

# INDIRECT EFFECTS IN MARINE ROCKY INTERTIDAL INTERACTION WEBS: PATTERNS AND IMPORTANCE<sup>1</sup>

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**Abstract.** To determine the patterns of occurrence and importance of indirect effects relative to direct effects in natural communities, I analyzed experimentally based studies from 23 rocky intertidal habitats. The vehicle of analysis was the construction of interaction webs, or the subset of species in food webs involved in strong interactions. The analysis focused on indirect effects involving changes in abundance, or interaction chains, since little information was available on other types of indirect effects (behavioral, chemical response, environmental). As expected, number of direct (= strong) interactions, indirect effects, interaction sequences producing indirect effects, and types of indirect effects (e.g., keystone predation, apparent competition, etc.) all increased with web species richness. Less expected, when these measures were adjusted to a per species basis, positive relationships with species richness were still observed for all measures but the number of types. In other words, with increasing web diversity, each species interacted strongly with more species, was involved in more indirect effects, and was part of more interaction pathways. The analysis identified 83 subtypes of indirect effect, including the seven previously identified types. Many of the 76 additional types could be reclassified into the seven types if the original definitions of these “classic” types were expanded to include interactions having similar effects but differing in the specific mechanism (e.g., both interference competition and inhibition of recruitment [preemption] have negative effects involving a spatial resource). Two new types of indirect effect, termed “apparent predation” and “indirect defense” were also identified, producing a total of 9 general types of indirect effect divided among 565 specific indirect effects. Of these, keystone predation (35%) and apparent competition (25%) were most common and exploitation competition (2.8%) was least common in these webs.

Two methods of analysis suggested that indirect effects accounted for  $\approx 40\%$  of the change in community structure resulting from manipulations, with a range of 24–61%. The proportion of change due to indirect effects was constant with web species richness, indicating that strong direct interactions and indirect effects produce roughly the same level of alteration of community structure regardless of the level of web complexity.

Several potential artifacts and biases were evaluated. Most importantly, neither variation in level of taxonomic resolution nor intensity of experimentation varied significantly with web size (species richness). Despite a bias toward manipulation of consumers over manipulation of basal species, some predator-initiated indirect effect types were scarce while some basal species-initiated types were common. While the frequency of exploitation competition may have been underestimated, it is unlikely that the frequency of this indirect effect would change dramatically: changes due to this effect should have been detected in many of the studies and reported; and the most intensively studied individual webs did not report frequencies differing much from the average. This analysis suggests investigators effectively identified and first manipulated those species responsible for most indirect effects and that more experiments added decreasing numbers of indirect effects. Moreover, the frequencies and importance of indirect effects may be more predictable than expected on the basis of theory.

*Key words:* apparent competition; community; competition; connectance; direct effects; food webs; keystone predation; indirect effects; interaction chains; interaction webs; predation; rocky intertidal; species richness; strong interactions.

## INTRODUCTION

Until recently, community models emphasized “direct” effects such as competition or predation, where

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changes in abundance of a species resulted from its interaction with another species. Another potential cause of variation in community structure is “indirect” effects, where a species can, through its direct interactions with some species, indirectly alter the abundance of other species with which it does not interact directly. Four general categories of indirect effect have

been recognized: trophic linkage (= ecological or abundance), behavioral, environmental, and chemical response (Miller and Kerfoot 1987, Strauss 1991, Pennings 1994). Trophic linkage indirect effects are mediated through changes in abundance; behavioral indirect effects are mediated through changes in behavior independent of abundance; environmental indirect effects are mediated through the alteration of abiotic conditions; and chemical response indirect effects are mediated through chemical pathways. More recently, Wootton (1993) has termed trophic linkage indirect effects "interaction chains" and behavioral indirect effects "interaction modifications" to focus attention on the qualitative distinction between these interrelated effects. In this paper, the primary focus will be on trophic linkage or abundance indirect effects.

Although indirect effects have long been a well-established empirical fact of experimental studies in aquatic communities (e.g., Paine 1966, Hall et al. 1970, Dayton 1971, Menge 1976, Lubchenco and Menge 1978), the broader significance of these effects was initially unclear. Theoretical explorations of indirect effects began in the 1970s (e.g., Levine 1976, Holt 1977), and both theoretical and empirical work has burgeoned (Menge 1978, 1983, Paine 1980, Vandermeer 1980, Morin 1983, Underwood et al. 1983, Bender et al. 1984, Dethier and Duggins 1984, Holt 1984, 1987, Fairweather 1985, Dungan 1986, Menge et al. 1986a, b, Abrams 1987, 1992, Holt and Kotler 1987, Kerfoot and Sih 1987, Schmitt 1987, Yodzis 1988, Wootton 1992, 1993, 1994).

Despite this increased interest, the actual role of indirect effects in the regulation of natural communities is still far from clear. What are the ideas concerning their influence? Bender et al. (1984) noted that indirect effects could in several ways confound the interpretations of "press" experiments, or experiments in which the manipulation was sustained for a relatively long period. Indirect effects could cancel each other, could be larger than direct effects, and could take a long time to become apparent. They suggested that detailed knowledge of the natural history of the system was crucial in interpreting results. The analytical models of Levine (1976), Holt (1977, 1984), and Vandermeer (1980) indicated that indirect effects could alter the predictions of models, and produce "apparent" direct effects such as "apparent competition" or "apparent mutualism." Abrams (1987, 1992) showed that, theoretically, the variety of possible types of indirect effects is almost unlimited. For instance, indirect effects can result from changes in per capita rates of population growth, stability of population dynamics, level of risk to prey, and existence of equilibrium points as well as the more usually considered equilibrium population size. Moreover, all possible signs (+, 0, and -) of indirect effects can result from even a single kind of indirect effect (e.g., apparent competition; Abrams 1987); such counterintuitive results of indirect effects

may lead to false interpretations (Abrams 1992). Abrams (1992) also noted that indirect effects could potentially be more important than direct effects and that the largest effects are expected on species at the end of interaction chains. Yodzis (1988) showed that indirect effects can introduce a high level of indeterminacy in food web models, that is, the influence of a specific perturbation (e.g., maintained increase in abundance of a species) may very often be the opposite of that expected if only direct effects are considered. He further argued that results of press experiments may often be inconclusive with respect to revealing indirect effects: influences of both direct and indirect effects are intermingled, experiments are often too short to detect indirect effects, and experimentation is not generally systematic and exhaustive enough to reveal community dynamics. Strictly speaking, manipulation of every species in a community is necessary to quantify community dynamics. Realistically, however, the feasibility of gaining such knowledge is quite low.

Theoretical studies thus suggest that when indirect effects are considered, prediction of the effect of a particular type of interaction on community structure may be difficult. Empirical studies so far have done little to alter this view. Although some outstanding experimental work has been done in a variety of systems, most empirical research is still in early stages of documentation and discovery. Thus, for instance, we have little knowledge of either the frequency or importance of indirect effects in real communities (e.g., Strauss 1991).

Determining the patterns of occurrence of indirect effects, and particularly their importance relative to that of direct effects, is of major ecological interest (e.g., Pennings 1994). From both a theoretical and a management standpoint, we face two extreme scenarios. In the first, more desirable case, the occurrence and relative importance of indirect effects in communities will be predictable to the extent that much of the dynamics of a novel or little studied community can be understood without having to perform intensive field experiments. Under this scenario, reasonably accurate forecasts of the outcome of natural perturbations or of proposals to manage or exploit some or all of the community would be feasible. In the second, less desirable instance, little to no prediction will be possible even for systems whose natural history is well studied, and the relative importance of direct and indirect effects will have to be determined case by case using intensive field manipulations. Under this scenario, forecasting would be useless, and the role of ecology in adjusting to impending perturbations such as those envisioned under global change scenarios would be reduced.

Reality undoubtedly lies somewhere between these extremes. At present, however, our state of knowledge, both of theoretical and empirical research, is insufficient to allow even preliminary judgments regarding where reality lies on a continuum between these ex-

tremes. The lack of specific predictions on where in the food web, and under what environmental conditions, indirect interactions will be important suggests that one avenue of further progress in this area may involve a search for patterns in sets of interacting species in systems that already have been subjected to intensive investigation. A first step in this direction has been taken by Schoener (1993), who attempted to quantify the relative importances of direct and indirect effect in six experimental studies of community regulation in terrestrial and aquatic habitats. After developing a protocol enabling comparisons among these disparate communities, he concluded that direct effects were usually greater in magnitude and less variable than were indirect effects and that short-chain indirect effects were stronger than long-chain effects. Similar patterns seemed apparent in a larger but less intensive survey, suggesting real systems may exhibit a simpler form of indirect effect structure and dynamics than expected on the basis of theory.

Prompted by the theoretical conclusions noted above (and independently of Schoener's [1993] analysis), here I present an analysis that takes advantage of the substantial body of knowledge aquatic ecologists have accumulated on strong direct interactions in communities and their indirect effects. In particular, detailed experimental studies have been performed in a variety of marine benthic communities, and the level of both natural history knowledge and mechanistic understanding of the causes of change in community structure in these habitats is particularly high. It thus seemed appropriate to examine this body of knowledge for insight into the importance and patterns of occurrence of indirect effects in natural communities.

My aims in this paper are to survey experimentally evaluated marine intertidal food webs with the intentions of (1) identifying the patterns of indirect interactions and (2) suggesting methods of determining their importance. I will attempt to answer several questions: Do indirect effects vary with the number of species in the web? With trophic structure? With the trophic status of the affected organism(s)? Do the types or number of indirect effects vary if direct interactions are within vs. between trophic level? How should importance be defined? How does one detect and evaluate the relative importance of indirect effects? What is the feasibility of determining the importance of indirect effects? How important are indirect vs. direct effects, and to what extent can their relative importances be predicted?

I quantified the patterns of indirect effects observed in a set of rocky intertidal interaction webs (sensu Menge and Sutherland 1987) and examined their importance in determining community structure. Below, I first define direct effects, indirect effects, and interaction webs. Second, I describe the data set, explain my protocol in analyzing patterns of indirect effects, consider potential artifacts, and describe approaches to quantifying the importance of indirect effects. Third, I

examine overall patterns of indirect effects in relation to aspects of interaction web structure, such as species number and number of direct effects. Among other things, this analysis indicates that, with increasing web size (species number), numbers of both strong interactions and indirect effects per species increase. Fourth, I examine patterns of occurrence of "classic" models of indirect effects, as well as of "expanded definition" and new types of indirect effects. Keystone predation and apparent competition were the most frequent types while exploitation competition was the least frequent of nine types of indirect effects. Finally, I present two methods of analysis of the importance of indirect effects. Both suggest that indirect effects account for  $\approx 40\%$  of the change in community structure resulting from experimental manipulations.

## DEFINITIONS

### *Direct effects*

Direct interactions can be classified according to the sign of their effects on each interactor (e.g., May 1973). For instance, for interactors A and B, a + - interaction (here termed "predation" [see Lubchenco 1979], a general term that includes carnivory, herbivory, and parasitism) involves A having a negative effect on B and B having a positive effect on A. Interference competition is a - - interaction, in which A and B have direct, mutually negative effects on each other. In theory, all possible combinations of +, -, and 0 (neutral) effects can occur in pairwise interactions (May 1973).

Field experiments do not always document reciprocal effects. For example, studies of predation may document the negative effect of a predator on its prey, but usually the positive effect of a prey on its predator is assumed. This assumption may often be appropriate, but it is conceivable that a predator can have a strong negative effect on a prey that contributes little to its overall food intake (Abrams 1992). Similarly, interference competition is generally asymmetric (i.e., stronger in one direction than another; Schoener 1983), and reciprocal effects are not always demonstrated experimentally. For these reasons, and because single indirect effects result from a unidirectional sequence or chain of direct effects, I treat reciprocal effects separately. Thus, reciprocal effects in a predator-prey interaction (+ -) are food (+) and predation (-). Interference competition effects (- -) may be either interference competition (-) and interference competition (-), or, if the reverse effect is 0 or not known or easily inferred, simply interference competition (-) with no reciprocal effect.

The most common direct effects observed in the webs described below thus included (Table 1):

**Predation** (a trophic interaction, between levels; coded as "p"), and

**Interference competition** (a nontrophic interaction, within levels; coded as "c"), both defined as above.

TABLE 1. List of direct interactions involved in sequences leading to indirect effects in 23 rocky intertidal interaction webs. Letters in parentheses are codes used in later tables and in the text.

Direction	Negative interactions		Positive interactions	
	Trophic	Nontrophic	Trophic	Nontrophic
Vertical				
High to low trophic levels	Predation (p)	Inhibit recruitment (ir)	...	...
Low to high trophic levels	...	Inhibit recruitment (ir)	Food (f)	Enhance recruitment (er)
	...	Inhibit feeding (if)	...	Provide habitat or shelter (hs)
Horizontal	...	Interference competition (c)	...	Enhance recruitment (er)
		Inhibit recruitment (ir)		Provide habitat or shelter (hs)

These are the most intensively studied direct interactions (e.g., Connell 1983, Schoener 1983, Sih et al. 1985), and it is reasonable to expect that many if not most indirect effects will involve these interactions.

Other types of interactions exist, of course, and one interesting result of my analysis is the relatively high frequency of these less-studied, "nontraditional" types of interactions. As shown in Table 1, all such interactions are nontrophic effects but can occur both between trophic levels as well as within levels. Included are:

**Inhibition of recruitment** ("ir," a negative effect), an established occupant of a habitat, whether mobile or sessile, reduces the rate of successful invasion of the habitat by recruiting stages of another species. For example, limpets can inhibit recruitment of barnacles by "bulldozing," or pushing recent settlers off the rock (Dayton 1971). This interaction is regarded as passive, distinguishing it from interference competition, which involves directed aggression or overgrowth. I use "recruitment inhibition" rather than "preemptive competition," which I consider a more specific form of passive inhibition resulting when a sessile species displaces other sessile species by colonizing, establishing, and monopolizing space before other colonists can arrive.

