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Press perturbation experiments and the indeterminacy of ecological interactions: effects of taxonomic resolution and experimental duration

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The outcomes of press perturbation experiments on community dynamics are difficult to predict because there is a high degree of indeterminacy in the strength and direction of ecological interactions. Ecologists need to quantify uncertainties in estimates of interaction strength, by determining all the possible values a given interaction strength could take and the relative likelihood of each value. In this study, we assess the degree to which fish effects on zooplankton and phytoplankton are indeterminate in direction using a combination of experimental data and Monte Carlo simulations. Based on probability distributions of interaction strength (i.e. effect magnitude), we estimated the probability of each fish interaction being negative, positive or undetermined in direction. We then investigated how interaction strength and its predictability might vary with experimental duration and the taxonomic resolution of food web data. Results show that most effects of fish on phyto- and zooplankton were indeed indeterminate, and that the effects of fish were more predictable in direction as the taxonomic resolution of food web data decreased and the experimental duration increased. Results also show that most distributions of interaction strength were not normal, suggesting that normal based statistical procedures for testing hypothesis about interaction strength may be misleading, as well as predictions of food web models assuming normal distributions of interaction strength. By considering the probability distributions and confidence intervals of interaction parameters, ecologists would better understand the outcomes of species interactions and make more realistic predictions about our perturbations in natural food webs.

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A central goal for ecologists is to understand and predict the outcome of species interactions in natural communities. Ecologists need to know which species in a food web are particularly sensitive and which species are resistant to perturbations by poisoning, extinction, invasion, exploitation or stocking of some other species (Yodzis 1988). However, understanding and predicting the outcomes of species interactions require knowledge about which species are dynamically coupled, either directly or indirectly through intermediate species, as well as the strengths and directions of such interactions (Schmitz 1997).

Interaction strength is the magnitude of the effect of one species on another (Paine 1980), whereas interaction direction is the sign of the effect (positive or negative). Measuring the strength and direction of ecological interactions in a given community has become a core requirement for food web models and a central goal for community ecologists (Lawton 1992, Paine 1992).

Press perturbation experiments are those in which the densities of one or more species are continually altered and held at higher or lower levels by means of continual addition or removal of individuals of a particular species (Bender et al. 1984). These experiments are quite common empirical approaches used to measure the strength and direction of species interactions (Yodzis 1988). However, the outcomes of such experiments are highly probabilistic and difficult to predict partly because they are highly sensitive to the strength and direction of interactions among species, which are highly variable in time and space (Yodzis 1988).

Press experiments involve both direct and indirect effects of a perturbation (Bender et al. 1984). When indirect effects are stronger than direct ones, theory predicts that we may expect highly unpredictable outcomes of such experiments (Yodzis 1988, Schoener 1993). Yodzis (1988) argued that due to the prevalence of indirect effects in natural communities, even our most elementary expectation for press experiment (e.g. that adding predators will result in fewer prey) should not be taken for granted. Yodzis (1988) found that due to indirect effects the long-term outcomes of press experiments are highly indeterminate, in terms of the signs of the responses and even in terms of the identities of those species that suffer the largest responses.

The implications of such indeterminacy is that the response of a given species to a press perturbation in any single replicate can be opposite to the expected response (Yodzis 1988, Schoener 1993, Schmitz 1997). Moreover, if variation among replicates is sufficiently large and the mean response is weak one can conclude that there is little or no statistically significant effect of such press perturbation (Schmitz 1997). Such conclusions based only on the statistical significance of the mean treatment effect may be very misleading (Schmitz 1997).

There is a high degree of indeterminacy in the strength and direction of ecological interactions and ecologists need to quantify and describe the nature of this indeterminacy, by determining all the possible values a given interaction parameter could take and determining the relative likelihood of each value. This is done with probability distributions, which give both the range of values that a variable could take (minimum to maximum) and the likelihood of occurrence of each value within the range. In the present study, we used Monte Carlo simulations to estimate the probability distributions and confidence intervals of interaction strengths between a fish species (*Perca fluviatilis*) and several phyto- and zooplankton taxa. We also used these sampling distributions of interaction strength to estimate the probability of each interaction being negative, positive or undetermined in direction.

In this study, we investigate whether conventional experiments designed to test for species interactions might be biased toward concluding that there are no interactions when in fact interactions are strong but unpredictable. There are good theoretical reasons to expect that this might be the case (Yodzis 1988) and it is therefore of considerable interest to determine if these conjectures are true. In addition, we evaluate the degree to which interaction strength and its predictability might vary with time and taxonomic scale. These are important questions that are at the forefront of current experimental work in community ecology. We demonstrate that most effects of fish on phyto- and zooplankton were indeed indeterminate, and that the effects of fish were more predictable in direction as the taxonomic resolution of food web data decreased and the experimental duration increased. The implications of these findings for the statistical analysis and interpretation of data from press perturbation experiments on community dynamics are discussed.

