerous famous examples of trophic cascades in natural communities, such as the shift in the Lake Victoria community with the introduction of an exotic cichlid, the general importance of trophic cascades in large complex communities has been a matter of intense debate. Many

factors (omnivory, prey resistance, and predator competition and interference) tend to limit trophic cascades within communities and enormous variability is seen in the extent and magnitude of these cascades (see reviews listed above and Morin and Lawler 1995). Thus predicting whether a trophic cascade will occur and how large it will be depends again on knowing the community composition and the strengths of interactions between species.

Given the need to make predictions concerning contaminants given less than ideal information on the community, we explored characteristics of target species that might suggest that they will be better predictors of community impact. Simple characteristics of the target species, such a whether it is a generalist or specialist, is at a high or low trophic level, or is abundant or rare, did not increase the predictive value of the target species in our analyses. Based on dynamic food web models, the measurement of lethality of a contaminant – even with knowledge of the trophic level, abundance, or linkages of the target – species cannot be assumed by itself to indicate its potential impact on a community. The same weak link between impact and species characteristics has been found previously in analyses of keystone species (species that have a disproportionately high impact on a community). There may be general trends, such as species at higher trophic levels are more likely to be keystone, but there are as many exceptions to this rule as there are adherents to to it (Power et al. 1996).

In addition, we studied the relative impacts of mortality changes versus sublethal effects, namely sublethal changes in predator-prey, fecundity, or intraspecific competition rates. We found that these sublethal changes may be equally or more important than changes in mortality. In 2 out of the 4 model communities, the community was more sensitive to changes in predator-prey, fecundity, or intraspecific competition rates than to changes in the mortality rates. In the other communities, sensitivities were similar. In our analyses, we compared proportionately equal changes in mortality and sublethal rates. For example, we compared a 0.1% decrease in mean life span with a 0.1% decrease in prey capture rates. The sensitivity of these model communities to proportionately equal changes in mortality and sublethal rates suggests that we need to pay attention the magnitude of changes in sublethal rates

(especially prey capture and fecundity rates) relative to changes in mortality rates.

5.1 Where to Go From Here?

At first glance, our results paint a very discouraging picture and suggest that simple assays may not anticipate community-level consequences of toxicants. But the absence of incredibly simple answers does not mean it is hopeless. Rather, we feel further exploration of community models could yield hypotheses about assays of impact that are of mid-level complexity. For example, it could be that although the responses of single species yield little predictive power, studies that focus on 3-4 interacting species are effective assays. For example, empirical studies of microcosms or extracts of communities could be good indicators of community impacts. This possibility could be tested with models, and the models could be used to identify what type of microcosms offer the greatest benefit. Second, it may be that field studies which directly measure several community features capture the impact of contaminants. But here again, we will need theory to suggest possible ways of summarizing an entire community's response to a pollutant. Lastly, our analyses suggest that it is important to focus on the relative change in fecundity and predator-prey or feeding rates versus the change in mean life spans. Of course, short-term behaviors translate easily into population-level parameters in simple models, but whether this translation occurs in nature is less clear. However, if changes in behavior do translate into population level changes in predation, capturability, fecundity or competition rates, this can have an equal or greater dynamical impact on the community compared to equal changes in mortality rates. The summary message from this analysis of dynamical food web models is that when we evaluate contaminants in the environment, methods developed largely with simple lab systems as their model are not likely to work. Environmental toxicology needs to be as sophisticated as nature, if it is to understand and manage the risks associated with environmental contamination.

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Appendix: Models and Parameters

Three-Species Food Web

From Fig. 1, c1 = S3, h1 = S2, p1 = S1, for the notation in the model below. For the parameters, a_{ij} is the impact of species Sj on species Si.

$$dS1/dt = S1(b_1 - a_{1,1}S1 - a_{1,2}S2)$$
$$dS2/dt = S2(-d_2 + a_{2,1}S1 - a_{2,3}S3) \qquad (3)$$
$$dS3/dt = S3(-d_3 + a_{3,2}S2)$$

Plant-Mammal-Mammal A: $b_1 = 7, a_{11} = .7, a_{12} = 100, a_{23} = 3000, a_{21} = .1, a_{32} = 8, d_2 = .4, d_3 = .2$

Plant-Mammal-Mammal B: $b_1 = 7, a_{11} = .7, a_{12} = .05, a_{23} = 10, a_{21} = 10, a_{32} = .08, d_2 = 4, d_3 = 2$

Plant-Insect-Insect A: $b_1 = 7, a_{1,1} = .7, a_{1,2} = .05, a_{2,3} = 10, a_{2,1} = 10, a_{3,2} = .08, d_2 = 4, d_3 = 2$

Plant-Insect-Insect B (univoltine): $b_1 = 7, a_{11} = .7, a_{1,2} = .05, a_{2,3} = 10, a_{2,1} = 10, a_{3,2} = .08, d_2 = 1, d_3 = 1$

Plant-Insect-Parasitoid: $b_1 = 7, a_{1,1} = .7, a_{1,2} = .05, a_{2,3} = 10, a_{2,1} = 10, a_{3,2} = .8, d_2 = 4, d_3 = 2$

Plant-Insect-Disease: $b_1 = 7, a_{1,1} = .7, a_{1,2} = .05, a_{2,3} = .01, a_{2,1} = 10, a_{3,2} = 10, d_2 = 4, d_3 = 10$

Six-Species Food Web

The subscripts on the parameters correspond to the species in Fig. 2: $1 = $ p1, $2 = $ p2, $3 = $ p3, $4 = $ h1, $5 = $ h2, $6 = $ c1.

$$dS1/dt = S1(b_1 - a_{1,1}S1 - a_{1,3}S3)$$

$$dS2/dt = S2(b_2 - a_{2,2}S2 - a_{2,3}S3 - a_{2,4}S4)$$

$$dS3/dt = S3(-d_3 + a_{3,1}S1 + a_{3,2}S2 - a_{3,5}S5)$$

$$dS4/dt = S4(-d_4 + a_{4,2}S2 + a_{4,6}S6 - a_{4,5}S5)$$

$$dS5/dt = S5(-d_5 + a_{5,4}S4 + a_{5,3}S3)$$

$$dS6/dt = S6(b_6 - a_{6,6}S6 - a_{6,4}S4)$$

(4)