**Inhibition of feeding** ("if," a negative effect), an interactor, whether mobile or sessile, reduces the feeding activity of another species, usually mobile. For example, adult barnacles can reduce the foraging success of herbivores such as limpets or chitons by presenting the forager with rugged terrain upon which it is difficult to crawl and feed (van Tamelen 1987, Farrell 1991). This is an interaction between established individuals.

**Enhancement of recruitment** ("er," a positive effect), a prior occupant of a habitat, whether mobile or sessile, increases the rate of successful invasion of the habitats by offering favored attachment sites or otherwise raising the probability of colonization. For example, barnacles can enhance the recruitment of mussels, apparently by providing interstices between the barnacles to which mussels either prefer to settle or in which they experience reduced early mortality (Menge 1976). Like recruitment inhibition, this is an interaction

between juvenile colonizing stages and established individuals.

**Provision of habitat or shelter** ("hs," a positive effect), an organism increases the survival of associates, or attracts migrants to itself, because it offers a more attractive microhabitat than exists away from the organism. For example, seaweeds provide a cool, dark, moist habitat for limpets and other organisms (Dethier and Duggins 1984). This is an interaction between established species.

**Mutualism** (+ +) and **commensalism** (0 +) are not listed as direct effects for two reasons. First, direct mutualism was not reported as a direct effect in any of the webs evaluated here. Second, although positive effects were observed, I chose to give these effects more specific names (enhance recruitment, provide habitat or shelter) rather than use the more general term commensalism.

#### *Models of indirect effects*

Prior studies have identified a set of at least seven models of indirect effect sequences (e.g., Kerfoot and Sih 1987, Fairweather 1990; see Fig. 1):

**Keystone predation**, where a predator indirectly increases the abundance of competitors of its prey via consumption of the prey (e.g., Paine 1966, 1969, and many others) was perhaps the earliest interaction identified as having an important indirect effect.

**Tri-trophic interactions**, or an increase in plant abundance caused by the control of herbivores by predator (Hairston et al. 1960), have more recently been labelled **trophic cascades** (Paine 1980, Carpenter et al. 1985), the term used here, and recognized as an important kind of indirect effect (e.g., Strauss 1991).

**Exploitation competition** is a reduction in a consumer resulting from the reduction of its prey by another consumer species. Although a primary focus of ecology for years, exploitation competition was not appreciated as an indirect effect until relatively recently (e.g., Kerfoot and Sih 1987, Strauss 1991).

**Apparent competition**, or reduction of a species resulting from increases in a second species which enhances

MODELS OF INDIRECT EFFECT SEQUENCES

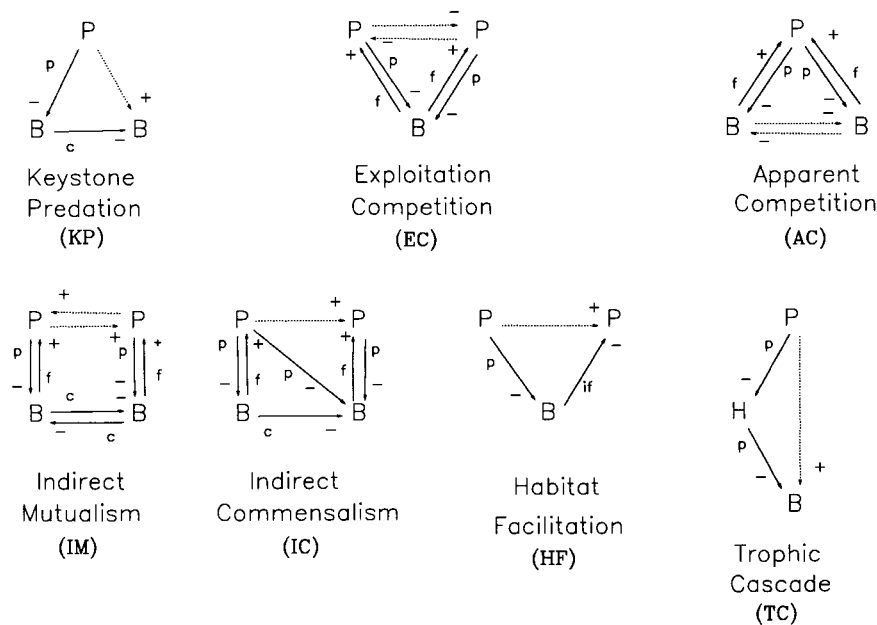


FIG. 1. Models of indirect effect sequences. P, predator; H, herbivore; B, basal species. Solid arrows represent direct effects, dashed arrows represent indirect effects. +, positive effect; -, negative effect. p, predation; c, interference competition; f, provision of food; if, inhibition of feeding.

predation by a shared enemy, was first postulated as an indirect effect by theorists (Levine 1976, Holt 1977) and later demonstrated in nature by Schmitt (1987).

**Indirect mutualism**, or positively correlated changes in two species resulting from predation by each on the competitor of the other's main prey, was evidently first defined by Vandermeer (1980), who suggested it was likely to be important in natural communities. Stimulated by Vandermeer's model, Dethier and Duggins (1984) documented a variant of indirect mutualism in their field studies in a marine plant-herbivore system, which they termed

**Indirect commensalism**, and argued may be more common than indirect mutualism. Indirect commensalism results when one potential indirect mutualist is more generalized in diet and also feeds on the main prey of the other indirect mutualist (Fig. 1). Finally,

**Habitat facilitation** occurs when one organism indirectly improves the habitat of a second by altering the abundance of a third interactor (Fairweather 1990).

These models are undoubtedly not the only types of indirect effects. However, all have been documented in real communities, and several (keystone predation, trophic cascade, exploitation competition) are widely believed to be common. Questions remain regarding the number of other types of indirect effects, their frequency in natural communities, and their importance in structuring communities relative to direct effects.

*The interaction web concept*

As has been stressed earlier (Paine 1980, Menge and Sutherland 1987), an **interaction web** represents that subset of species in a food web that interact strongly through both trophic and nontrophic interactions. Interaction webs are identifiable through the results of manipulations of web components, with the importance of a link ("interaction strength") being a direct reflection of the magnitude and impact on community structure of the experimental result. An interaction web (synonymous with "functional" web; Paine 1980) is one of three types of webs that can be defined in a community.

As defined here, **food webs** include species associated only by consumer-prey linkages, and can be based purely on observation. The linkages in food webs ("connectivity") may include no information about their magnitude or strength. For instance, for prey populations consisting of thousands of individuals, consumption of a single individual by one predator in some observation interval is unlikely to have a proportionately significant impact on the prey, while consumption of thousands of individuals of the same species by a second predator is likely to have a large effect. In food webs, because links are usually unweighted, both predators would be considered equivalent.

Like food webs, **energy-flow webs** are based on description, with links representing the magnitude of en-

TABLE 2. Summary of interaction web statistics by web number. Component species include "trophic" plus biological species, where trophic species are aggregates of two or more ecologically equivalent biological species ("biospecies"); level number is the longest chain of vertical interactions possible in a web; omnivores are either component species consuming both

Characteristic	Web number								
	1	2	3	4	5	6	7	8	9
Component species number	3	3	4	4	4	5	6	8	8
Level number	1	2	2	3	3	3	3	3	2
Prop. omnivores (animal/plant)	0	0	0	0	0	0	0	0	0
Prop. omnivores (food chain)	0	0	0	0	0	0	0	0.13	0
Prop. predators	0	0	0	0.25	0.25	0.2	0.17	0.13	0.13
Prop. herbivores	0	0.33	0.25	0.25	0.25	0.4	0.17	0.38	0
Prop. basal species	1.0	0.67	0.75	0.5	0.5	0.4	0.67	0.5	0.88
Prop. biospecies	0.67	0.67	0.5	0.75	1.0	0.8	0.5	0.75	1.0
Prop. manipulated	0.33	0.33	0.5	0.25	1.0	0.6	0.67	0.75	0.13
Interaction connectance	0.67	0.33	0.42	0.42	0.42	0.2	0.3	0.46	0.39
Total connectance	0.67	0.5	0.58	0.58	0.58	0.35	0.37	0.64	0.45

ergy, biomass, or nutrients moving between web components. Such fluxes are important currencies of ecosystem dynamics and can thus provide a measure of importance, but often correspond poorly with interaction strength (Paine 1980). Hence, energy-flow webs are intermediate between food webs and interaction webs with respect to community dynamics.

Despite these seemingly important ecological distinctions, Pimm (1991:364) recently criticized the distinction between food and interaction webs, arguing that the food web definition can be stretched to include interactions other than predation, thereby avoiding "inventing a piece of jargon such as 'interaction webs'." Pimm (1991) also implicitly includes interaction strength in his use of "food web," although weak and strong links are not distinguished in food web analyses.

I argue that, contrary to Pimm's assertion, use of the term food web to refer to both descriptive and experimentally defined webs effectively equates community dynamics to community structure, thereby obscuring important ecological distinctions. Thus, the interaction webs analyzed in this paper included only those species shown to interact strongly in experimental analyses of community regulation. Species whose interactions were statistically and/or ecologically insignificant were omitted from analysis.

#### METHODS

##### *Rocky intertidal interaction webs: assembly*

I assembled a collection of 23 interaction webs from the literature, in some cases with additional input from the authors, and from my own work. To be included in the analysis, studies had to be experimental, had to have quantified responses to manipulation at the community or subweb levels of organization, and had to include sufficient natural history information to permit interpretation of whether effects were direct or indirect. In only one case were all species in the interaction web manipulated, and in no cases were all species in the community or subweb manipulated. Most workers focused on macrofauna and macroflora, so no study pre-

sented data on roles or responses of meso- or micro-organisms. All investigators assumed such very small organisms were present in all treatments, and none reported evidence of differential responses of such groups to manipulations. Of course, this does not mean small organisms were unimportant, just that they were largely unstudied in the context of community regulation. Experimental approaches were either removal/additions involving no artificial devices or enclosure/enclosures involving barriers (mesh cages, roofs, walls, etc.). In my judgment, all studies were controlled adequately for experimental treatments.

For the purposes of this paper, searches for new webs to add to the set ceased in December 1992. Each web is listed by number, in order of number of species in Appendix 1. For each web, I list the geographic location of the study, the tidal level on the shore (high, mid, low), the degree of exposure to wave forces (exposed, intermediate, protected), and the sources used to construct the web. As explained below, steps in the analysis included (1) determining the direct interaction matrix, (2) summarizing web statistics, (3) listing web components, and (4) evaluating indirect effects. This latter evaluation consisted of determining all indirect effect sequences or chains, assigning codes to each (numeric, interaction, sign of effect, and type of interaction), and counting the number of types, sequences/type, and actual indirect effects.

The web summary (Table 2) lists web statistics. Web components ("species") include trophic species, where a trophic species is a set of two or more species considered to be ecologically equivalent (Schoener 1989, Cohen et al. 1993), and biological species. I made an effort to resolve all components to biological species to the fullest extent possible, but all but two studies included one or more trophic species. For example, because encrusting coralline algae are difficult to distinguish, most ecologists have categorized what are undoubtedly several species (e.g., Steneck 1986, Steneck and Paine 1986) into a single ecological category. Algae are treated thus most often, but other taxonomically

animals and plants (animal/plant), or feeding on more than one level (food chain); basal species are sessile animals plus plants; prop. manipulated is the proportion of component species manipulated in experiments forming the basis of the webs; and interactive and total connectances are as defined in *Methods: Rocky intertidal interaction webs: assembly*.

Web number														
10	11	12	13	14	15	16	17	18	19	20	21	22	23	
8	8	9	9	10	10	10	10	12	13	14	18	21	23	
4	2	2	3	2	3	2	3	3	3	3	3	4	3	
0	0	0	0	0	0	0	0	0	0	0	0	0.19	0	
0.25	0	0	0	0	0.1	0	0	0	0	0	0	0.29	0.09	
0.5	0	0	0.11	0	0.1	0.3	0.2	0.17	0.08	0.07	0.11	0.19	0.18	
0.25	0.2	0.22	0.22	0.3	0.2	0	0.1	0.17	0.23	0.14	0.11	0.14	0.18	
0.25	0.8	0.78	0.67	0.7	0.7	0.7	0.7	0.67	0.69	0.79	0.88	0.48	0.64	
0.88	0.25	0.67	0.67	0.5	0.8	0.9	0.6	0.67	0.85	0.71	0.94	0.9	0.73	
0.63	0.38	0.67	0.78	0.4	0.1	0.3	0.7	0.42	0.38	0.57	0.28	0.52	0.43	
0.21	0.38	0.35	0.40	0.17	0.38	0.31	0.39	0.14	0.13	0.27	0.23	0.21	0.18	
0.36	0.50	0.38	0.49	0.21	0.52	0.41	0.47	0.17	0.20	0.31	0.29	0.31	0.26	

difficult groups have also been so categorized. Other statistics listed in Table 2 include the proportions in the web of: predators, omnivores (both consumers of animals and plants [animal/plant omnivory] and consumers feeding on more than one level [food chain omnivory]; Table 2), herbivores, basal species, species which are single biological species ("biospecies"), and species which were manipulated ("manipulated"). Finally, the number of web levels, "interaction" connectance, and "total" connectance are also presented for each web. These statistics were used in analyses of interaction web pattern.

The measures of connectance used here are somewhat different from earlier usage (e.g., Briand 1983, Yodzis 1980, Martinez 1991). Interaction connectance was calculated as  $I/S(S - 1)$ , where  $I$  = interspecific strong interactions including predation, interference competition, inhibition or enhancement of recruitment or feeding, and provision of habitat or shelter; and  $S$  = number of species. Total connectance was calculated as  $(I + F)/S(S - 1)$ , where  $F$  = provision of food. Interaction connectance was calculated largely to devise a measure more comparable to some earlier measures, which did not include energy transfers as a link, and total connectance provided a measure using all links including food. Intraspecific effects were excluded because most studies in the data set did not investigate such interactions.