Methods

Experimental design

We conducted an enclosure experiment from 12 August to 10 September 1997 including a control treatment (*C*) with natural planktonic densities and no addition of fish and a fish treatment (F) with natural planktonic densities and addition of three perch (*Perca fluviatilis*) 7–9 cm long. Treatments were replicated four times. Enclosures were made of thin, clear polyethylene formed into cylindrical tube, suspended from a wooden frame buoyed by styrofoam floats, sealed at the bottom and open to the atmosphere at the top. The diameter of the enclosures was 1.6 m and the depth 1.5 m, yielding a volume of approximately 3 m^3. Fish were also fed with 3 g of dead chironomids twice a week and the same amount of chironomids were added to the control treatment to avoid biased enrichment of the fish treatment.

Zooplankton and phytoplankton samples were collected at the start of the experiment and after 14 and 28 d from the start. Samples were taken from the surface to the bottom with a Plexiglas tube at five different locations of each enclosure. These five samples were pooled to obtain a representative sample for each enclosure. From each pooled sample, 100-mL subsamples were taken for phytoplankton analysis and 1-L subsamples were filtered through a 10-μm mesh for zooplankton analysis. Phytoplankton and zooplankton samples were preserved with acid Lugol's solution. Phytoplankton were counted at 250 × magnification with an inverted microscope on permanent slides of each sample (HPMA; Crumpton 1987). In each slide a minimum of 10 fields or 200 cells were counted. The length and width of 20 individuals of each algal species were measured and the biovolumes were calculated using different formulae according to their geometric shape. Zooplankton were counted at 100 × magnification with an inverted micro-

scope after sedimentation in 10-mL chambers. At least 200 organisms were counted per zooplankton sample. The length of 20 individuals of each zooplankton species were measured in each sample and zooplankton biomass was calculated using species or genus specific length-weight regression equations reported in Dumont et al. (1975) and Bottrell et al. (1976).

Quantifying interaction strength

We measured per capita interaction strength (effect size) of fish on the per capita growth rate of the phytoplankton and zooplankton populations, because per capita interaction strength is considered to be the most useful index to measure the magnitude of the effect of a manipulated species on a given target species (Laska and Wootton 1998). Here, the effect of fish on a given target taxa was assessed as the difference between the per capita growth rates of the target taxa in the fish treatment and in the control. We calculated per capita growth rates for phytoplankton and zooplankton over 14- and 28-d periods. However, 14 d could include as many as 10–12 generations of phytoplankton, especially smaller species. Thus, the estimated growth rates of phytoplankton actually represent net growth rates over the time span of the experiment.

We used the metric proposed by Osenberg and coworkers (Osenberg and Mittelbach 1996, Osenberg et al. 1997) to estimate per capita interaction strength. This metric considers one control treatment (c) and one experimental treatment (e), and assumes that the resulting dynamics of the target population can be described by an exponential model. The per-unit (per-predator) effect on the per capita growth rate of a given population is then estimated as:

$$\Delta r = r_e - r_c = \mathrm{d}N_e/N_e \, \mathrm{d}t - \mathrm{d}N_c/N_c \, \mathrm{d}t$$
$$= [\ln(N_{te}/N_{0e}) - \ln(N_{tc}/N_{0c})]/tP$$

where r_e and r_c are the per capita growth rates of the target population in the experimental and control treatments, respectively; N_{te} and N_{tc} (or N_{0e} and N_{0c}) are the densities of the target population after t d (or at the start, $t = 0$) in the experimental and control treatments; t is the experimental duration (14 or 28 d) and P is the densities of the predator in the experimental treatment (three fishes).

This metric was chosen because it makes no equilibrium assumptions and is therefore considered to be the most informative metric for short-term experiments (Laska and Wootton 1998, Berlow et al. 1999). Although there is little guidance on how short is a short-term experiment, Yodzis (1988) suggests the following rule of thumb for long-term experiments: A press perturbation should run for at least twice the generation time of the longest lived prey species to allow the

system to settle near its new equilibrium. For our system, this would be in excess of some months so that we can be confident that our manipulations at least do not satisfy Yodzis' long term criterion. Furthermore, the metric used here is the best measure of proportional effects if both negative and positive effects are being compared, because it behaves symmetrically about zero (Berlow et al. 1999). Another advantage of this metric is that the densities of the target population at the start of the experiment is taken into account so that variations in interaction strength resulting from different initial conditions in the control and experimental treatment are excluded (Laska and Wootton 1998).