Plant-Mammal-Mammal: $b_1 = 7, a_{1,1} = .7, a_{1,3} = 100, a_{1,4} = 6, b_2 = 7.1, a_{2,2} = .77, a_{2,3} = 7, a_{2,4} = 101, a_{3,5} = 3000, b_6 = 2, a_{6,6} = 1.4, a_{6,3} = 20, a_{6,4} = 30, a_{3,6} = .02, a_{4,6} = .5, a_{4,5} = 3000, a_{3,1} = .05, a_{4,1} = .01, a_{3,2} = .01, a_{4,2} = .15, a_{5,3} = 8, a_{5,4} = 9, d_3 = .2, d_4 = .3, d_5 = .1$

Plant-Insect-Insect: $b_1 = 7, a_{1,1} = .4, a_{1,3} = 100, a_{1,4} = 6, b_2 = 4.1, a_{2,2} = 2.1, a_{2,3} = .07, a_{2,4} = .01, a_{3,5} = 300, b_6 = 2, a_{6,6} = 1.4, a_{6,3} = .06, a_{6,4} = .08, a_{3,6} = 10, a_{4,6} = 15, a_{4,5} = 200, a_{3,1} = 20, a_{4,1} = 22, a_{3,2} = 12, a_{4,2} = 13, a_{5,3} = 8, a_{5,4} = 9, d_3 = 3, d_4 = 4, d_5 = 1.1$

Mono Lake

The parameter subscripts correspond to the species in Fig. 3: $1 = $ algae, $2 = $ brine flies, $3 = $ plovers, $4 = $ phytoplankton, $5 = $ brine shrimp, $6 = $ gulls.

$$dS1/dt = S1(b_1 - a_{1,1}S1 - a_{1,2}S2)$$

$$dS2/dt = S2(-d_2 + a_{2,1}S1 - a_{2,3}S3 - a_{2,6}S6)$$

$$dS3/dt = S3(-d_3 + a_{3,2}S2)$$

$$dS4/dt = S4(b_4 - a_{4,4}S4 - a_{4,5}S5)$$

$$dS5/dt = S5(-d_5 + a_{5,4}S4 - a_{5,6}S6)$$

$$dS6/dt = S6(-d_6 + a_{6,2}S2 + a_{6,5}S5)$$

(5)

$b_1 = 7, a_{1,1} = .7, a_{1,2} = 100, a_{2,3} = 3000, a_{2,1} = .1, a_{3,2} = 8, d_2 = .4, d_3 = .2, b_4 = 7, a_{4,4} =$
$.7, a_{4,5} = 100, d_5 = .4, d_6 = .2, a_{5,4} = .065, a_{5,6} = 3000, a_{6,2} = 4, a_{6,5} = 8, a_{2,6} = 2000$

California Salt Marsh

The parameter subscripts correspond to the species in Fig. 4: 1 = terrestrial plants, 3 = terrestrial invertebrates, 6 = shrews, 8 = rails, 10 = passerines, 11 = small rodents, 12 = rats, 13 = raptors.

$$dS1/dt = S1(b_1 - a_{1,1}S1 - a_{1,10}S10 - a_{1,11}S11 - a_{1,12}S12 - a_{1,3}S3 - a_{1,8}S8)$$

$$dS3/dt = S3(-d_3 + a_{3,1}S1 - a_{3,10}S10 - a_{3,11}S11 - a_{3,12}S12 - a_{3,6}S6 - a_{3,8}S8)$$

$$dS6/dt = S6(-d_6 - a_{6,13}S13 + a_{6,3}S3)$$

$$dS8/dt = S8(-d_8 + a_{8,1}S1 - a_{8,12}S12 - a_{8,13}S13 + a_{8,3}S3)$$

$$dS10/dt = S10(-d_{10} + a_{10,1}S1 - a_{10,13}S13 + a_{10,3}S3)$$

$$dS11/dt = S11(-d_{11} + a_{11,1}S1 - a_{11,13}S13 + a_{11,3}S3)$$

$$dS12/dt = S12(-d_{12} + a_{12,1}S1 - a_{12,13}S13 + a_{12,3}S3 + a_{12,8}S8)$$

$$dS13/dt = S13(-d_{13} + a_{13,10}S10 + a_{13,11}S11 + a_{13,12}S12 + a_{13,6}S6 + a_{13,8}S8)$$

$$(6)$$

$b_1 = 7, d_3 = 13, d_6 = 1.5, d_8 = .7, d_{10} = .75, d_{11} = 1.2, d_{12} = .85, d_{13} = .2, a_{1,1} =$
$.10, a_{1,3} = .2, a_{1,8} = 5.1, a_{1,10} = 24, a_{1,11} = 37, a_{1,12} = 5, a_{3,1} = 10.12, a_{3,6} = 14, a_{3,8} =$
$13, a_{3,10} = 25, a_{3,11} = 13.3, a_{3,12} = 14.4, a_{6,3} = 2.2, a_{6,13} = 14.55, a_{8,1} = .4, a_{8,3} = .33, a_{8,12} =$
$2.4, a_{8,13} = 12.2, a_{10,1} = .3, a_{10,3} = .35, a_{10,13} = 10.2, a_{11,1} = .5, a_{1,13} = .87, a_{11,13} = 44.5, a_{12,1} =$
$.21, a_{12,3} = .86, a_{12,8} = .07, a_{12,13} = 22.4, a_{13,6} = .3, a_{13,8} = .45, a_{13,10} = .27, a_{13,11} = .42, a_{13,12} =$
$.46$