Earlier connectance measures differed in various ways from these measures. Most importantly, all were calculated for food webs rather than interaction webs. That is, connectance was based on observations of trophic links (most early connectances; "interactive connectance" as used by Martinez [1991]) rather than on experimentally determined strong interactions. Further, other measures of connectance included other types of linkages. "Upper connectance" included interspecific exploitation competition by adding a link each time two consumers shared a prey (Martinez 1991). "Directed connectance" included cannibalism and mutual predation (Martinez 1991). I used the measures defined above rather than these earlier measures because (1)

interaction webs are a subset of food webs, (2) exploitation competition may or may not occur if consumer species share a prey species, i.e., such overlaps may be trivial and cannot be assumed equivalent to a strong interaction, and (3) no marine intertidal study of community regulation has experimentally investigated cannibalism or mutual predation.

In marine benthic communities, the presence of sessile animals produces alternative concepts of "trophic level." If species are categorized strictly by trophic status, the second (herbivore) level should include both mobile grazing and browsing animals such as limpets, chitons, crabs, and sea urchins and sessile filter-feeding animals such as bivalves, barnacles, sponges, and bryozoans. Carnivorous anemones would be placed at the third (carnivore) level (although many species include symbiotic dinoflagellates or zooxanthellae in their tissues and are therefore functionally at least partly "plants"). However, in terms of space use, these groups generally interact somewhat differently. Mobile herbivores are not fixed to the substratum, and generally do not monopolize space (for an exception, see Branch and Griffiths 1988 and webs 14 and 18 in Appendix 1). Sessile animals are fixed to the substratum (and are thus relatively immobile) and have varying abilities to compete for, and monopolize space (e.g., Connell 1961, Paine 1966, Sebens 1976, 1982, Jackson 1979). In this sense, they are like sessile marine plants. For this reason, Pimm (e.g., 1982) termed the bottom "trophic level" the "basal" level, and organisms on this level (filter-feeding or carnivorous sessile animals and macrophytes) were termed "basal species." Here I follow this usage, and use the term "level" to avoid the complications that would result from using the term "trophic level" to refer to these difficult-to-categorize species. Strictly defined, level number for a given web was the number of species in the longest vertical interaction chain in the web.

The 23 webs include 6 from New England (webs 1, 2, 4, 13, 17, 20); 5 from southern California (webs 3, 9, 12, 15, 16); 3 from the Pacific Northwest coast (webs 7, 11, 23); 2 each from the Gulf of Panama (webs 10,

22), Chile (webs 19, 21), and South Africa West Coast (webs 14, 18); and 1 each from the Gulf of California (web 5), Costa Rica (web 6), and Eastern Australia (web 8). Webs from New England and Panama were at least partly based on studies done by J. Lubchenco and me while all other webs were based on studies of other investigators. Some webs, generally the simpler ones, were based on single investigations (e.g., webs 1, 2, 3, 9, 11), while other webs were based on a series of investigations generally produced by a particular laboratory group (e.g., webs 8, 18, 21, 22, 23). Classified by climatic region, 10 webs were from cold temperate regions (all webs from New England, the Pacific Northwest, and one Chilean web), 9 were warm temperate (all webs from southern California and South Africa, a Chilean web, and the Eastern Australia web), 1 (Gulf of California web) was subtropical, and 3 were tropical (Panama and Costa Rica webs).

#### *Analysis of indirect effects*

The existence of ecologically significant indirect effects was, in most cases, as indicated by the results of field manipulations combined with natural history knowledge. Occasionally indirect effects were inferred from repeated direct observations through time of the consequences of a change in abundance of a particular species. For instance, in two webs (4, 6), invasions or migrations of whelks through areas previously unoccupied by these predators triggered a series of changes in abundance of prey and other species (Sutherland 1990; B. Menge and J. Lubchenco, *personal observations*). While whelks were not directly manipulated, other experiments in these systems and natural history knowledge suggested both the structure of the interaction webs characterizing these systems and which effects were indirect.

To analyze for indirect effects, I examined each study for changes resulting from manipulations. A change was defined as ecologically significant if the resulting change was both (1) large and (2) statistically significant. Generally, ecologically significant changes in abundance (percent cover, density) were those  $\geq 10\%$ . While a change of a few percent (e.g.,  $< 10\%$ ) could be statistically significant, it would be too small to be considered ecologically significant unless small changes in several ecologically similar species (e.g., foliose algae, barnacles, etc.) totalled to a large change, and comparable changes did not occur in controls. I reasoned that a change of 71% cover to 75% cover, for example, could be well within the range of normal temporal fluctuation rather than a treatment effect, and was therefore ecologically trivial, particularly if comparable changes occurred in controls. Examples of the magnitude of change are given in Appendix 3.

Once large changes had been determined, I constructed a "Direct Interaction Matrix" for those changes that were unambiguously a result of direct interactions as indicated by the authors of each study or

my own knowledge of the system (Appendix 1). Species were included only if they were involved in a strong interaction. Species were coded as predators (letter code, P<sub>i</sub>; numeric code, 1), herbivores (H<sub>i</sub>; 2), competitively dominant basal (sensu Pimm 1982) species (D<sub>i</sub>; 3), competitively intermediate basal species (I<sub>i</sub>; 4), and competitively subordinate basal species (S<sub>i</sub>; 5), where  $i = 1$  to  $n$  species of that particular type in the web. Species causing direct effects are in columns and species affected are in rows. Interspecific effects are listed by sign and were positive (+) or negative (-). Zeros in the matrix indicate cases either where the nature of the interaction was not directly investigated (most cases) or where no effect was observed in experiments (few cases). Because the distinction between these two types of "zero effects" was often ambiguous, I did not attempt to separate them. Intraspecific effects are listed as "X" if unknown, and are otherwise listed by sign. In a few cases, a species had both positive and negative effects on another; in such cases, both effects are listed (e.g.,  $\pm$ ).

With this matrix, I examined the remaining changes and determined which were indirect results of the direct interactions. Many of these indirect effects were explicitly identified and discussed by the investigators, while others had to be inferred with the aid of natural history information from the particular system, from different but similar systems, and in some cases from my personal knowledge or experience with a system. For instance, changes in seaweed abundance occurring in manipulations of carnivorous seastars or whelks must have been indirect effects, since the predators do not consume plants. In all interpretations I was conservative. Change without either a clear mechanism or a clear sequence of direct effects leading to the change was not included in the analysis. Such instances were rare, however.

At both taxonomic and ecological levels, every community is unique in many respects. While such detail is fascinating, stimulating, and cannot be ignored if true insight into a system is to be gained, detection of pattern requires devising some means of categorizing species and interactions in ways that allow comparisons and analyses that are free of many of the unique characters of each community. Thus, I devised a hierarchical system of classification of species and interactions, which was aimed at allowing the detection of generalities in indirect effects, if indeed they existed.

After all indirect effects had been identified, I constructed "indirect effect sequences" (= Wootton's [1994] interaction chains) for each. Sequences consist of two or more direct effects and one or more indirect effect. For example, in web 3 (Appendix 1), the indirect effect sequence  $H_1 - S_2 - S_1(+)$  is read as "H<sub>1</sub> (a limpet) had a negative direct effect on S<sub>2</sub> (an alga), S<sub>2</sub> had a negative direct effect on S<sub>1</sub> (a barnacle), and H<sub>1</sub> (the limpet) had an indirect positive effect on S<sub>1</sub> (the barnacle). A virtually identical sequence in this web

involved alga  $S_3$  in place of alga  $S_2$  [i.e.,  $H_1 - S_3 - S_1(+)$ ]; such nearly identical indirect effect sequences are listed together [e.g.,  $H_1 - S_{2,3} - S_1(+)$ ] to save space and provide a first step of categorization. Thus, in this case, limpet removal directly increased algal abundance and indirectly decreased barnacle abundance. Conversely, in the presence of the limpet, algae were scarce and barnacles were abundant. In this example the effect of the limpet on barnacles had to be indirect because limpets had no direct effect on barnacles (the matrix entry for the effect of  $H_1$ , the limpet on  $S_1$ , the barnacle is 0).

Each sequence was coded further into "numeric" and "interaction" codes, "effect sequences," and "direct interaction sequences" to ease categorization (Appendix 1). Numeric codes listed each sequence by the number categorizing each species in the sequence. For example, "255" for the example in the previous paragraph indicates a sequence involving a herbivore, a subordinate competitor, and another subordinate competitor. Numeric codes were used in sorting and grouping of sequences.

Interaction codes lump all basal species (letter codes D, I, and S; numeric codes 3, 4, and 5) into a single group coded "B" (for "basal"), and dropped the numeric subscripts linking each letter code to each specific web component. Further, the indirectly affected species were distinguished by underlining and boldface. Thus, interaction codes such as "HB-**B**" are read as "a herbivore directly affected a basal species and indirectly affected another basal species through a direct interaction between the basal species." This is a rather general category of interaction and is simpler than the original indirect effect sequence but lacks potentially important details of the sign of the effects (+, - or *p*, *n* [for *p*ositive and *n*egative]) and the specific interactions involved in the sequence (e.g., predation, competition, inhibition of recruitment, etc.).

To recover these details and permit categorization into specific subtypes of indirect effect, sequences/subtype, and total number of indirect effects, I determined "effect sequences" and "direct interaction sequences" for each indirect effect sequence. Effect sequences list the sign of the direct (by symbol) and indirect effects (by italicized lowercase letter) in the order they occurred in the indirect effect sequence. In our example, "*- - p*" means both the first and second direct effects were negative, and the indirect effect was positive. The direct interaction sequence "*p/ir*" means that the specific interactions, or mechanisms involved in the sequence were predation (*p*) and inhibition of recruitment (*ir*). Together, the interaction code (**HB**), effect sequence (*- - p*), and direct interaction sequence (*p/ir*) uniquely categorize each indirect effect sequence into a particular subtype, where a subtype represents one of several possible variants of a more general "type" of indirect effect (keystone predation, exploitation competition are types; see Fig. 1, Appen-

dix 2, and Table 5 for more complete listing of types). This particular subtype had two sequences [i.e., the two different pathways by which limpets indirectly increased barnacles;  $H_1 - S_{2,3} - S_1(+)$ ] but produced a total of only one indirect effect (the increase in barnacles). As this example demonstrates, in general, species were often indirectly similarly affected by a manipulated species via several different pathways through similar intermediate species in the chain. Hence, the number of indirect effect sequences was greater than the number of indirect effects.

Most indirect effect sequences involved three species but some sequences included >3 components. Again returning to web 3, the second sequence [ $H_1 - S_3 - S_1(+)$  -  $H_1(-)$ ] includes four species, three direct effects, two indirect effects, and three specific interactions. In this sequence, the limpet indirectly reduced its own abundance by directly reducing an alga which in direct interactions reduced barnacles, which in turn directly reduced limpet abundance. Only a single new indirect effect (the reduction in limpet abundance) resulted, however, since the indirect increase in barnacles was recorded in the previous sequence. Finally, for this web, experiments showed that barnacles inhibited feeding (= if) of the limpet, which in turn reduced alga  $S_2$ , so barnacles indirectly increased the abundance of alga  $S_2$ .

One final detail of the protocol was that if a given web component was indirectly affected in two distinct indirect effect sequences of the same subtype but by manipulations of different species, the total number of indirect effects was recorded as two. I reasoned that since different species produced the indirect effect, and thus the effects of each might occur at different times or be of different magnitude, each should be counted separately.

To permit visual, statistical, and graphical examination of these indirect effect patterns, I summarized the data in Appendix 2 by web, subtype, and type of interaction. Interaction sequences were grouped by whether or not they were "vertical" (included links between levels) or "horizontal" (included only links within a level), by the level of the species initiating the sequence (predator, herbivore, or basal species), and by the number of species in the sequence (range, 3-6). Overall, 83 subtypes of interactions were recorded in the 23 webs; 925 specific sequences producing 565 indirect effects were identified, and 22 of 23 webs had indirect effects. Details of the analysis are presented in the *Results*.

#### *Potential artifacts*

As in all such studies, potential artifacts exist that could also affect patterns of indirect effects. Degree of taxonomic resolution, intensity of study, or experiment duration could all vary among webs or with web species richness, leading to false conclusions. For instance, the number or frequency of indirect effects could be

greater (or less) in webs that were taxonomically highly resolved, i.e., webs with a high proportion of biological species vs. trophic species (e.g., Martinez 1991). More intensively studied webs (ones with a high proportion of species manipulated) might also be expected to have a high frequency of indirect effects. Experiments may not have lasted long enough to detect indirect effects.

To check for some of these biases, I examined correlations between aspects of web structure and the proportions of biospecies and of species manipulated (Table 2, Appendix 1). The potential influence of experiment duration was also analyzed in detail, the results of which are presented elsewhere (B. A. Menge, unpublished manuscript). For the purposes of this paper, these latter analyses indicated that indirect effect patterns were not biased by running experiments for insufficient time.

Another possible problem is that I may have misinterpreted or overinterpreted the study. As indicated above, I attempted to be conservative in my interpretations. In addition, in many cases the original investigators either examined my interpretations of their work (e.g., webs 3, 5, 7, 8) or actually provided the web following my protocol (webs 14 and 18). Some webs were based completely or partly on my own work (webs 1, 2, 4, 13, 17, 20, 22), were done in systems with which I was familiar (web 6), or were from work being done simultaneously in a system in which I was working at the time (webs 10 and 23). Several studies were quite explicit in identifying direct and indirect effects (webs 11, 12, 21), or such effects were quite clear from the authors' descriptions (webs 9, 15, 16, 19), and I based my interpretations directly on the authors' findings without additional inference regarding other possible effects.