However, this metric provides estimates for the theoretical coefficient of interaction strength only under the following limited set of conditions: when prey are initially rare, far from equilibrium and exhibiting exponential growth (Berlow et al. 1999). Like other metrics commonly used to estimate interaction strength in the field, this metric also assumes no density dependence in the interaction strength with respect to prey or predators (Berlow et al. 1999). Therefore, whether or not it actually measures the theoretical coefficient of interaction strength depends critically on whether the system at hand meets the assumption of the underlying exponential model of population growth (Laska and Wootton 1998, Berlow et al. 1999). Our system clearly does not meet some of these assumptions for most phytoplankton and some small zooplankton taxa (e.g. rotifers). Therefore, in the context of our study, this metric should be viewed as a measure of the magnitude (strength) of treatment effects. However, even if our interaction strength estimates are not directly translatable into model parameters, they can provide ecologically meaningful information about how interaction strength are distributed among species in a given community (Berlow et al. 1999) and how these patterns may vary with the degree of taxonomic resolution and experimental duration.

Assessing the indeterminacy of ecological interactions

We used a parametric bootstrap technique for determining the range of possible values a given effect size could take, and the relative likelihood of each value within this range, given the structure of the existing data. First, we calculated the size (magnitude) of the fish effect on a given taxon as described in the previous section, for each possible combination of control and fish treatment replicates (4×4 replicates = 16 estimates of effect size). Then, we assigned these 16 estimates of effect size (i.e. interaction strength) to an histogram and its density function was entered as input in a Monte Carlo simulation (Fig. 1). Before the simulation, we calculated the mean, standard deviation, skewness and

kurtosis of the input distribution and we found which of 28 distribution types fit best our input data. We used the software BestFit from Palisade Corporation
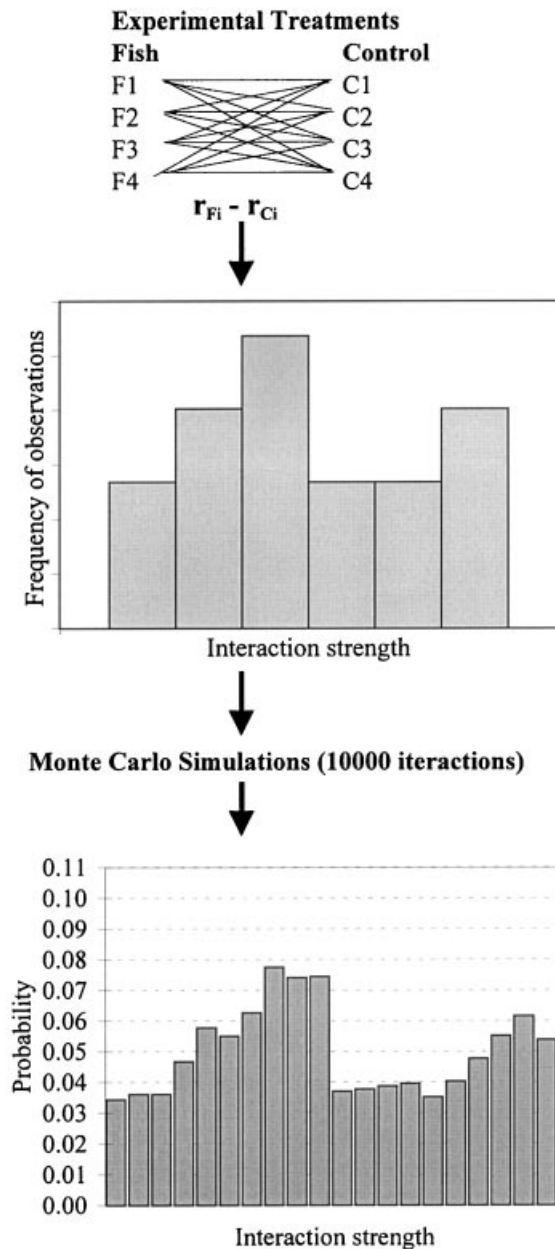

Fig. 1. Procedure used to quantify the uncertainty associated with a given interaction strength measure. Interaction strength was first calculated for each possible combination of replicates between the fish and control treatments. These interaction strength values were then assigned to input frequency distributions. The density functions of these frequency distributions were entered as inputs in a Monte Carlo simulation with 10000 iterations. The Monte Carlo simulation generated output probability distributions describing all the possible outcomes of each interaction strength and their respective likelihood of occurrence.

(www.palisade.com), which goes through the following steps when finding the best fit for our input data: 1) for each distribution type, a first guess of parameters is made using maximum-likelihood estimators, 2) the fit is optimized using the Levenberg-Marquardt method, 3) the goodness-of-fit is measured for the optimized function and 4) all functions are compared and the one with lowest goodness-of-fit value is considered the best fit. The goodness-of-fit test used here was the Kolmogorov-Smirnov test which does not depend on the number of intervals (i.e. frequency classes) selected.