French Frigate Shoals

The model for the French Frigate Shoals (Fig. 5) was a series of 15 ordinary differential equations for each species in the web. Each equations for each species was of the form:

$$dSi/dt = Si(q_1 + a_{i,1}S1 + a_{i,2}S2 + a_{i,3}S3 + a_{i,4}S4 + a_{i,5}S5 + a_{i,6}S6$$

$$+ a_{i,7}S7 + a_{i,8}S8 + a_{i,9}S9 + a_{i,10}S10 + a_{i,11}S11 + a_{i,12}S12 \qquad (7)$$

$$+ a_{i,13}S13 + a_{i,14}S14 + a_{i,15}S15)$$

with $a_{i,j}$ parameters as below. Missing $a_{i,j}$ parameters equal zero. Parameter values are from Polovina (1984). The parameter subscripts correspond to species in Fig. 5. 1 = tiger sharks, 2 = birds, 3 = monk seals, 4 = reef sharks, 5 = turtles, 6 = small pelagics, 7 = jacks, 8 = reef fishes, 9 = lobsters, 10 = bottom fishes, 11 = tuna, 12 = zooplankton, 13 = benthos, 14 = phytoplankton, 15 = benthic producers.

$a_{1,1} = -0.95, a_{1,2} = 10, a_{1,3} = 0.63, a_{1,4} = 0.44, a_{1,5} = 0.38, a_{1,6} = 0.021, a_{1,7} = 0.064, a_{1,8} = 0.009, a_{1,9} = 0.058, a_{1,11} = 0.23, d_1 = -0.455, a_{2,1} = -90, a_{2,6} = 1.97, a_{2,7} = 1.39, a_{2,8} = 0.054, a_{2,11} = 2.45, a_{2,12} = 0.27, d_2 = -1.62, a_{3,1} = -5.71, a_{3,8} = 0.17, a_{3,9} = 0.37, d_3 = -2.76, a_{4,1} = -3.97, a_{4,6} = 0.0047, a_{4,8} = 0.011, a_{4,9} = 0.007, d_4 = -0.008, a_{5,1} - 3.46, a_{5,12} = 0.015, a_{5,15} = 0.002, d_5 = -0.005, a_{6,1} = -0.19, a_{6,2} = -29.18, a_{6,4} = -0.102, a_{6,6} = -0.21, a_{6,7} = -0.16, a_{6,10} = -0.24, a_{6,11} = -1.36, a_{6,12} = 1.04, d_6 = -0.056, a_{7,1} = -0.58, a_{7,2} = -20.56, a_{7,6} = 0.015, a_{7,8} = 0.018, a_{7,9} = 0.035, d_7 = -0.017, a_{8,1} = -0.084, a_{8,2} = -0.80, a_{8,3} = -2.27, a_{8,4} = -0.23, a_{8,7} = -0.20, a_{8,8} = -0.066, a_{8,10} = -0.11, a_{8,11} = -0.028, a_{8,12} = 0.257, a_{8,13} = 0.009, a_{8,15} = 0.005, d_8 = -0.075, a_{9,1} = -0.52, a_{9,3} = -4.99, a_{9,4} = -0.16, a_{9,7} = -0.38, a_{9,10} = -0.054, a_{9,12} = 0.011, a_{9,13} = 0.006, d_9 = -0.026, a_{10,6} = 0.021, a_{10,8} = 0.01, a_{10,9} = 0.005, a_{10,10} = -0.96, a_{10,11} = -4.76, a_{10,12} = 0.033, a_{10,13} = 0.001, d_{10} = -0.017, a_{11,1} = -2.045, a_{11,2} = -36.36, a_{11,6} = 0.17, a_{11,8} = 0.003, a_{11,10} = 0.59, a_{11,12} = 0.24, d_{11} = -0.029, a_{12,2} = -4.028, a_{12,5} = -0.35, a_{12,6} = -7.010, a_{12,8} = -1.63, a_{12,9} = -0.17, a_{12,10} = -0.38, a_{12,11} = -1.92, a_{12,14} = 9.57, a_{12,15} = 0.049, d_{12} = -2.009, a_{13,8} = -0.057, a_{13,9} = -0.104, a_{13,10} = -0.012, a_{13,13} = -0.018, a_{13,15} = 0.034, d_{13} = -0.15, a_{14,12} = -66.96, a_{14,14} = -1.84, b_{14} = 73.49, a_{15,5} = -0.042, a_{15,8} = -0.032, a_{15,12} = -0.34, a_{15,13} = -0.14, a_{15,15} = -0.017, b_{15} = 13.12$
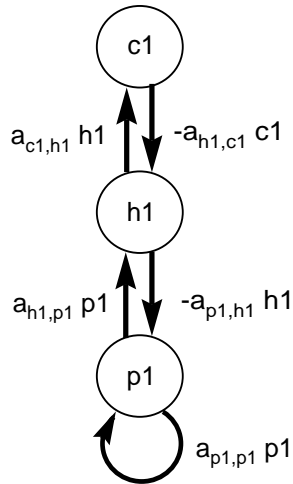
Fig. 1. Simple 3 species food web. The interactions rates between species (shown by the arrows) are a linear function of density.
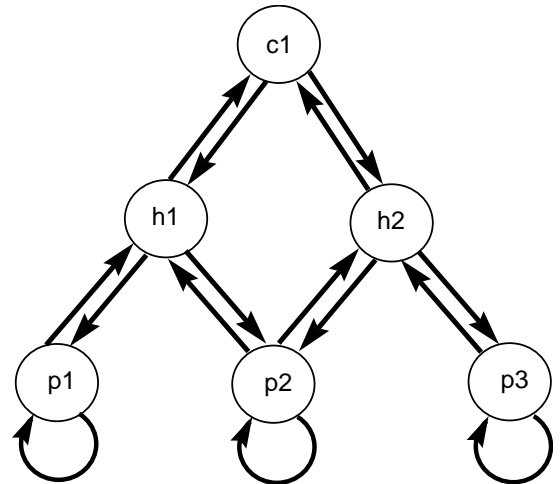