A unique problem in this data set was encountered in one of the South African webs (web 14). In this community, a major (external) input at the basal level is drift kelp from the subtidal region. This drift is the major source of energy for the dominant grazer *Patella granatina* and is a key element in understanding the dynamics of this particular community (G. M. Branch and R. Bustamante, personal communication). Because it is not a "resident" of the web 14 community, however, drift kelp does not fit easily into my categorization scheme. I have labelled it  $S_6$  in the South Africa sheltered web, but drift kelp is clearly a unique category of basal species.

#### Web definitions

The above analyses yielded information on two features of these webs, species structure and interaction structure. Species structure was defined by the number of species ( $S$ ), levels ( $L$ ), and proportions of predators ( $p_p$ ), herbivores ( $p_h$ ), omnivores ( $p_o$ ), and basal species ( $p_b$ ). Interaction structure was defined by the number of direct interactions or links, indirect effects, indirect effect sequences, subtypes, and types. In some analy-

ses, each of these measures of interaction structure was divided by the number of species to determine if changes in the frequency of each measure was independent of the number of components in webs.

#### Importance of indirect effects

Because the above analyses were done on interaction webs and not food webs, and were thus based primarily on the results of experiments, the frequency of occurrence of particular types of indirect effects should actually reflect the importance of the effects. However, the actual magnitude of the effects on community structure are not likely to be clearly indicated by frequencies of occurrence. Some indirect effects might cancel each other, for example, while others could enhance the effect of another (Yodzis 1988, Pennings 1994). Moreover, the effects of some strong interactions are likely to be greater than others (e.g., Paine 1992). Finally, the effects quantified in the above web analyses are focused on biological or trophic species, and simply counting up the number of species affected by, for example, keystone predation does not provide a good measure of the importance of the effect of keystone predation in particular or indirect effects in general.

Two approaches were used to quantify the relative importance of indirect vs. direct effects on community structure. The first involved obtaining an estimate of the total amount of change in community structure by the manipulations in a given community, and determining the proportion of this change that was due to indirect effects. Total change was estimated by adding up the absolute values of the changes in abundance of both sessile and mobile organisms as determined by differences between control and experimental treatments. For example, in the low intertidal zone of New England sites, predator exclusions led to increased cover of barnacles and mussels and decreased cover of algae while little change occurred in controls (Lubchenco and Menge 1978). Total change in these organisms was thus estimated as the absolute value of the total difference between exclusions and controls in cover of barnacles + mussels + algae.

The ceiling of 100% cover can be exceeded when considering cover of seaweeds (secondary or understory, and tertiary or canopy layers; Dayton 1971, Lubchenco et al. 1984). Values exceeding 100% cover were recorded only twice in the 18 webs analyzed, however, and these were only modestly higher than 100% (111 and 125%; Appendix 3). Little bias would be introduced by these values to measures of overall change.

Changes in abundance of mobile organisms were less straightforward because densities are not constrained by upper and lower limits as are sessile organisms (cover cannot be  $<0\%$  and, for primary space at least, cannot be  $>100\%$ ). To standardize densities of mobile organisms, I calculated change in manipulations as the percent above or below the maximum density recorded in control treatments. Maximum rather than mean den-

sity was used to reduce the influence of sometimes very large percent changes that resulted in using means. In other words, if the mean density was a relatively small number (e.g., 0.2 individual/m<sup>2</sup>) and treatment densities increased by orders of magnitude (e.g., 2.0 individuals/m<sup>2</sup>), then very large percent changes could result from what were often relatively small absolute changes. Use of maximum densities reduced the magnitudes of such unduly large influences. This was still not an ideal measure, because values below the maximum can =100% while those above the maximum could be >100%. This was not a common occurrence, however, so this aspect of the protocol probably introduced little bias.

Nineteen (of 23) webs were included in the analysis of magnitude of change. Indirect effects in webs 2 and 4 were based partly on observations rather than controlled experiments, so direct estimates of the magnitude of change resulting from manipulation were not available from these webs for this analysis. Webs 14 and 18, from South African shores, which were kindly provided by G. M. Branch and R. Bustamante (*personal communication*), were based in part on unpublished results and did not include magnitudes of change resulting from manipulations.

Excepting the estimates of percent change for density data discussed above, data resulting from this analysis were based primarily on differences between mean values because these were the typical form of the published results. Moreover, measures of variance were sometimes either not presented, or were not presented in a usable form. As a result, no estimates of variance could be made, and the data presented below and any conclusions advanced must be regarded with caution.

A second method of estimating the importance of indirect effects used analysis of variance techniques to analyze results of factorial design studies (ANOVA, multivariate ANOVA). Ideally, such a design would involve simultaneous manipulation of all important interactors in a web. Practically, this approach is severely constrained: simultaneous manipulations of webs with >5 species would in most systems constitute an immense effort and would be impractical. Strict application of this method is thus likely to be infrequent, although the general attributes of such an approach might be retained using less restrictive approaches. For example, one alternative might involve obtaining estimates of variation due to direct and indirect effects using fractional factorial designs. As another alternative, serially executed factorial designs involving subwebs of 2–5 species in interaction webs consisting of >5 species could be employed. Both of these approaches are likely to provide underestimates of indirect effects, since if there are more species than treatments, some indirect effects might be masked by reciprocal changes within the lumped categories.

This approach assumes that variation due to direct effects is estimated by the “main effects” in an ANO-

VA, and that variation due to indirect effects is estimated by statistical interaction terms (e.g., Worthen and Moore 1991). Thus, a significant interaction implies that a substantial amount of variation in the species affected (dependent variables) results from synergisms or antagonisms between the main effects included in the interaction term in question. Use of MANOVA to analyze the simultaneous response of species in the community (dependent variables) to the factors manipulated (independent variables) captures the total response of the community to the manipulations. An orthogonal design, in which each independent variable (= main effect) is manipulated with respect to all the others allows the partitioning of total variance into those proportions due to direct effects (main effects) and indirect effects (interaction terms).

#### *Statistical analysis*

Pearson product-moment correlations were used to suggest the degree of association between web structure and indirect effect structure. Correlations that appeared ecologically meaningful were analyzed further using regression techniques. Because these statistical methods are univariate, involving pairwise associations between single variables, while many statistical associations involved simultaneous changes of multiple variables, multivariate statistical techniques were also employed (Dillon and Goldstein 1984). Specifically, canonical correlation analysis and multivariate ANOVA were used to explore the correlation patterns between web structure and indirect effect structure in the 23-web sample, and in the New England example estimating the importance of direct vs. indirect effects. All analyses were done on a personal computer using SYSTAT (Wilkinson 1990, 1992).

Assumptions of both univariate and multivariate statistics include (1) samples are taken at random, (2) error terms are independently distributed and (3) are normally distributed, and (4) variances of a set of samples are equal (e.g., Sokal and Rohlf 1981, Dillon and Goldstein 1984). Because percent cover and proportional data tend to have bimodal rather than normal distributions, all such data were transformed with the arcsine transformation prior to analysis (Sokal and Rohlf 1981). Similarly, count data, which are often skewed towards small values, were transformed as  $\ln(x)$ , or if  $x = 0$  in any data set, then the entire set was transformed as  $\ln(x + 1)$ . To determine if errors around the mean were independent and normally distributed, residuals were plotted against estimated values and visually inspected. In multivariate tests, bivariate or multivariate normality (Dillon and Goldstein 1984) was checked by examining plots of residuals for each variate. With analysis of variance, the assumption of homogeneity of variances was tested by (1) plotting studentized residuals against estimated values (Wilkinson 1990) and (2) Cochran's test (Underwood 1981, Winer et al. 1991). With a few exceptions discussed below

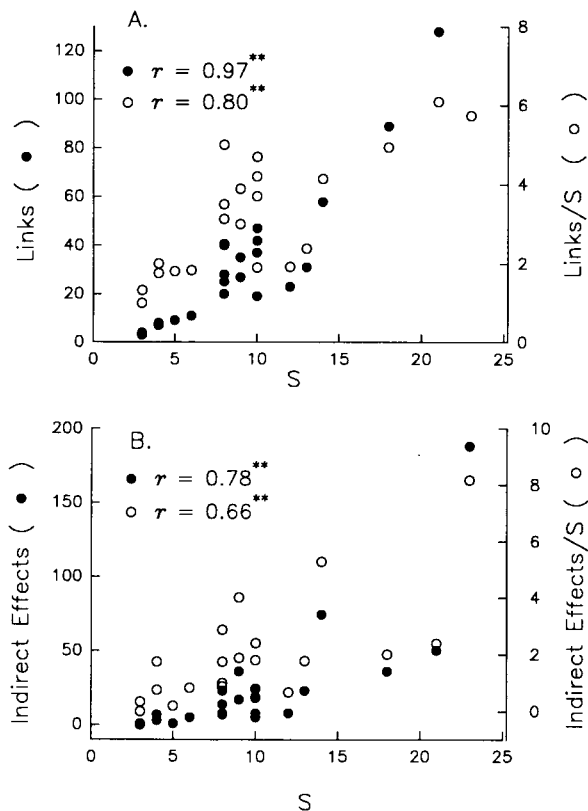


FIG. 2. Web species richness ( $S$ ) vs. (A) direct interactions ("links," ●) and direct interactions per species ("links/ $S$ ," ○); (B) indirect effects (●) and indirect effects/ $S$  (○). Pearson product-moment correlation coefficients ( $r$ ) are shown for each plot in this figure and in Figs. 3 and 5–10. \*\*  $P < 0.01$ ; \*  $P < 0.05$ ; NS,  $P > 0.05$ .

for the relevant cases, most analyses met these assumptions.

## RESULTS

### *Relationships between interaction structure and species number: univariate analyses*

Interaction structure appeared strongly dependent on the number of species in each web. Ln-ln relationships generally provided the best fit between variables, but in some cases linear regressions had higher significance levels. Despite this, however, examination of residuals in linear regressions sometimes demonstrated departure from either normality or independence of error terms, while all assumptions were met using ln-ln regressions. All regressions were therefore performed on ln-transformed data (untransformed data are given in most figures to ease translation to real values).

The number of strong direct interactions (DE) was highly correlated with the number of species ( $= S$ ; Fig. 2A, Table 3), accounting for  $\approx 90\%$  of the variance in DE. Similar relationships were observed between  $S$  and indirect effect structure. Number of indirect effects ( $= IE$ , Fig. 2B), sequences ( $= Q$ ) and subtypes ( $= T$ , Fig. 3A, B) were all significantly correlated with  $S$  (Table 3), accounting for 69, 71, and 31% of the variance, respectively. Thus, with increasing web size, each measure of indirect interaction structure increased exponentially.

These relationships are not particularly surprising. One would expect that with more interacting species the number of direct and indirect effects should increase (e.g., Bender et al. 1984, Martinez 1992). Of

TABLE 3. Regression equations between interaction web measures and potential artifacts, and species richness ( $s$ , shown in italic boldface for clarity) in 23 rocky intertidal food webs. Transformation (transf.) codes: 1, ln-ln; 2, arcsine-ln; 3, none.

Dependent variable	Equation	Transf.	Regression statistics			
			$F$	$P$	$R^2$	df
<b>Indirect effect structure</b>						
Direct interactions (DE)	$DE = 0.66s^{(1.691)}$	1	230.6	$\leq 0.0001$	0.913	1, 21
Indirect effects (IE)	$IE = 0.19s^{(1.929)}$	1	42.4	$\leq 0.0001$	0.663	1, 20
Sequences (Q)	$Q = 0.10s^{(2.34)}$	1	59.8	$\leq 0.0001$	0.746	1, 19
Types of indirect effect (T)	$T = 0.77s^{(0.865)}$	1	5.74	0.026	0.184	1, 20
Direct interactions/species	$DE/S = 0.66s^{(0.691)}$	1	38.5	$< 0.0001$	0.631	1, 21
Indirect effects/species	$IE/S = 0.19s^{(0.930)}$	1	9.86	0.005	0.297	1, 20
Sequences/species	$Q/S = 0.10s^{(1.347)}$	1	19.7	0.0003	0.484	1, 19
Types of indirect effect/species	$T/S = 0.76s^{(0.133)}$	1	0.14	0.72	0.000	1, 20
Sequences/indirect effect (minus web 21)	$Q/IE = 1.57s^{(0.129)}$	1	2.15	0.16	0.054	1, 19
Three-chains observed	$3Ob = 0.84s^{(0.814)}$	1	8.10	0.01	0.244	1, 21
Three-chains observed/possible	$3Ob/Pos = 1.88s^{(0.215)}$	2	36.6	$< 0.0001$	0.640	1, 19
Four-chains observed	$4Ob = 0.41s^{(0.641)}$	1	7.82	0.01	0.237	1, 21
Four-chains observed/possible	$4Ob/Pos = 1.01s^{(0.002)}$	2	0.06	0.81	0.000	1, 17
Total connectance	$TConn = 0.58 - 0.017s$	3	15.7	0.0007	0.400	1, 21
Interaction connectance	$IConn = 0.45 - 0.014s$	3	11.2	0.003	0.318	1, 21
Change due to indirect effects	$Change = 36.8 \pm 0.257s$	3	0.13	0.72	0.000	1, 17
<b>Potential artifacts</b>						
Proportion of biospecies	$pBio = 0.65 + 0.008s$	3	1.16	0.29	0.007	1, 21
Proportion manipulated	$pMan = 0.53 - 0.005s$	3	0.36	0.56	0.000	1, 21
Experiment duration	$Dur = 8.33s^{(0.269)}$	1	1.14	0.31	0.010	1, 12

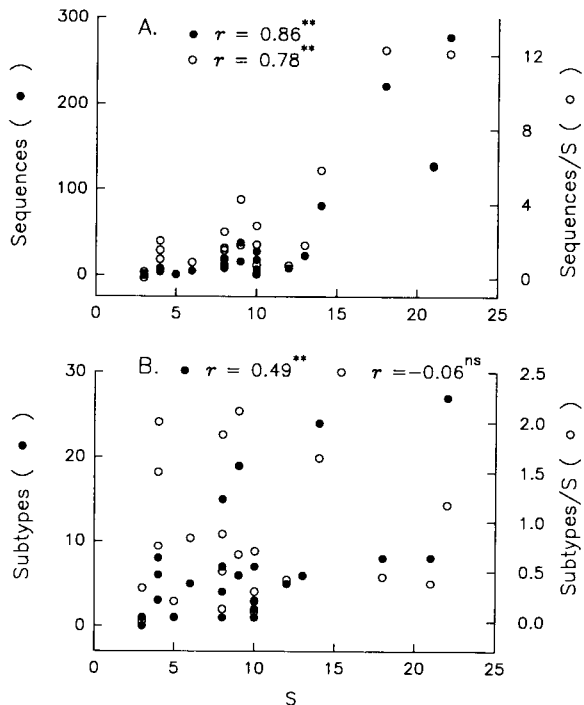


FIG. 3. Web species richness (S) vs. (A) number of distinct sequences leading to indirect effects (●) and sequences/S (○); (B) number of types of indirect effects (●) and types/S (○). See Fig. 2 for explanation of asterisks, ns.

more interest is that when the number of direct and indirect effects and indirect effect sequences (= pathways producing indirect effects) are expressed on a per species basis, positive regressions still result (Table 3). That is, the number of direct interactions per species increases exponentially with an increase in web size (Fig. 2A). Similarly, per species, both the number of indirect effects (Fig. 2B) and the number of pathways producing indirect effects (Fig. 3A) increase with increasing S. Only the number of subtypes of indirect effect per species was independent of interaction web size (Fig. 3B). Thus, with increasing numbers of species in the web, on average (1) each species interacted directly with more species and (2) each species generated an increasing number of indirect effects and indirect effect sequences. Equally interesting is that (3) the number of subtypes of indirect effect per species remained constant across webs of different size. Note that the first of these relationships, an increase in the number of species with which each species interacts with increasing web size, is consistent with that observed by others (e.g., Martinez 1992, Bengtsson et al. 1994), although I analyzed interaction webs and others analyzed food webs. I return to this point in the *Discussion*.