The density function of an histogram is described by its minimum and maximum values and by the probability weight p of each frequency class. These probability weights were normalized so that their sum was equal to 100% (i.e. by summing all weights and dividing each weight by this sum). The density function was then expressed as a cumulative probability distribution, with a 0 to 1 scale in the Y axis which represented the cumulative probabilities of the corresponding interaction strength values in the X axis. The scale of 0 to 1 was the range of possible numbers that was randomly sampled by the Monte Carlo simulation. The computer generated random numbers between 0 and 1 which were used to select the corresponding values of interaction strength from the X axis of the cumulative probability distribution. In our simulation, 10000 random samples (iterations) from 0 to 1 were taken from a given input distribution to generate the corresponding output distribution. This high number of iterations was needed for all the output distributions to reproduce the structure of the given data. During the simulation, we monitored the mean, the standard deviation and the average percent change in percentile values of the output distributions. After 10000 iterations the average percent change in percentile values of all output distributions was less than 1.5%, the convergence criterion used in this study. The Monte Carlo simulation was performed with the software @RISK, a risk analysis software for Excel spreadsheets, also from Palisade Corporation.

The cumulative probability distributions of interaction strength generated by the Monte Carlo simulation were used to classify the direction of each interaction. Here, we will consider the effect of fish on a given taxon negative if in a random sample of interaction strength, the probability of the effect to be lower or equal than zero is ≥ 0.9 and we will consider the effect positive if its probability to be greater than zero is ≥ 0.9. Effects that are neither negative nor positive will be considered undetermined in direction. Thus, if an effect is considered positive, we can be 90% confident that it will not be negative or undetermined in direction (Fig. 2). This criterion of 90% probability to delimit effects as positive or negative is of course arbitrary. However, we checked whether our major results and
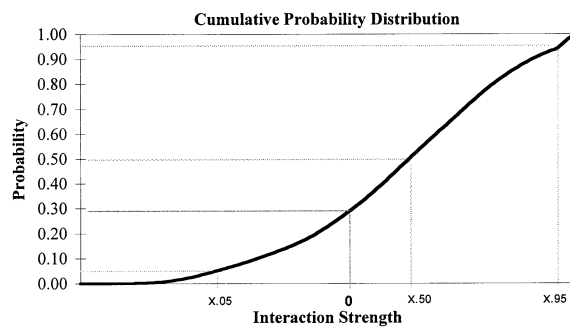
Fig. 2. The cumulative probability distribution for a hypothetical interaction strength between the manipulated species (fish) and a target taxon or taxonomic group. The probability for this hypothetical interaction being less than or equal to 0 (negative) is 0.3 and the probability for the interaction being greater than 0 (positive) is $1-0.3 = 0.7$. As the probability for the interaction being positive or negative is < 0.9, such interaction would be classified in this study as undetermined in direction. The interaction strength value $x_{.50}$ corresponding to the 50th percentile represent the median of the distribution. The interaction strength values $x_{.05}$ and $x_{.95}$ corresponding to the 5th and 95th percentiles represent the central 90% of the distribution or the 90% confidence limits of this hypothetical interaction strength.

conclusions would differ if we used a less conservative criterion of 80% probability to classify the direction of the interactions and we found that results were actually robust when we used the less conservative criterion.

From our classification of interactions, we quantified the number of interactions undetermined in direction after 14 and 28 d of experiment, for different levels of taxonomic resolution. The number of undetermined interactions was divided by the total number of interactions at the respective level of taxonomic resolution. These proportions of undetermined interactions were then used to evaluate the effects of taxonomic resolution and experimental duration on the degree of indeterminacy of the interactions.

Taxonomic aggregation was first performed by lumping the 15 most important (in biovolume) phytoplankton genera into five classes and the five most important (in biomass) zooplankton genera plus copepods nauplii into two groups (i.e. copepods and cladocerans). Rotifers were not resolved to genus level but was included as a group at the order/class level of taxonomic resolution. The second taxonomic aggregation was performed by lumping the five algae classes into a single phytoplankton cluster and the three zooplankton groups into a single zooplanktonic cluster. Therefore, the food web investigated in this study was analysed at three different levels of taxonomic resolution (Table 1). Since phytoplankton and zooplankton operate on different time scales, especially phytoplankton (days) vs copepods (months), we also investigate the effects of experimental duration on the indeterminacy of the fish interactions with phyto- and zooplankton separately.

Results

Planktivorous fish had positive effects on the per capita growth rates of total phytoplankton, Cyanophyceae, *Microcystis* and rotifers after both 14 and 28 d of experiment (Table 2). Fish also had positive effects on the growth rates of *Pandorina* after 14 d as well as on the growth rates of *Snowella*, total zooplankton, cladocerans, rotifers, *Bosmina*, *Cyclops* and nauplii after 28 d of experiment (Table 2). The effect of fish on other taxa or taxonomic groups was undetermined in direction (Table 2).