Fig. 2. Six species food web. The web has 3 plant producers, 2 herbivores and 1 top predator.
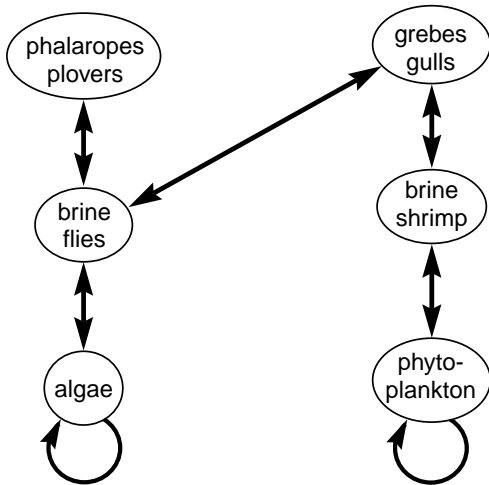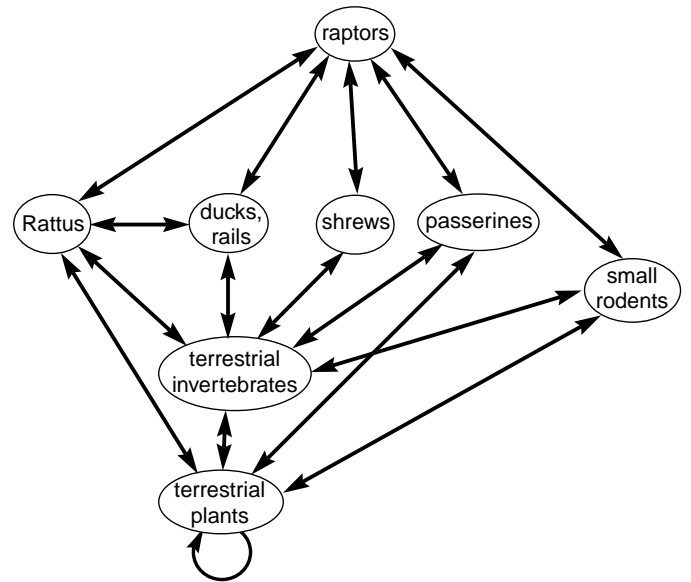

Fig. 3. Food web of the Mono Lake ecosystem.