Theory suggests that the frequency of long interaction chains (i.e., sequences with  $>3$  species) should increase with web complexity. In these intertidal webs,

chains of three, four, five, and six species were observed (Appendices 1 and 2). The number of both three-chains and four-chains observed did increase with web size (Fig. 4A, B, Table 3; too few five- and six-chains were observed for analysis). However, the number of possible three- and four-chains both increase exponentially with richness and at a much greater rate than the number observed (Fig. 4A, B). For example, in a 10-species web, a conservative estimate (see Fig. 4 legend) of the number of possible three-, four-, five-, and six-chains is 720, 5040, 30 240, and 151 200, respectively. Thus, proportionately, the number of three- and four-chains observed compared to the number possible decreased sharply with web size (Fig. 4, Table 3). That

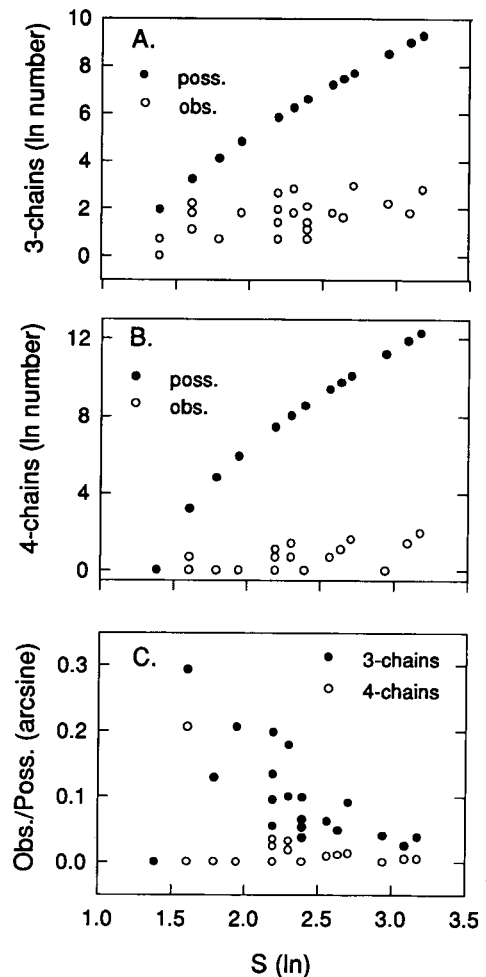


FIG. 4. Web species richness (S) vs. (A) number of observed and possible three-chains, (B) number of observed and possible four-chains, and (C) proportion of three- and four-chains possible that were actually observed. Number (N) of possible chains of length n for a web size (S), was calculated as  $N = S(S - 1)(S - 2) \dots [S - (n - 1)]$ , where it is assumed that links exist in only a single state. Since in fact links can be + or - and can represent at least seven direct interactions (Table 1), this is a conservative estimate of the number possible.

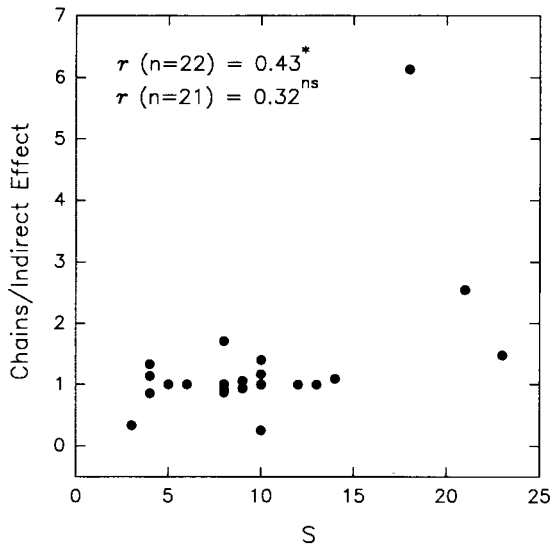


FIG. 5. Number of sequences or chains per indirect effect vs. web species richness ( $S$ ). With the data point from web 21 ( $r$  for  $n = 22$ ), the correlation is significant; without it ( $r$  for  $n = 21$ ) the correlation is not significant. See Fig. 2 for explanation of asterisks, NS.

is, relatively fewer interaction chains of length three and four (or longer) were observed in more complex webs despite the potentially huge numbers possible.

In arguing that diverse food webs are more stable, MacArthur (1955) postulated that more complex webs should have more alternative pathways for energy transfer, and thus that loss of species from a species-rich web should have less effect on the community than loss of a species from a species-poor web. Since links in complex webs may also represent interactions, it is of interest to examine the relationship between the number of pathways per indirect effect vs. web richness. Inclusion of all but web 1 (which had no indirect effects) in a regression analysis of the number of sequences/indirect effect vs.  $S$  suggests these variables are significantly positively related ( $P = 0.047$ ). However, web 21 from central Chile, which had an unusual number of sequences per IE, represented an extreme outlier in the analysis (Fig. 5), and its removal produced an insignificant regression (Table 3;  $P = 0.16$ ). The unusual value for web 21 resulted from an unusually high number of chains involving a highly diverse group of foliose algae, all of which directly or indirectly affected a small number of target species, generating many pathways for relatively few indirect effects. This result may be a consequence of a high level of resolution, but may also be an artifact (e.g., from my mistakenly inferring in analyzing this study that species were strong interactors when they were actually weak interactors).

Assuming that this data point is anomalous, the number of sequences per IE averages ( $\pm 1$  SE) slightly above one ( $1.13 \pm 0.09$ ,  $n = 21$ ) and evidently does not vary with species richness (Fig. 5). In this data set at least, there is little evidence that there are more

alternative pathways leading to indirect effects with increasing web size.

#### Evaluation of possible artifacts

Such patterns could result from several possible artifacts, such as variation in the proportion of species manipulated in studies of each web, in the proportion of web components that were biological species vs. trophic species, or experiment duration (e.g., Bender et al. 1984). For instance, the fraction of web components manipulated could have increased with  $S$ , resulting in the observed increase in strong interactions and indirect effects. Alternatively, the fraction of biospecies may have increased with web size and produced a spurious increase in interaction structure complexity. For example, if more resolved webs (i.e., webs including a higher proportion of biospecies) yield more links per species, as found by Martinez (1991) for Little Rock Lake, Wisconsin, then we might expect increases in the interaction complexity in webs with higher proportions of biospecies.

Neither taxonomic resolution nor intensity of investigation underlies the relationships described in the previous section. Although the proportion of biospecies increased with web size (Fig. 6A;  $r = 0.23$ ), the slope

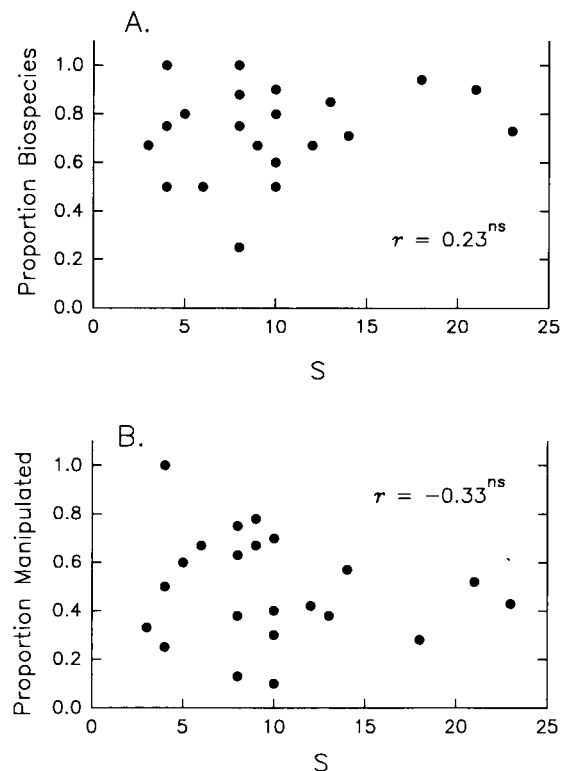


FIG. 6. Web species richness ( $S$ ) vs. (A) proportion of the species per web that were biological species (as opposed to "trophic" species); (B) proportion of the species per web that were manipulated in field experiments. See Fig. 2 for explanation of asterisks, NS.

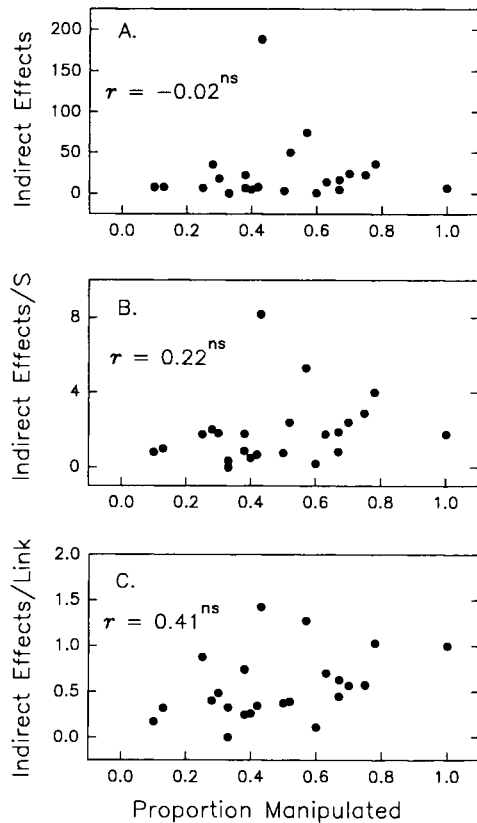


FIG. 7. Proportion of species manipulated vs. (A) number of indirect effects, (B) number of indirect effects/S, and (C) number of indirect effects/direct interaction. S = web species richness. See Fig. 2 for explanation of NS.

of this relationship was not significantly different from 0 (Table 3,  $P = 0.29$ ). The proportion of species manipulated actually decreased with S (Fig. 6B;  $r = -0.33$ ), but again, the slope was indistinguishable from 0 (Table 3,  $P = 0.56$ ). Similarly, experiment duration (months; details of analysis to be presented in B. A. Menge, *unpublished manuscript*) was unrelated to S as well (Table 3,  $P = 0.31$ ).

Statistical power of these analyses (the probability of concluding there is no difference when in fact there is a difference), assuming a minimally significant correlation coefficient of 0.413 ( $P = 0.05$ ,  $df = 21$ ; Rohlf and Sokal 1981: Table 25) is 0.502, i.e., not particularly high. However, ecologically, such a low correlation coefficient would generally be regarded as of marginal importance. Assuming a more rigorous stance, i.e., expecting a higher correlation coefficient (0.6 or greater), would provide statistical power of well above 0.8 (e.g.,  $r = 0.618$ ,  $P = 0.001$ ,  $df = 21$ ; power = 0.898). Since most significant correlation coefficients were relatively high (Figs. 2 and 3) and regression analyses indicated the probabilities of most significant regressions were low (generally  $P < 0.01$ ; Table 3), the conclusion that these potential artifacts do not vary with S seems reasonably robust.

Interaction structure also seemed unaffected by these potential artifacts. Number of indirect effects, number of indirect effects/S, and number of indirect effects/link were independent of both the proportion manipulated (Fig. 7) and the proportion of biospecies (Fig. 8). In all cases, assumptions of normal and independent error terms were met. For these webs, at least, indirect effect structure seems unrelated to the intensity of experimentation or the degree of taxonomic resolution.

These data suggest that investigations involving relatively few experiments somehow identified and manipulated the most indirect effect-rich interactions, and that the number of additional indirect effects revealed declined with more experiments per web. Similarly, in this analysis, indirect effect structure seemed unaffected by the extent of variation in degree of resolution of taxa in the webs.