The Kolmogorov-Smirnov test of goodness-of-fit revealed that the normal distribution fit best less than half of the distributions of interaction strength (Table 3). Because several distributions of interaction strength were skewed, the median were a better measure of central tendency than the mean. The median of the interaction strength distributions indicate that after 14 d, *Snowella* and *Ankyra* had the strongest positive and negative response to fish, respectively (Fig. 3). On the other hand, fish had the strongest positive effect on *Microcystis* and the strongest negative effect on *Ankyra* after 28 d of experiment (Fig. 4). Despite of their strongest positive and negative responses to fish, *Snowella* and *Ankyra* had responses undetermined in direction (Table 2).

Results show that most 90% confidence intervals of the fish effects included zero (Figs 3, 4). These confidence intervals indicate that if we were to test the null hypothesis that the effects of fish were equal to zero, the resulting P-value will be < 0.1 only for total phytoplankton, Cyanophyceae, *Microcystis*, *Pandorina* and

Table 1. Degrees of taxonomic resolution of phytoplankton and zooplankton.

	Phytoplankton	Zooplankton
Lowest	Total phytoplankton	Total zooplankton
Intermediate	Cyanophyceae Chlorophyceae Diaptomophyceae Conjugatophyceae Cryptophyceae	Rotifera Cladocera Copepoda
Highest	*Anabaena* *Fragillaria* *Mycrocystis* *Staurastrum* *Surirella* *Cosmarium* *Cryptomonas* Green colony *Monoraphidium* *Ankyra* *Oocystis* *Pandorina* *Pseudoanabaena* *Scenedesmus* *Snowella*	*Bosmina* *Diaphanosoma* *Ceriodaphnia* *Cyclops* *Eudiaptomus* Nauplii

Table 2. Probability (P) for the fish effects on phyto- and zooplankton being positive after 14 and 28 d of experiment. The probability for an effect being negative or equal than zero is $1 - P$. Probabilities >0.90 are marked with bold letters to indicate positive effects. The other effects were considered undetermined in direction.

Phytoplankton	14 d	28 d	Zooplankton	14 d	28 d
Total phytoplankton	**0.95**	**1.00**	Total zooplankton	0.76	**0.99**
Chlorophyceae	0.49	0.41	Copepods	0.66	0.88
Conjugatophyceae	0.72	0.72	Cladocerans	0.59	**0.93**
Cryptophyceae	0.81	0.77	Rotifers	**0.99**	**1.00**
Cyanophyceae	**1.00**	**1.00**	*Bosmina*	0.78	**1.00**
Diaptomophyceae	0.27	0.47	*Ceriodaphnia*	0.30	0.79
Anabaena	0.46	0.42	*Diaphanosoma*	0.23	0.56
Fragillaria	0.31	0.48	*Cyclops*	0.75	**1.00**
Microcystis	**1.00**	**1.00**	*Eudiaptomus*	0.37	0.52
Staurastrum	0.71	0.62	Nauplii	0.66	**1.00**
Surirella	0.28	0.33			
Cosmarium	0.72	0.58			
Cryptomonas	0.81	0.77			
Green colony	0.89	0.83			
Monoraphidium	0.54	0.88			
Ankyra	0.22	0.12			
Oocystis	0.45	0.40			
Pandorina	**1.00**	0.37			
Pseudoanabaena	0.86	0.71			
Scenedesmus	0.87	0.75			
Snowella	0.75	**1.00**			

Rotifera after 14 d (Fig. 3) and only for total phytoplankton, Cyanophyceae, *Microcystis*, *Snowella*, total zooplankton, Rotifera, *Bosmina*, *Cyclops* and nauplii after 28 d (Fig. 4).

The median and 90% confidence intervals of the interaction strength distributions also shows that individual taxa or taxonomic groups may respond to fish in the opposite direction of the aggregate variables (Figs 3, 4). The amplitude of these confidence intervals indicate that there is usually much more uncertainty in the interaction strength estimates of genera than of aggregate variables such as total phyto- and zooplankton (Figs 3, 4).

We quantified the proportion of interactions undetermined in direction after 14 and 28 d of experiment, for each level of taxonomic resolution (Table 4). These proportions of undetermined interactions were then used to evaluate the effects of taxonomic resolution and experimental duration on the degree of directional indeterminacy of the interactions.

Effects of taxonomic resolution

At the lowest level of taxonomic resolution, the effect of fish was undetermined in direction on one (total zooplankton) of the two aggregate variables (50%) after 14 d of experiment. At the intermediate level of taxonomic resolution, the effect of fish was undetermined in direction on 6 out of 8 taxonomic groups (75%), while at the highest level of taxonomic resolution, the effect of fish was undetermined in direction on 19 out of 21 taxa (90%). Therefore, increasing the degree of taxonomic resolution after 14 d, the effects of fish became

more undetermined in direction. A similar trend was also observed after 28 d of experiment. The proportion of fish effects undetermined in direction increased from 0 to 76% increasing the degree of taxonomic resolution after 28 d (Table 4).