Fig. 4. Food web of a California salt marsh (from Briand 1983). The small rodents are *Microtus, Reithrodontomys, and Mus.* The raptors are *Circus* and *Asia.*
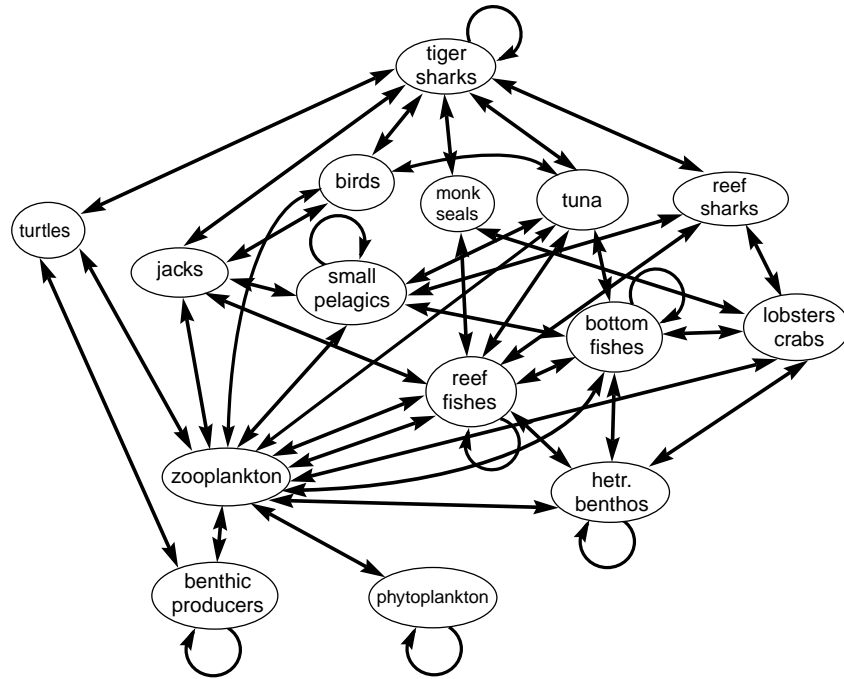
Fig. 5. Food web of the French Frigate Shoals (from Polovina 1984).
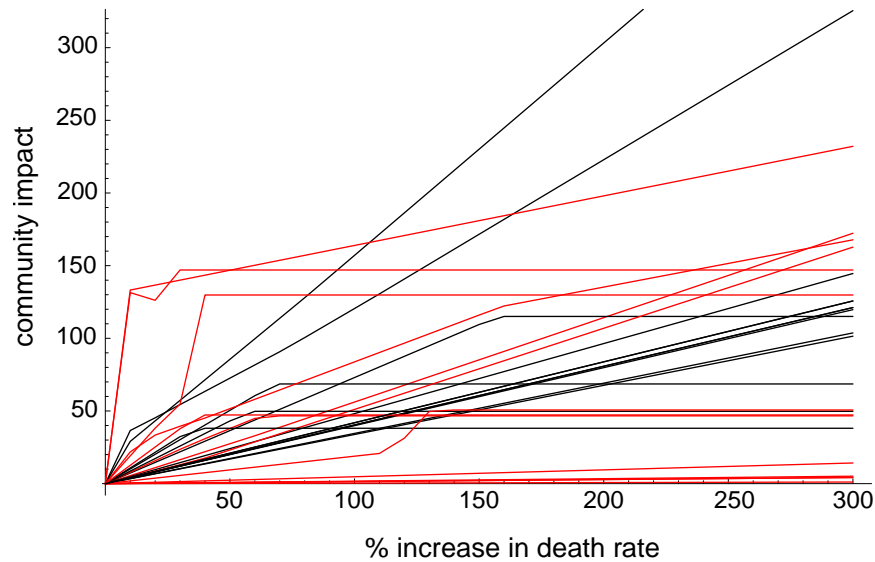
Fig. 6. Impact of an increase in the death rate of 1 species on species abundances in the community as a whole. Community impact is defined as the percent change of the average species in the community. Black lines indicate species at the top of the food web. Thick grey dashed lines indicate species at lower trophic levels. These results include the 6 3-species webs giving 6 top-predator lines and 6 lower trophic level lines, the 2 6-species webs giving 2 top-predator lines and 4 lower trophic level lines, the Mono Lake web giving 2 top-predator lines and 2 lower trophic level lines, and the California salt marsh web giving 1 top-predator line and 6 lower trophic level lines.
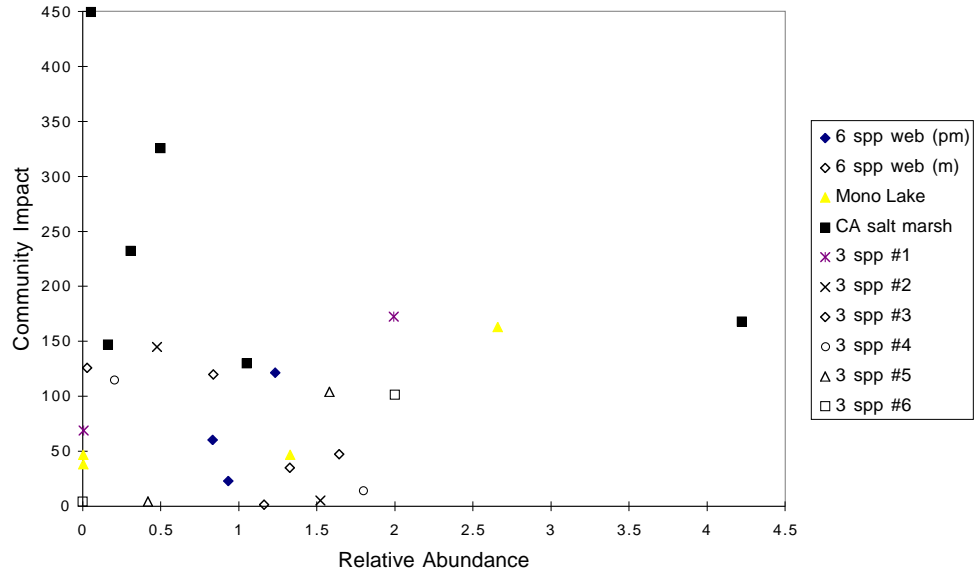
Fig. 7. The relative abundance of a species in a community versus the community impact resulting from a 300% increase in that species' death rate (which corresponds to a 75% decrease in mean life span). The relative abundance is abundance divided by the mean abundance of all non-producers in the community. Results are shown for the following webs, Mono Lake, CA salt marsh, 2 6-species webs (m: plant-mammal-mammal and pm: plant-phytophagus insect-mammal) and 6 3-species webs 1: plant-mammal-mammal A, 2: plant-mammal-mammal B, 3: plant-insect-insect A, 4: plant-insect-insect B, 5: plant-insect-parasitoid, 6: plant-insect-disease (see appendix for parameters).
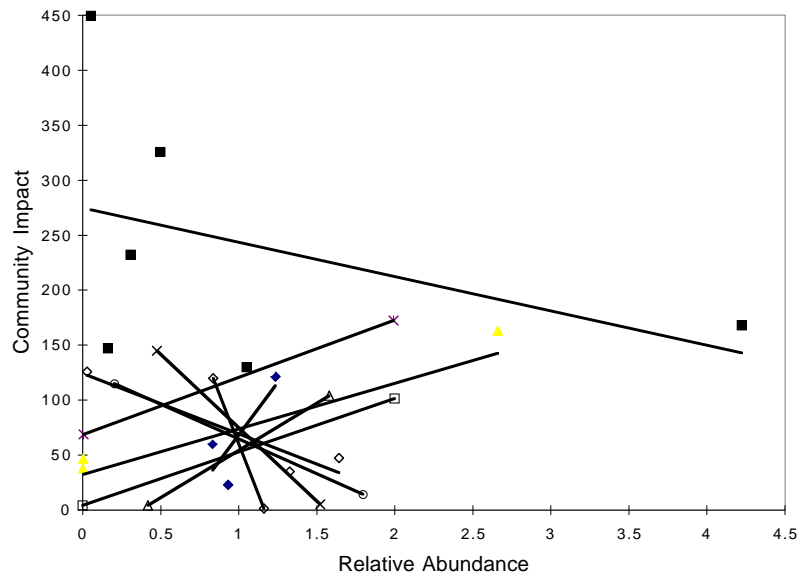
Fig. 8. Abundance versus community impact. This is the same data as in Fig. 7 with trendlines for each of the 10 communities. For 5 communities, impact increases with abundance, and for 5 impact decreases with abundance.
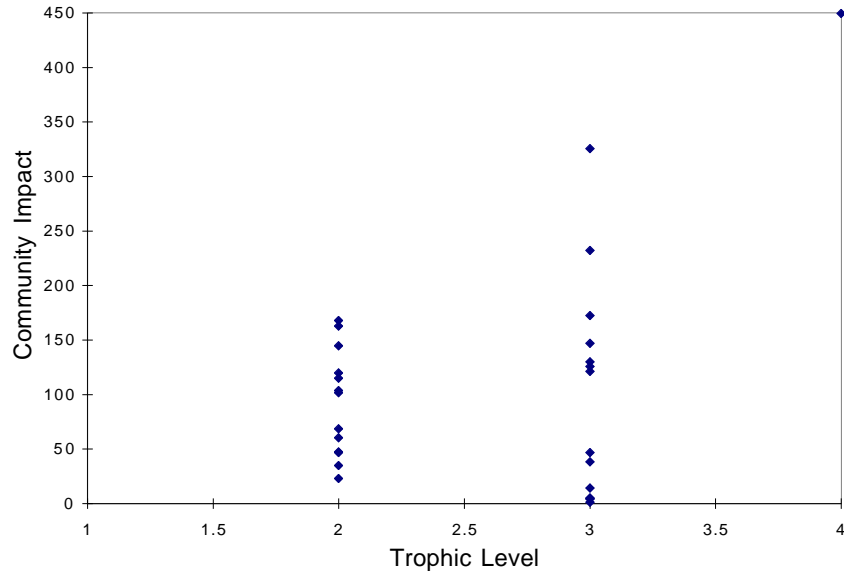
Fig. 9. Trophic level of a species versus the community impact resulting from a 300% increase in that species' death rate. Data for all species in all 10 communities are lumped together. At this level, there is a positive trend of trophic level with community impact. However, as discussed in the text, there is no consistent trend when the data is examined at the level of individual communities.
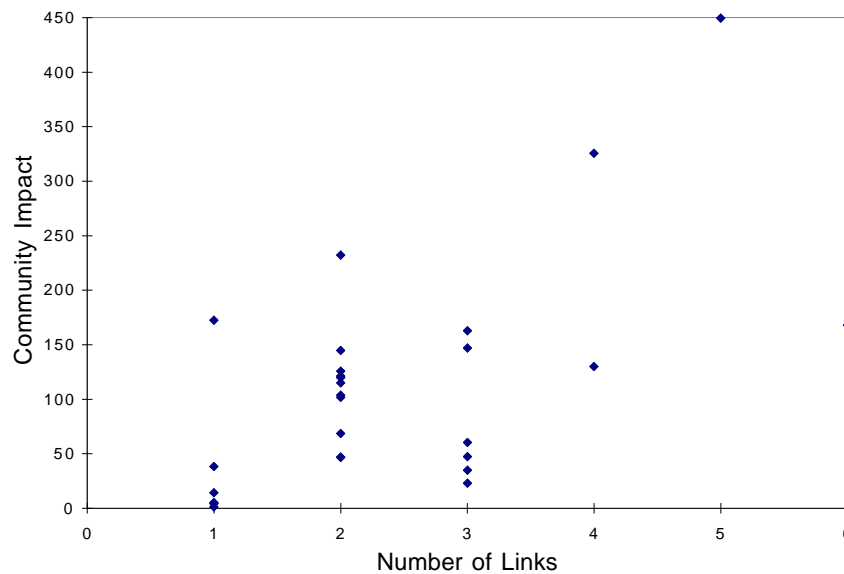
Fig. 10. Number of links versus the community impact resulting from a 300% increase in death rate. Data for all species in all 10 communities are lumped together. In the lumped data, there is a positive trend between the number of links a species has with other species and the impact of an increase in the death rate of that species. However as discussed in the text, there is no consistent trend when the data is examined at the level of individual communities. Half of the communities show a positive trend and half show a negative trend.