#### *Relationships between interaction structure and other aspects of web structure*

Univariate correlations between indirect effect structure and other measures of web structure such as the

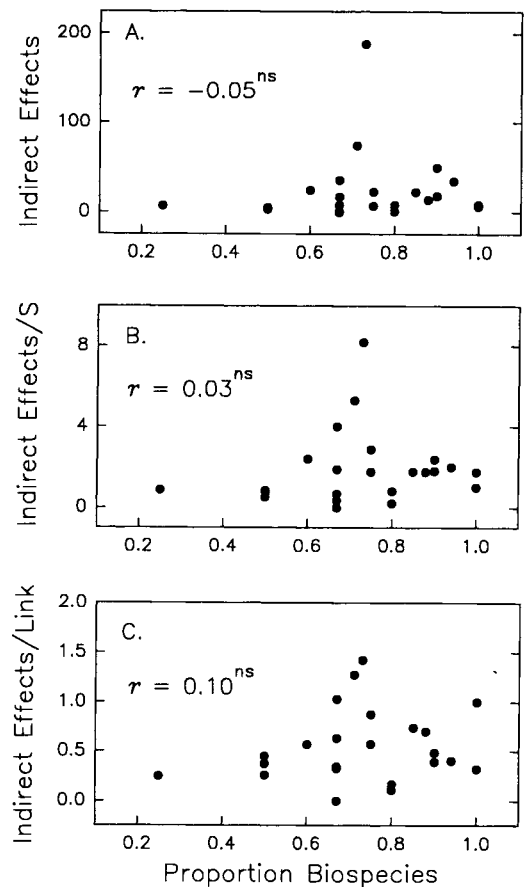


FIG. 8. Proportion of species that were biological species vs. (A) number of indirect effects, (B) number of indirect effects/S, and (C) number of indirect effects/direct interaction. S = web species richness. See Fig. 2 for explanation of NS.

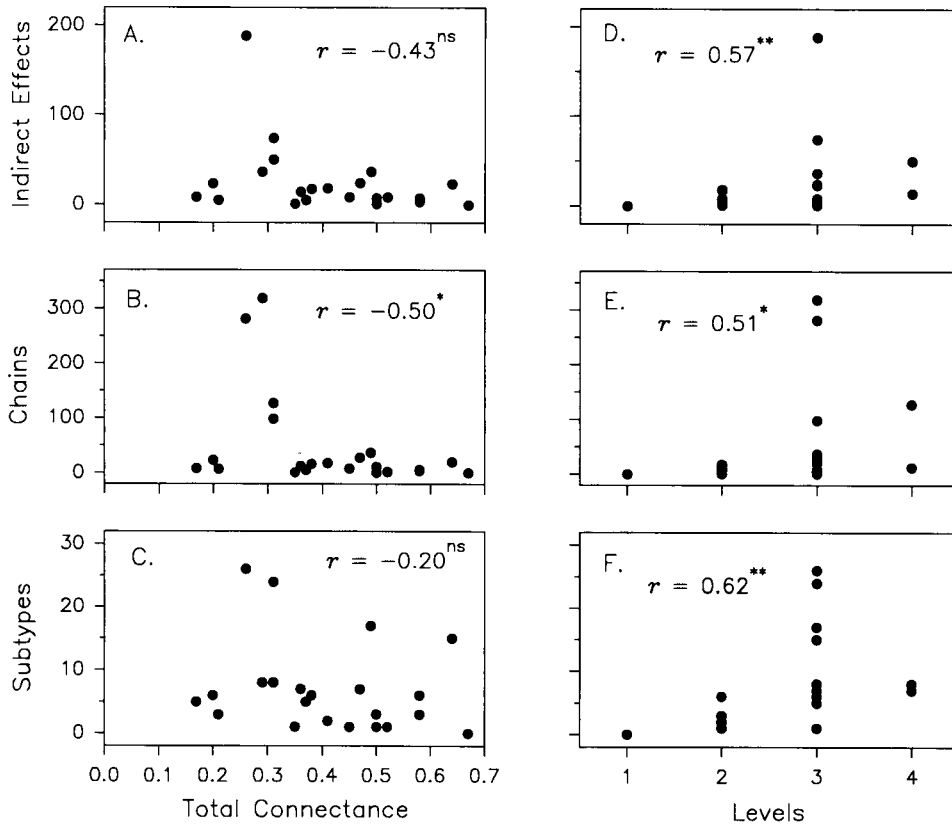


FIG. 9. Correlations between number of indirect effect, chains, and subtypes and total connectance (A, B, and C, respectively) and number of levels (D, E, and F, respectively). See Fig. 2 for explanation of asterisks, ns.

proportions of predators, herbivores, and basal species were mostly weak and nonsignificant ( $P > 0.05$ ). Correlations between total connectance and number of indirect effect chains (= sequences) were significant, but this relation was dependent on two high values (Fig. 9B). Deleting these and reanalyzing yielded a nonsignificant correlation ( $P = 0.12$ ,  $df = 1, 19$ ). Further, neither number

of indirect effects nor subtypes was related to total connectance (Fig. 9A, C). Further examination of relationships between connectance and other web measures, involving only direct links and not indirect effects, are beyond the scope of this paper, although it is worth noting that both measures of connectance vary inversely with  $S$  (Fig. 10, Table 3). This pattern is, of course, consistent with similar relationships observed in collections of food webs (e.g., Martinez 1992).

Correlations between the number of levels and the numbers of indirect effects, indirect effect sequences and subtypes were statistically significant (Fig. 9D–F), suggesting the complexity of interaction structure tends to increase with an increase in the number of levels in the web. Again, however, the scatter in the data, especially for webs of three levels, lends uncertainty to the ecological significance of these relationships.

*Multivariate analysis*

The above analyses are all univariate and are useful both in distinguishing the small set of variables on which to focus from among the larger set of variables, most of which are not correlated, and in evaluating possible artifacts. Like many ecological problems, however, the question being addressed is multivariate,

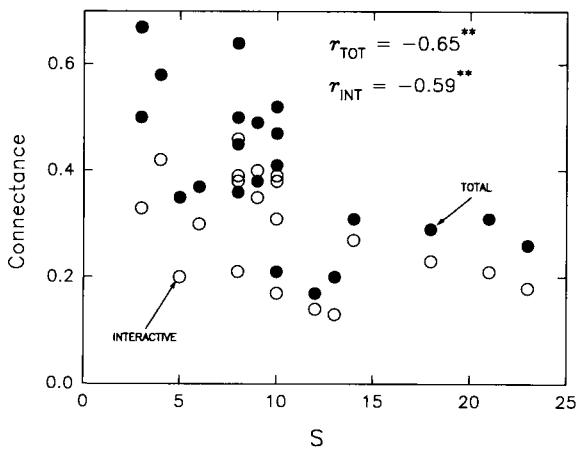


FIG. 10. Correlations between total (●) and interactive (○) connectance and  $S$ . See Fig. 2 for explanation of asterisks.

TABLE 4. Canonical correlation analysis relating indirect effect structure (dependent set of variables; number of indirect effects, number of indirect effect sequences, and number of types of indirect effect) and web structure (independent set of variables; number of trophospecies, number of trophic levels, proportion of herbivores). Numerical data were log transformed and proportional data were arcsine transformed. Boldface values are significant at  $P < 0.05$ .

Variables	Canonical variates					
	1		2		3	
	Loadings	Wts.	Loadings	Wts.	Loadings	Wts.
<i>Y<sub>i</sub></i> Indirect effect structure (criterion variables)						
Number of indirect effects	<b>0.891</b>	1.015	-0.452	0.087	-0.042	-3.229
Number of sequences	<b>0.896</b>	0.579	-0.352	0.874	0.272	2.889
Number of types	0.533	-0.794	<b>-0.834</b>	-1.615	0.145	0.527
Percent of variance	62.7		34.1		3.2	
<i>X<sub>i</sub></i> Web structure (predictor variables)						
Number of species	<b>0.976</b>	0.882	0.161	0.033	0.150	0.963
Number of trophic levels	0.408	0.062	<b>0.845</b>	0.689	-0.346	-1.137
Proportion of herbivores	-0.455	-0.251	<b>0.773</b>	0.548	0.443	1.044
Percent of variance	44.2		44.6		11.3	
Canonical correlations	0.932**		0.597*		0.093 <sup>NS</sup>	
Redundancy coefficients ( $R^2_{v_i}$ )			66.9%			
( $R^2_{x_i}$ )			54.4%			
Multivariate statistics						
Statistic	<i>F</i>		df		<i>P</i>	
Wilks' lambda = 0.08	8.54		9, 41		<0.0001	
Pillai Trace = 1.30	4.84		9, 57		<0.0001	
Hottelling-Lawley = 7.09	12.4		9, 47		<0.0001	
Univariate <i>F</i> tests						
Variable	ss	df	ms	<i>F</i>	<i>P</i>	
<i>Y</i> set						
Number of indirect effects	25.177	3	8.392	20.42	<0.0001	
Error	7.808	19	0.411			
Number of sequences	34.775	3	11.592	18.24	<0.0001	
Error	12.072	19	0.635			
Number of types	8.071	3	2.690	6.21	0.004	
Error	8.325	19	0.433			
<i>X</i> set						
Included in final model						
Number of species	4.717	3	1.572	32.49	<0.0001	
Error	0.920	19	0.048			
Number of levels	0.376	3	0.125	4.23	0.019	
Error	0.562	19	0.030			
Proportion of herbivores	0.102	3	0.034	4.13	0.021	
Error	0.156	19	0.008			
Others tested, not in final model						
Connectance (total)	0.117	3	0.039	1.95	0.156	
Error	0.381	19	0.020			
Proportion of predators	0.181	3	0.060	1.27	0.314	
Error	0.904	19	0.048			
Proportion of omnivores	0.132	3	0.044	1.37	0.281	
Error	0.609	19	0.032			

not univariate. That is, indirect effect structure (the dependent variables) includes not one but three variables per web: the number of indirect effects, the number of interaction pathways or sequences leading to these indirect effects, and the number of specific subtypes of pathway leading to indirect effects. Hence, the problem of their dependence on aspects of web structure is a multivariate, not a univariate problem. We must seek to evaluate the simultaneous relationships among them, not the pairwise relationships (Dillon and Goldstein 1984). As indicated above, the number of

indirect effects can be greater or less than the number of alternative interaction pathways, while the number of subtypes of indirect effect is generally considerably less than either of these measures.

The multivariate analog of univariate correlation analysis is canonical correlation analysis. This method determines the linear association between a set of "predictor" variables ( $X$ ; in this case, web structure) and another set called "criterion" variables ( $Y$ ; in this case, indirect effect structure). Measures of web structure included in the final model were number of species ( $S$ ),

number of levels, and the proportion of herbivores. Analyses including other possible web structure measures such as the proportion of predators, proportion of omnivores, and total connectance indicated these factors contributed insignificantly to variation in indirect effect structure (Table 4).

Canonical correlation analysis identified two statistically significant canonical variates (Table 4). All multivariate statistics were highly significant (Table 4), indicating a strong association between the criterion and predictor variables. Although the assumptions of multivariate normality and independence of error terms cannot be tested directly, residuals of each variate were normally distributed and independent.

The first variate, with a canonical correlation coefficient of 0.932, indicated that the number of indirect effects and the number of sequences jointly depended on the number of species. Canonical loadings (equivalent to simple correlation coefficients; Dillon and Goldstein 1984) for the dependent set (indirect effects and sequences) were both high (0.891 and 0.896, respectively); the only high loading for the independent set in variate 1 was species number (0.976). Hence, as indicated by the univariate analysis, multivariate analysis suggests both indirect effects and sequences increased with increasing species number (Table 4). Estimates of the amount of variation in the criterion and predictor sets of variate 1 can be calculated by squaring the canonical loadings and dividing by the number of variables in each set (Dillon and Goldstein 1984). This analysis indicates that variate 1 accounts for 62.7% of the variability in indirect effect structure and 44.2% of the variability in web structure.

Canonical variate 2, with a canonical correlation coefficient of 0.597, suggested that the number of types of indirect effect (canonical loading of 0.834) was a joint function of the number of trophic levels and the proportion of herbivores (loadings of 0.845 and 0.773, respectively; Table 4). Number of types of indirect effects increased with simultaneous increases in trophic level number and proportion of herbivores (Table 4). Variate two accounts for 34.1% of the variability in indirect effect structure and 44.6% of the variability in web structure. A third canonical variate, with a canonical correlation coefficient of 0.093, was not significant ( $P = 0.69$ ) and contributed little of the variability in either the criterion set (3.2%) or the predictor set (11.3%).

Large and highly significant canonical correlations are possible without explaining much of the overall variation in the dependent and independent sets (Dillon and Goldstein 1984). In this case, calculation of redundancy coefficients, which measure the amount of variance in the  $Y$  set accounted for by the  $X$  set (or vice versa), indicates that these sets explain substantial amounts of the variability in the other; 66.9% of the variance in the  $Y$  set is explained by the  $X$  set, while 54.4% of the variance in the  $X$  set is explained by the  $Y$  set (Table 4).

This analysis thus suggests that, in this set of interaction webs, indirect effect structure is dependent on several aspects of web structure. More indirect effects and more sequences leading to these effects occur with an increase in species number, while more types of indirect effect sequences occur in webs with both more levels and a greater proportion of herbivores. Most of these effects seem sensible: (1) with more species (and more links; Fig. 2A), there should be both more potential "targets" for indirect effects and more alternative pathways for these effects, and (2) with more levels, and more species at intermediate levels (i.e., herbivores), it seems reasonable to expect more types of interactions. It is not clear why the proportion of predators is unrelated to indirect effect structure, however. Although the proportion of predators was usually low (0.07–0.3, when present), so was the proportion of herbivores (0.1–0.38).

#### FREQUENCY OF INDIRECT EFFECTS

As detailed in Appendix 2, 83 subtypes of indirect effect chains were identified in this set of 23 webs. To determine how these 83 subtypes related to the seven types emphasized in the literature (Fig. 1), I further analyzed indirect effect patterns.