Effects of experimental duration

The effects of experimental duration on the degree of indeterminacy of fish interactions was investigated by looking at changes in the proportions of undetermined interactions for a fixed level of taxonomic resolution. In general, the proportion of fish effects undetermined in direction decreased with increasing the experimental duration from 14 to 28 d, for all levels of taxonomic resolution (Table 4). However, separating the effects of

Table 3. Statistical distributions that best fit the input data of interaction strength between fish and the 31 phyto- and zooplankton variables after 14 and 28 d of experiment. Number of times that each distribution best fit the data.

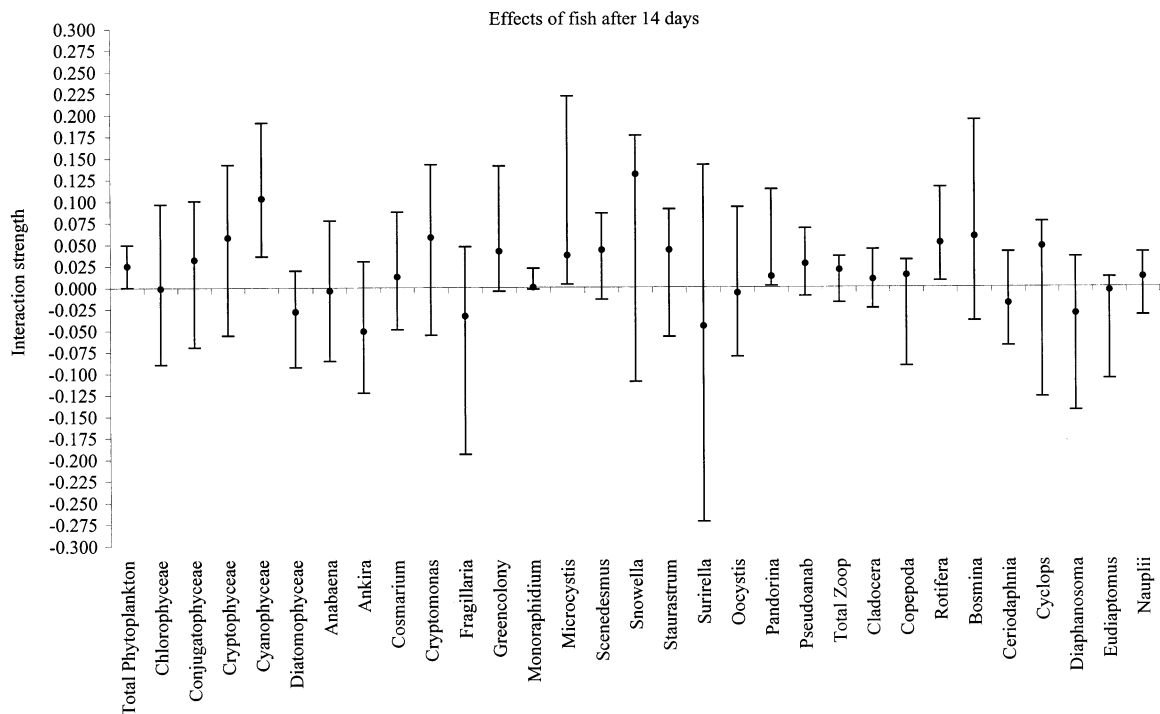| Distributions	14 d	28 d
Normal	13	14
Pearson VI	3	3
Logistic	2	3
Triangular	3	1
Uniform	2	1
Beta	2	1
Gamma	1	2
Extreme Value	1	2
Erf	1	2
Weibull	1	2
Log normal	1	0
Log logistic	1	0

Fig. 3. Median and 90% confidence intervals for the effect of fish on phytoplankton and zooplankton after 14 d of experiment.

fish on phytoplankton from those on zooplankton variables revealed that only the effects on zooplankton became less undetermined in direction with increasing experimental duration (Table 5). Results also show that fish had more predictable effects on zooplankton than on phytoplankton after 28 d but not after 14 d of experiment (Table 5).

Discussion

Our results indicate that some of the strongest effects of fish on phyto- and zooplankton were undetermined in direction. This has important implications for the statistical analysis of data from press perturbation experiments on community dynamics. Traditionally, ecologists evaluate the significance of treatment effects by statistical hypothesis testing. In the present study, if a test of the null hypothesis that a fish effect equals zero was conducted, one could conclude that fish had no significant effect on those taxa or taxonomic groups that actually had the strongest but directionally undetermined responses to fish, a conclusion that would be misleading. Field experiments generally suffer from low levels of replication and high variability among replicates and, therefore, are particularly susceptible to type II statistical errors (i.e. failure to detect a true effect). As this study illustrates, the failure to reject the null hypothesis of zero effect on those taxa which had

strong responses to fish, would clearly result from a lack of power, rather than a lack of fish effect.