b1	b2	d3	d4	d5	b6
1,1	.	1,3	.	.	.
.	2,2	2,3	2,4	.	.
3,1	3,2	.	.	3,5	.
.	4,2	.	.	4,5	4,6
.	.	5,3	5,4	.	.
.	.	.	6,4	.	6,6

Fig. 11. Sensitivity of the 6 species food web (Fig. 2) to changes in the death rates, fecundities and predation rates (using plant-mammal-mammal parameters). Left) The diameter of each circle represents the rel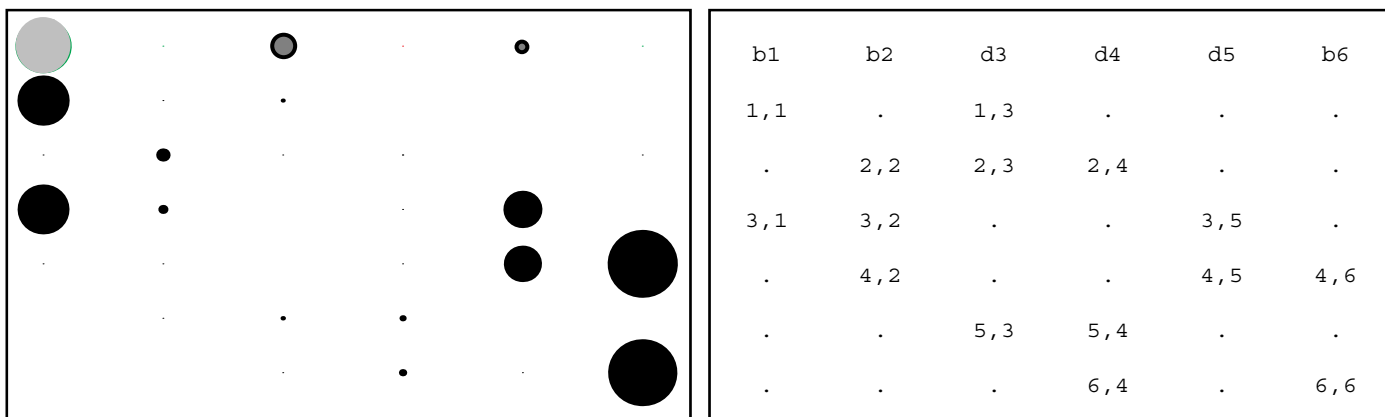ative community impact due to a small (.1%) change in the parameter at the corresponding position on the right. Relative impacts due to changes in death rates are shown with dark grey circles with black perimeter; in fecundities, with light grey circles; and in predator-prey rates, with black solid circles. Predator-prey rates denote both the rate that predators capture prey and the rate that prey (including plants) are eaten by predators or herbivores. Right) Parameters corresponding to the data points (circles) on the left. a_{ij} is the impact of species j on i. The subscripts on the parameters correspond to the species in Fig. 2: 1 = p1, 2 = p2, 3 = p3, 4 = h1, 5 = h2, 6 = c1.

b1	b2	d3	d4	d5	b6
1,1	.	1,3	.	.	.
.	2,2	2,3	2,4	.	.
3,1	3,2	.	.	3,5	.
.	4,2	.	.	4,5	4,6
.	.	5,3	5,4	.	.
.	.	.	6,4	.	6,6