First, I diagrammed each subtype of sequence listed in Appendix 2 (Figs. 11–17). I organized the types by category of the species which was manipulated to detect the effect and by the number of species included in the sequence ( $\geq 3$ ). For each type, I list the number of webs in which the type was identified and the number of indirect effects produced by each and by the type of indirect effect.

The majority (412 of 565 or 72.9%) of indirect effects resulted from sequences involving three species (Table 5), but substantial numbers (153, or 27.1%) resulted from sequences involving  $\geq 4$  species. Nearly half (281, or 49.7%) of all indirect effects resulted from manipulations of predators. Manipulations of herbivores produced 16.3% (92) of indirect effects, manipulations of basal species involving consumer levels produced 31.3% (177), and manipulations of basal species involving just basal levels produced 2.7% (15) of indirect effects (Table 5).

The 83 subtypes of interaction chains shown in Figs. 11–17 can be sorted into three major categories, "classic," "expanded-definition," and new types, each of which includes several major types of indirect effect. Classic types of indirect effect (i.e., those shown in Fig. 1) were the most frequent in these webs. Others include both expanded-definition types, ones similar to the classic types but differing in one or more of the direct effects in the sequence, and new, previously unnamed types (Figs. 18 and 19, Tables 5 and 6).

Keystone predation, with 34.7% (including both classic and expanded types) of the total number of indirect effects, was by far the most frequent type of indirect effect observed in these webs, occurring in 19

INDIRECT EFFECTS: PREDATOR MANIPULATIONS – THREE SPECIES

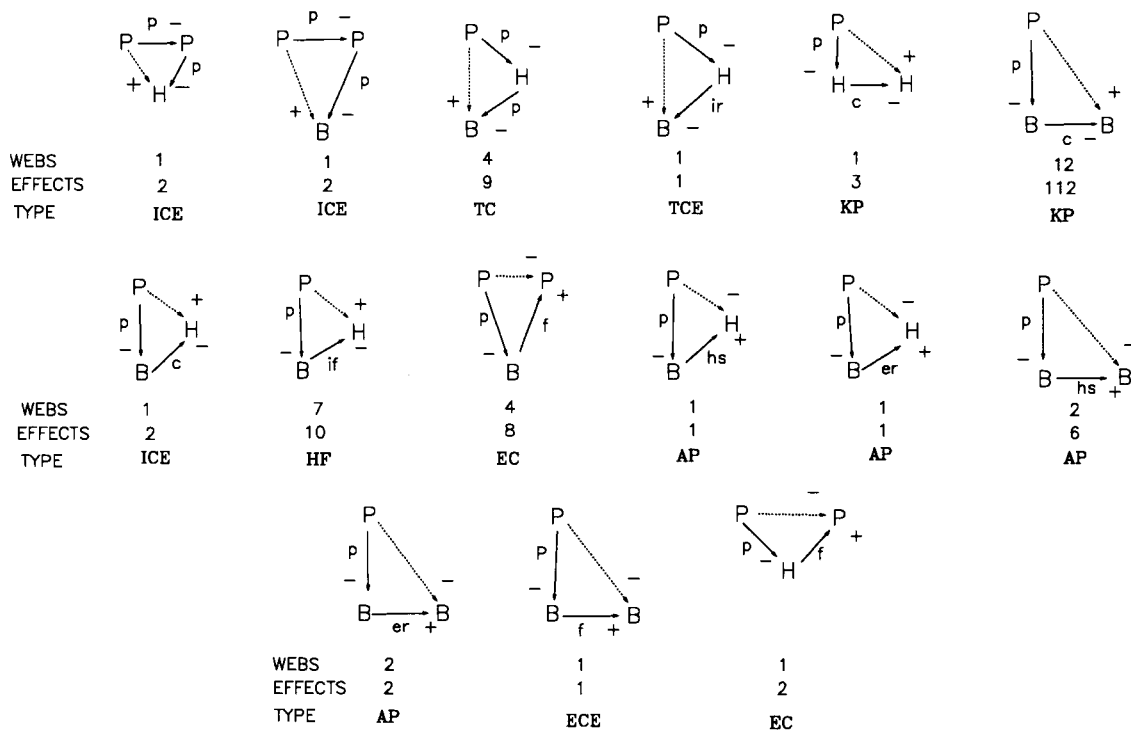


FIG. 11. Indirect interaction sequences involving three species from experiments in which predators were manipulated. See Fig. 1 for code to types of indirect effects; additional codes: ICE, indirect commensalism, expanded; TCE, trophic cascade, expanded; AP, apparent predation; ECE, exploitation competition, expanded. "Webs," number of webs in which the sequence was observed; "effects," number of indirect effects produced by the particular sequence. See Table 1 for code to direct interactions (lowercase letters).

webs (Figs. 11, 12, 14, 15, 18, Table 6). Unexpectedly, apparent competition between basal species, with 25.0% of the total, was the second most common type of interaction and occurred in 14 webs (Figs. 16–18, Table 6). Other classic types were less common. Trophic cascades made up 6.5% of indirect effects and occurred in only five webs (Figs. 11–13, 15, Table 6). Indirect mutualism and indirect commensalism made up 7.1 and 3.2% of the indirect effects, and occurred in 3 and 10 of the webs, respectively (Figs. 11, 15–17, Table 6). Interestingly, exploitation competition was not common. Only 2.8% of indirect effects spread over five webs were of this type (Fig. 18, Table 6).

Although fewer than the classic types, other types of indirect effects were still relatively frequent (Figs. 11–17, 19, Tables 5 and 6). Some of these, the expanded-definition types, are variations on the classic types (and are included in the numbers given above). For example, keystone predation involves a predator indirectly benefitting competitors of one of its main prey by alleviating competition. In the jargon used here, the interaction sequence is p/c, or predation (on the major prey)/competition (between the major prey

and its competitors). As is evident in Figs. 12, 14, and 15, other direct interactions can sometimes produce the same kind of effect produced by either predation or competition, leading to the same effect sequences (– – p) seen in keystone predation. In web 8, for example, predation on a basal species benefitted two other basal species, but the second interaction in the sequence was inhibition of recruitment, not competition (Fig. 12, second diagram in second row; Appendix 2). This indirect effect chain was thus classified as expanded type of keystone predation effect (Table 5). Similarly, all other expanded types were essentially similar to the classic models (Fig. 1) but involved one or more alternative types of direct interactions in the sequence (Fig. 19).

Other types of indirect effects included habitat facilitation (HF; discussed by Fairweather 1990 but not widely appreciated as an indirect effect), "apparent predation" (AP; see Holt 1977), and "indirect defense" (ID). Habitat facilitation of a nonprey species occurs when a predator removes a prey species that, when abundant, has a negative effect on the nonprey species. Seastars facilitate some limpet species, for example, by removing mussels that can inhibit limpet

INDIRECT EFFECTS: PREDATOR MANIPULATIONS – FOUR SPECIES

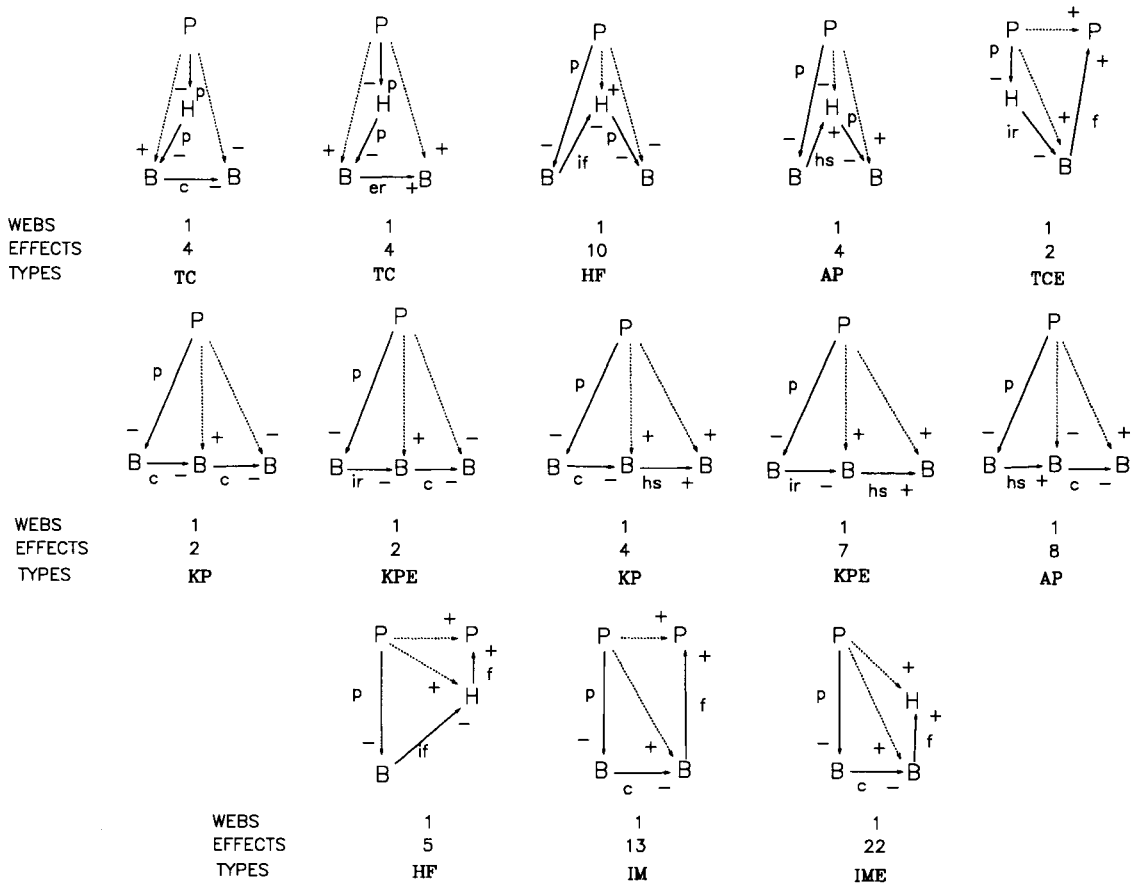


FIG. 12. Indirect effect sequences involving four species from experiments in which predators were manipulated. See legends to Figs. 1 and 11 for codes to types of indirect effect. Additional codes: KPE, keystone predation, expanded; IME, indirect mutualism, expanded. See Table 1 for code to direct interactions (lowercase letters).

foraging (and also crowd out the algal food of the herbivore, e.g., web 23, Appendices 1 and 2). In the presence of seastars, limpets are more abundant on rock surfaces because mussels are kept scarce. Habitat facilitation was relatively common, occurring in seven webs and producing 42 (7.4% of the total) indirect effects (Table 6). This effect resulted most often when predators were manipulated (Fig. 19).

Apparent predation, either (1) the indirect decrease in a nonprey produced by a predator or herbivore or (2) the indirect increase in a predator or herbivore produced by a nonprey, results under several circumstances. In the former instance, a predator or herbivore indirectly harms a nonprey species by reducing a prey species upon which the nonprey depends for habitat or shelter or which enhances recruitment (Figs. 11 and 12). For example, when whelks remove barnacles and thus eliminate shelters for littorine snails, abundance of the snail declines (web 20; Appendix 1). Another example of this type of apparent predation occurs when a prey herbivore increases predator abundance, which in turn reduces abundance of a barnacle prey. Indirectly, the herbivore apparently preys on the

barnacle (web 8; Fig. 14, lower right diagram; Appendices 1 and 2).

The alternative form of apparent predation is exemplified by an increase in a herbivore resulting when one nonprey basal species increases the abundance of a prey basal species via enhancement of recruitment or provision of habitat or shelter (Fig. 16, two lower right diagrams). Thus, for example, a nonprey fucoid alga provided a habitat for ephemeral algae, the major food of littorine snails, and thereby indirectly helped maintain high snail density (e.g., web 13; Appendices 1 and 2).

Indirect defense, the indirect reduction of a predator or herbivore by a nonprey, occurred in two ways (e.g., Fig. 16, middle row, two right diagrams). In one case, a nonprey basal species harmed a prey (via competition or recruitment inhibition), reducing the abundance of the consumer of the prey. For example, a nonprey foliose alga competitively reduced the abundance of ulvoid algae, the primary food of a grapsid crab (e.g., web 12; Appendices 1 and 2). A second form of indirect defense occurred when a prey basal species increased abundance of its predator, which then preyed more

INDIRECT EFFECTS: PREDATOR MANIPULATIONS  
FIVE AND SIX SPECIES

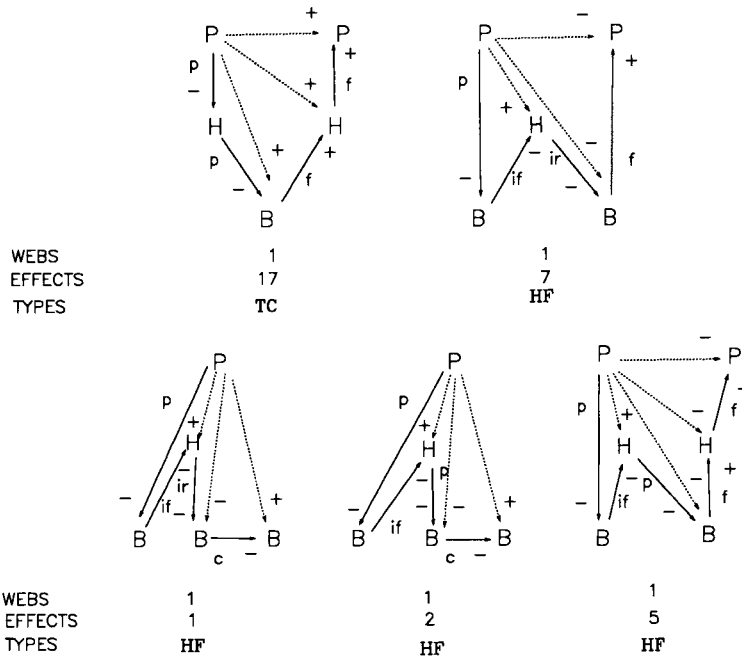


FIG. 13. Indirect effect sequences involving >4 species from experiments in which predators were manipulated. See Fig. 1 for codes to types of indirect effect.

heavily on a mobile prey species. For example, a barnacle indirectly reduced limpet abundance by increasing the abundance of a whelk, which then preyed more heavily on the limpet (e.g., web 8: Appendices 1 and 2). Indirect defense is thus a negative indirect effect of a prey species on a consumer species, while apparent predation is either a negative indirect effect of a consumer species on a prey or a positive effect of a prey on a consumer.