In many types of ecological experiments, statistical hypothesis testing have limited relevance because the quantities of primary interest are estimates of effect sizes and estimates of the errors to which they are subject. Test statistics (e.g. an F ratio or t value) and their corresponding P values are inappropriate measures of the biological magnitude of an effect and several arguments have been made against the use of such test statistics as indices of effect size (see Osenberg et al. 1997, 1999, Schmitz 1997). As this study illustrates, evaluating the effects of a manipulated species on other species by means of confidence intervals is biologically more meaningful and less misleading than traditional approaches based on null hypothesis testing. Confidence intervals provide both an estimate of the effect size and a measure of its uncertainty and are therefore more informative than test statistics and their corresponding P-values.

Monte Carlo simulations have often been used to calculate confidence limits for other population parameters such as growth rates (Alvarez-Buylla and Slatkin 1991), but it has not been used for calculating confidence intervals of interaction strength (but see Paine 1992). Here, we used Monte Carlo simulations to determine confidence intervals of interaction strength estimates. Our results show that most 90% confidence intervals were wide, indicating the high degree of uncer-
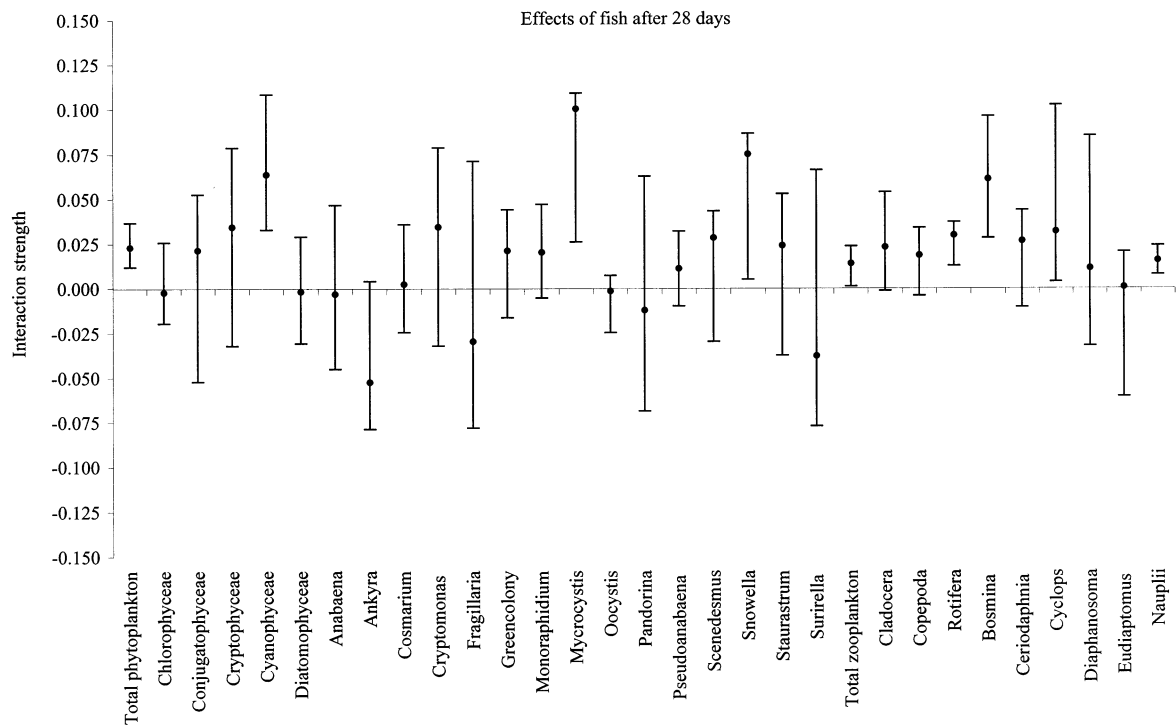
Fig. 4. Median and 90% confidence intervals for the effect of fish on phytoplankton and zooplankton after 28 d of experiment.

tainty associated with interaction strength measures. Statistical variation, systematic error, temporal and spatial variance and inherent stochasticity are all sources of uncertainty in interaction strength estimates, and it is important to estimate such uncertainty so that confidence intervals can be assigned to these interaction strength measures.

There is a high degree of indeterminacy in the outcomes of press perturbation experiments (Yodzis 1988) partly because the strength and direction of ecological interactions are context dependent and highly variable in time and space (Paine 1988, Menge et al. 1994, Power et al. 1996). This has often led to some pessimism about predicting the dynamics of complex natural communities (e.g. Lawton 1999). Despite this high degree of indeterminacy, we believe that the outcomes of press perturbation experiments can still be predictable but only in probabilistic terms.