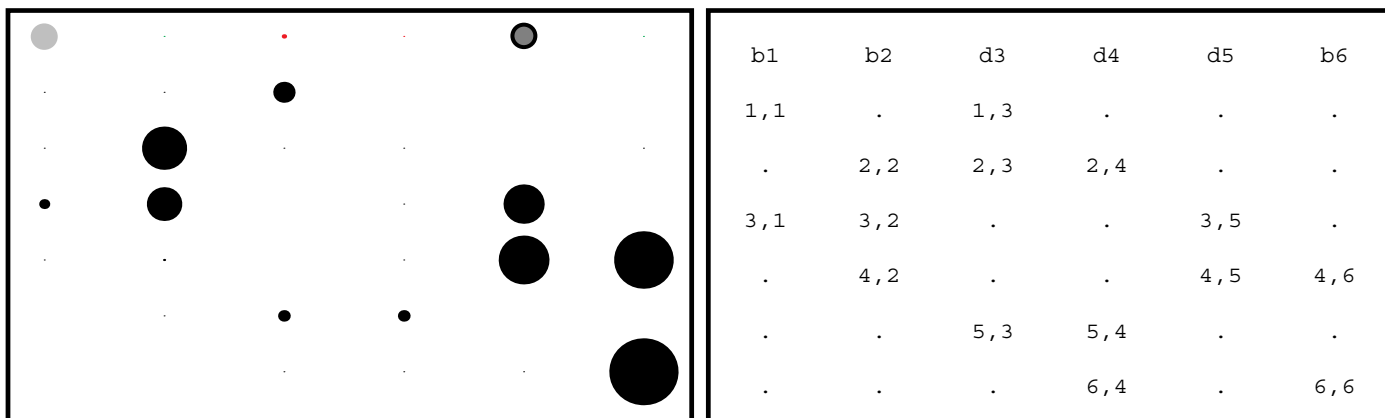Fig. 12. Sensitivity of the 6 species food web (Fig. 2) to changes in the death rates, fecundities and predation rates (using plant-phytophagus insect-mammal parameters). See Fig. 11 for an explanation of the figure. Right) parameters corresponding to the data points (circles) on the left.The subscripts on the parameters correspond to the species in Fig. 2: 1 = p1, 2 = p2, 3 = p3, 4 = h1, 5 = h2, 6 = c1.

b1	d2	d3	b4	d5	d6
1,1	1,2	.	.	.	.
2,1	.	2,3	.	.	2,6
.	3,2	.	.	.	.
.	.	.	4,4	4,5	.
.	.	.	5,4	.	5,6
.	6,2	.	.	6,5	.
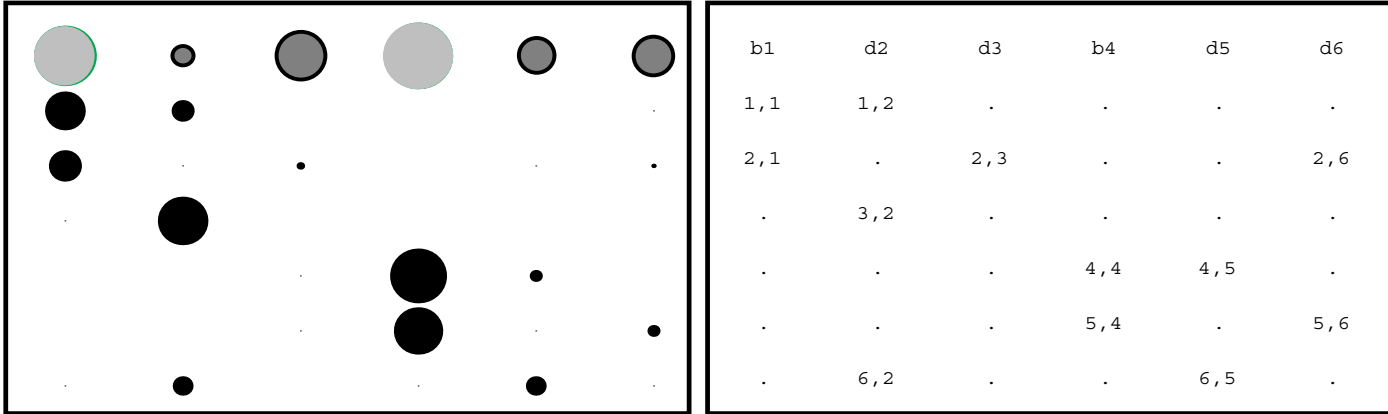
Fig. 13. Sensitivity of the Mono Lake food web (Fig. 3) to changes in the death rates, fecundities and predation rates. See Fig. 11 for an explanation of the figure. Parameters corresponding to the circles in on the left. The parameter subscripts correspond to the species in Fig. 3: 1 = algae, 2 = brine flies, 3 = plovers, 4 = phytoplankton, 5 = brine shrimp, 6 = gulls.

b1	d3	d6	d8	d10	d11	d12	d13
1,1	1,3	.	1,8	1,10	1,11	1,12	.
3,1	.	3,6	3,8	3,10	3,11	3,12	.
.	6,3	.	.	.	.	.	6,13
8,1	8,3	.	.	.	.	8,12	8,13
10,1	10,3	.	.	.	.	.	10,13
11,1	11,3	.	.	.	.	.	11,13
12,1	12,3	.	12,8	.	.	.	12,13
.	.	13,6	13,8	13,10	13,11	13,12	.

Fig. 14. Sensitivity of the California salt marsh food web (Fig. 4) to changes the death rates, fecundities and predation rates. See Fig. 11 for an explanation of the figure. Right) Parameters corresponding to the circles on the left. The parameter subscripts correspond to the species in Fig. 4: 1 = terrestrial plants, 3 = terrestrial invertebrates, 6 = shrews, 8 = rails, 10 = passerines, 11 = small rodents, 12 = rats, 13 = raptors.