The most complete and realistic statement which can be made about the outcome of a press perturbation experiment is a distribution of probabilities of possible outcomes (Hilborn and Mangel 1997). Here, we used Monte Carlo simulations to quantify the degree of uncertainty in the outcome of such experiments, by determining all the possible values a given treatment effect can take and by estimating the relative likelihood of each value. With this approach, we were able to estimate from probability distributions of interaction strength, the probability for a given interaction to be

positive, negative or undetermined in direction. One could also use these probability distributions to estimate the probability of a given interaction being lower or higher than any target value other than zero.

Monte Carlo simulations can also be used to determine the bias in the estimation of the mean interaction strength (i.e. the difference between the mean of the simulated and the actual interaction strength values), the accuracy of the associated standard error as well as the shape of the distributions of interaction strength. If interaction strength is not approximately normally distributed, one should avoid using parametric statistics to compare experimental estimates of interaction strength. In our study, slightly more than half of the distributions of interaction strength were not approximately normal, suggesting that normal based statistical procedures for comparing estimates of interaction strength

Table 4. Proportions of interactions undetermined in direction for each level of taxonomic resolution and experimental duration. The total number of elements, n, at each level of taxonomic resolution are given within brackets.

Taxonomic resolution	Experimental duration (d)	% undetermined
Level 1	14	50
($n = 2$)	28	0
Level 2	14	75
($n = 8$)	28	62
Level 3	14	90
($n = 21$)	28	76

Table 5. Proportions of interactions undetermined in direction for phytoplankton and zooplankton variables after 14 and 28 d of experiment.

Taxonomic resolution	Experimental duration (d)	% undetermined
Phytoplankton	14	81
($n = 21$)	28	81
Zooplankton	14	90
($n = 10$)	28	40

may often be misleading. Furthermore, our finding that most interaction strength distributions are not normal have important theoretical implications as these distributions are often assumed by food web modellers to be uniform or normal (Pimm 1991).

Effects of taxonomic resolution

Although we may be unable to predict which individual species will change in response to a press perturbation (Yodzis 1988), we may be able to predict how much the total density or biomass of a group of species will be changed (Pimm 1991). Thus, lumping species together into larger trophic or taxonomic categories may result in more predictable responses. Yodzis (1988) has investigated how the aggregation of biospecies into trophospecies affects the degree of indeterminacy of species interactions in plausible community matrices. He found that there seems to be a trend for directional indeterminacy to be more pronounced in more finely differentiated food webs. Thus, Yodzis' results suggest that lumping biospecies very coarsely into few trophospecies results in less directional indeterminacy. Our results suggest the same effect of taxonomic resolution on the directional indeterminacy of ecological interactions. In our study, the effect of fish on phyto- and zooplankton was more undetermined in direction in the more finely differentiated food web (genera level). This means that the response of a given taxon to a press perturbation is more unpredictable in direction than the response of taxonomic groups or aggregate variables such as total phyto- or zooplankton.

However, although the pooling of individual taxa into broad taxonomic groups might result in more predictable responses of such groups to press perturbations, such aggregation may lead to loss of information and sensitivity owing to compensatory responses of component taxa. If one wants to study the interactions between individual taxa and those taxa are aggregated into major taxonomic groups, they will lose their identities, each becoming part of an aggregate of several taxa (Yodzis 1996). Thus, the examination of species or genera-level responses to press-perturbation tend to be more sensitive, though less predictable, than

the pooling of individual taxa into major taxonomic groups (Cottingham and Carpenter 1998).

Effects of experimental duration

Our results show that increasing experimental duration did not change the degree of indeterminacy of the fish effects on phytoplankton. However, the time scale of our experiment was probably not appropriate to detect short-term responses of phytoplankton because 14 d could include as many as 10 generations of phytoplankton. On the other hand, results show that fish effects on zooplankton were less undetermined in direction after 28 d than after 14 d of experiment, suggesting that the direction of ecological interactions might become more predictable as experimental duration increase. Indeed, the analysis of even simple nonlinear models suggest that ecological systems may exhibit after a perturbation chaotic transient behaviour before approaching equilibrium (Hastings 1996). Thus, there are theoretical reasons to expect that the mid-term outcomes of a perturbation (transient stage of the dynamics) should be more unpredictable than the long-term outcomes closer to equilibrium.

Conclusions

There is a high degree of indeterminacy in the strength and direction of ecological interactions. Our results suggest that such indeterminacy should decrease with increasing experimental duration and decreasing taxonomic resolution. Ecologists need to quantify uncertainty in interaction strength estimates if we are to understand and predict the outcome of species interactions in natural communities. Ecologists would give a more complete and realistic picture of the outcomes of press perturbation experiments by reporting the probability distributions and confidence intervals of interaction strength estimates. This would make much more sense of the variation in the outcome of these experiments and would help us to frame hypotheses about experimental outcomes not as fixed directional changes but rather as probabilities of change, as suggested by Schmitz (1997). By considering the probability distributions and confidence intervals of interaction parameters, we would better understand the outcomes of species interactions and would make more realistic predictions about our perturbations in natural food webs.

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