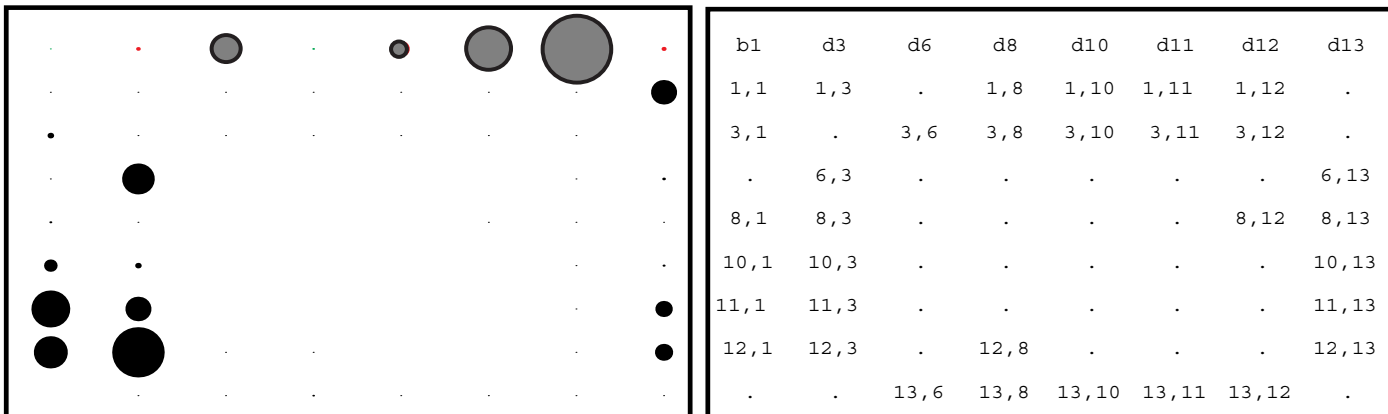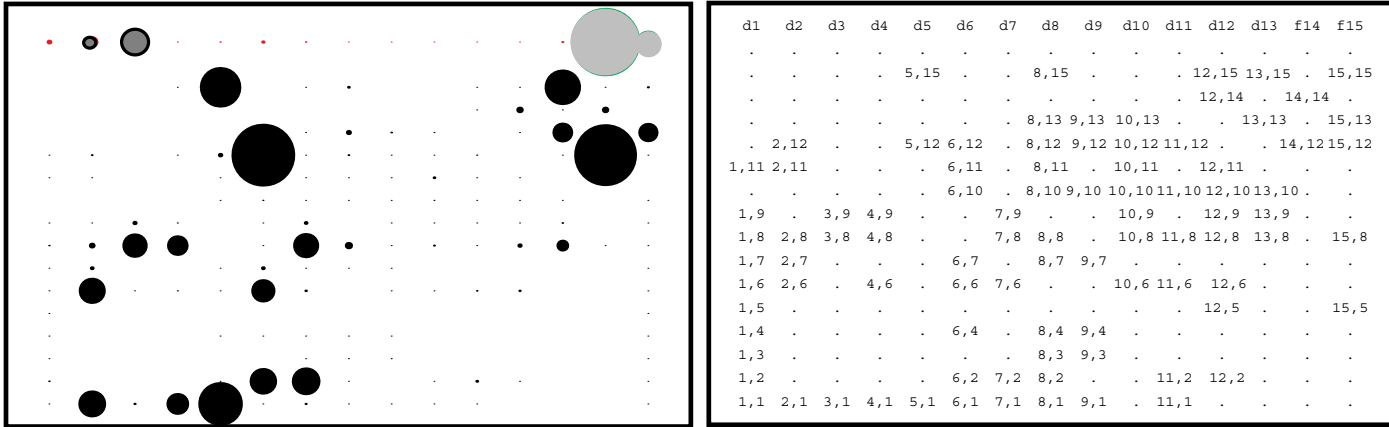| d1	d2	d3	d4	d5	d6	d7	d8	d9	d10	d11	d12	d13	f14	f15
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	5,15	.	.	8,15	.	.	.	12,15	13,15	.	15,15
.	.	.	.	.	.	.	.	.	.	.	12,14	.	14,14	.
.	.	.	.	.	.	.	8,13	9,13	10,13	.	.	13,13	.	15,13
.	2,12	.	.	5,12	6,12	.	8,12	9,12	10,12	11,12	.	.	14,12	15,12
1,11	2,11	.	.	.	6,11	.	8,11	.	10,11	.	12,11	.	.	.
.	.	.	.	.	6,10	.	8,10	9,10	10,10	11,10	12,10	13,10	.	.
1,9	.	3,9	4,9	.	.	7,9	.	.	10,9	.	12,9	13,9	.	.
1,8	2,8	3,8	4,8	.	.	7,8	8,8	.	10,8	11,8	12,8	13,8	.	15,8
1,7	2,7	.	.	.	6,7	.	8,7	9,7	.	.	.	.	.	.
1,6	2,6	.	4,6	.	6,6	7,6	.	.	10,6	11,6	12,6	.	.	.
1,5	.	.	.	.	.	.	.	.	.	.	12,5	.	.	15,5
1,4	.	.	.	.	6,4	.	8,4	9,4	.	.	.	.	.	.
1,3	.	.	.	.	.	.	8,3	9,3	.	.	.	.	.	.
1,2	.	.	.	.	6,2	7,2	8,2	.	.	11,2	12,2	.	.	.
1,1	2,1	3,1	4,1	5,1	6,1	7,1	8,1	9,1	.	11,1	.	.	.	.

Fig. 15. Sensitivity of the reef food web (Fig. 5) to changes in the death rates, fecundities and predation rates. See Fig. 11 for an explanation of the figure. Right) Parameters corresponding the circles on the left. The parameter subscripts correspond to species in Fig. 5. 1 = tiger sharks, 2 = birds, 3 = monk seals, 4 = reef sharks, 5 = turtles, 6 = small pelagics, 7 = jacks, 8 = reef fishes, 9 = lobsters, 10 = bottom fishes, 11 = tuna, 12 = zooplankton, 13 = benthos, 14 = phytoplankton, 15 = benthic producers.

Fig. 16.— Summary of the parameters causing the greatest changes in community abundances. The grey bars show the percentage of all sensitive parameters (large circles) that were of a particular type. This is contrasted to the black bars which show the percentage of all parameters (among all the models) that were of that type.