These additional types of indirect effects are collectively relatively common. Indirect defense, with 34 indirect effects (6.0% of the total), occurred in nearly half the webs (Fig. 19, Table 6). Apparent predation also occurred relatively frequently (41 indirect effects, 7.3% of the total, occurring in eight webs) and resulted from manipulations of species at all levels in the web (Fig. 19, Table 6).

The relative frequencies of different types of indirect effects in each web varies among webs (Table 6). Four webs (2, 6, 9, 15) had only one type of indirect effect, while two of these (2 and 6) had just one indirect effect and two (9 and 15) had >1 indirect effect. At the other extreme, one web (23) had eight different types of indirect effect, and five of these were frequent (i.e., proportions  $\geq 0.10$ ; Table 5).

In summary, this analysis suggests that as expected, several well-known types of indirect effect comprise the largest fraction of the total. Keystone

predation in the general sense produces the most indirect effects in the largest number of webs. Apparent competition also appears common and several other types, including previously known (trophic cascade), underappreciated (habitat facilitation), and previously unknown (apparent predation, indirect defense) indirect effects, also occur in rather substantial numbers. Exploitation competition, long a focus of intense ecological interest, was not a common type of indirect effect. The generality of these conclusions will be considered in the *Discussion*.

IMPORTANCE OF INDIRECT EFFECTS

*Magnitude of change: web analysis*

In the set of interaction webs (minus the webs with no estimate of change), the percent total change after manipulations accounted for by indirect effects ranged from 22 to 68% (Appendix 3) and averaged ( $\pm 1$  SE)  $41.6 \pm 3.2\%$  ( $n = 18$  webs) (Fig. 20A). As suggested in Fig. 17A and demonstrated explicitly in Fig. 20B, change magnitude was independent of web size ( $r = -0.12$ ; Fig. 20, Table 3). Plots of residuals showed that assumptions of normality and independence were met. Thus, on average, nearly half the total change resulting from experimental manipulations in these webs was due to indirect effects. Analyses presented elsewhere (B. A. Menge, *unpublished manuscript*) suggest that most experiments in this data set were run long enough

INDIRECT EFFECTS: HERBIVORE MANIPULATIONS – THREE SPECIES

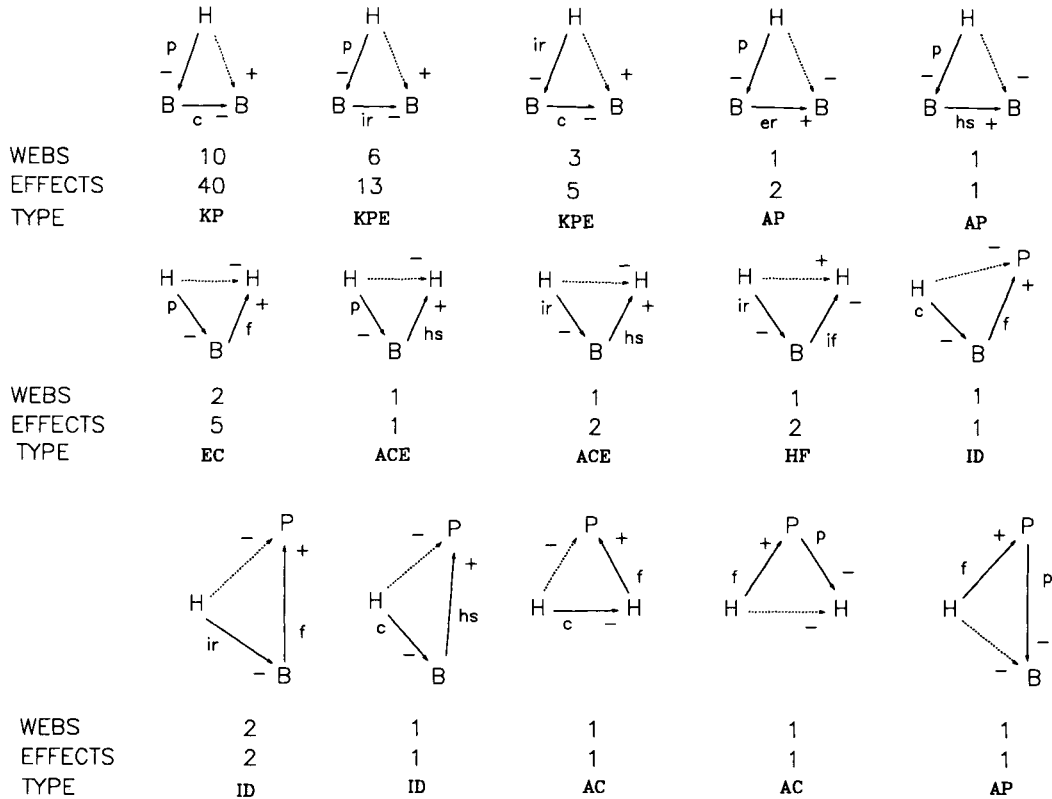


FIG. 14. Indirect effect sequences involving three species from experiments in which herbivores were manipulated. ID, indirect defense; ACE, apparent competition, expanded. See legends to Figs. 1, 11, and 12 for additional codes.

to see most indirect effects that would result from the manipulation and that experiment duration did not vary significantly with web species richness.

Proportion of variance in MANOVA

As an example of this method, I reanalyzed the results of an experiment done on a rocky shore at Grind-

stone Neck, Maine (B. A. Menge 1976, 1991b, unpublished data). The structure of the midzone community at this site was largely dependent on the reduction of barnacles (*Semibalanus balanoides*) and mussels (*Mytilus edulis*) by whelks (*Nucella lapillus*). This indirectly allowed fucoid algae, with associated epiphytes and herbivores, to dominate space on the rock (see

INDIRECT EFFECTS: HERBIVORE MANIPULATIONS – FOUR SPECIES

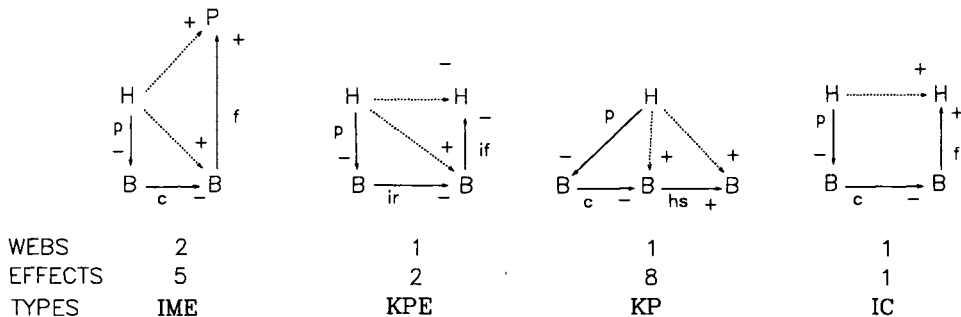


FIG. 15. Indirect effect sequences involving four species from experiments in which herbivores were manipulated. See legends to Figs. 1 and 12 for additional codes.

INDIRECT EFFECTS: BASAL-SPECIES MANIPULATIONS - THREE SPECIES, MULTI-LEVEL

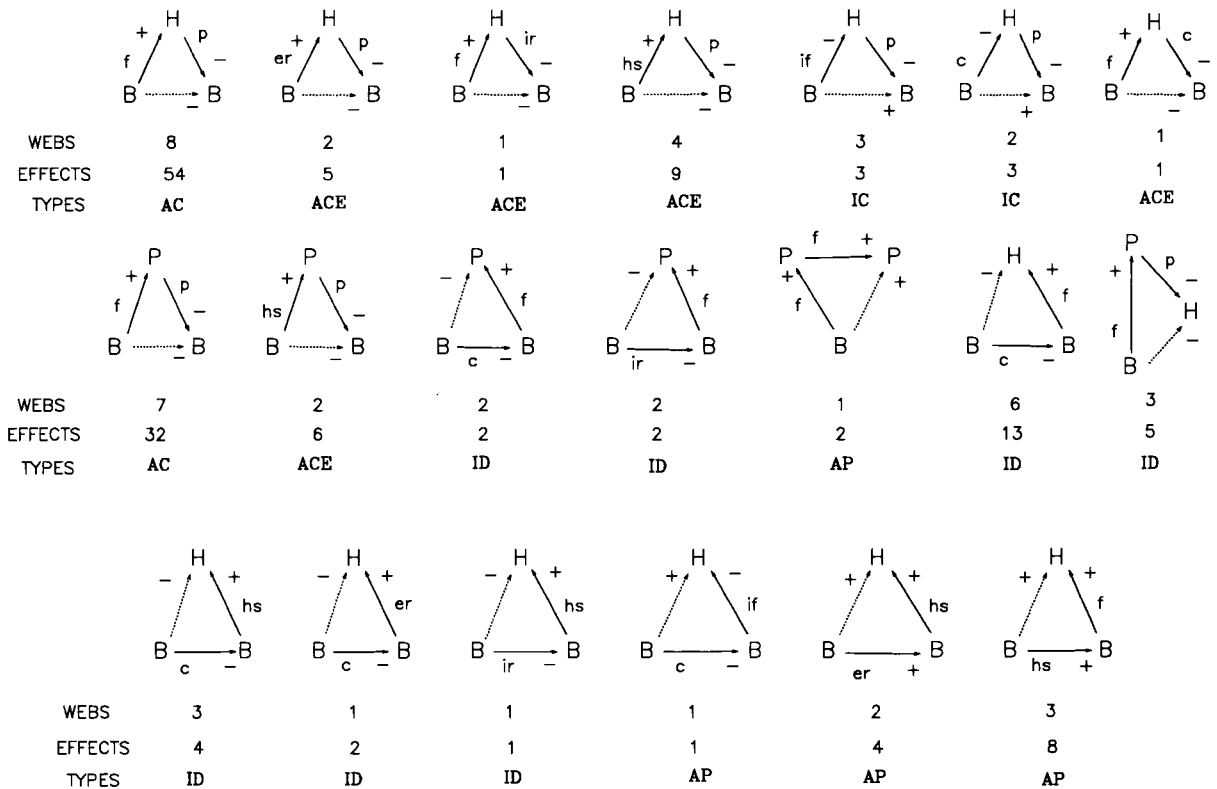


FIG. 16. Indirect effect sequences involving three species and spanning two web levels from experiments in which basal species were manipulated. See legends to Figs. 1, 11, and 14 for additional codes.

Appendix 1, web 13). The furoid canopy was not continuous, however, and large patches of substratum lacked an algal overstory (Menge 1976). Experiments done in these clearings, therefore, involved a very simple interaction subweb including whelks and their two main prey, barnacles and mussels.

These experiments, all conducted on smooth horizontal surfaces, included two treatments: whelks either had complete access to prey (sideless cages = roofs, and open marked plots) or no access to prey (complete cages), and mussels were manually removed or not (Menge 1976). These experiments were repeated annually from 1972 to 1975 during which recruitment of barnacles varied in both space and time, including, in some cases, complete failure to recruit (Menge 1991a). As a consequence of this variation, barnacle abundance was high in some cages and roofs and low in others. Here I treat these natural events (lack of barnacle recruitment vs. "normal" recruitment) as another experimental treatment. By combining the 1972-1975 experiments, the results provide an orthogonal data set: replicates of all combinations of + and - whelks, mussels and barnacles were available for multivariate ANOVA.

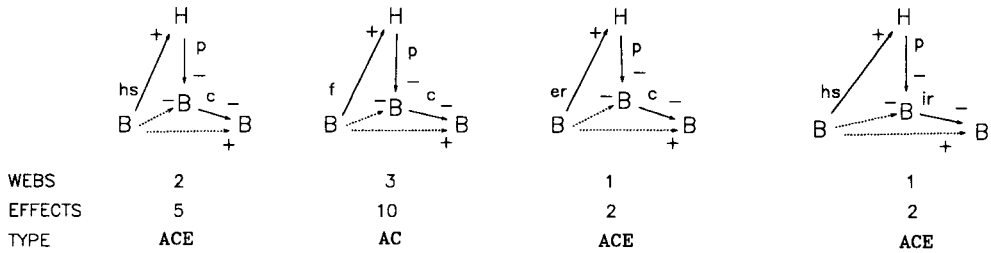
The results of these experiments were expressed as

monthly percent cover of barnacles and mussels (Fig. 21). These prey abundances were therefore the "community response" (= dependent variables) to the presence or absence of the three independent variables, whelks, mussels, and barnacles. Analyses were done on the abundances of prey in October, when the experiments were terminated.

The usual course of events is shown in the upper left panel of Fig. 21. Barnacles settled and temporarily became abundant until whelk predation caused a steady decline in their abundance. Mussels recruited later but, because whelk predation checked their abundance, reached only low cover by the end of the experiment. Removal of mussels (bottom left panel of Fig. 21) had little effect on the pattern of barnacle abundance, except that barnacles were less abundant overall, probably because all whelk predation was concentrated on barnacles in the absence of mussels.

In the absence of predators (Fig. 21 upper row, second panel from right), a similar pattern was seen for barnacles, but mussels invaded and reached nearly 100% cover by October, indicating that whelks controlled mussel abundance. That the interaction between mussels and barnacles represented competitive exclu-

INDIRECT EFFECTS: BASAL-SPECIES MANIPULATIONS  
FOUR SPECIES, MULTI-LEVEL



BASAL LEVEL, THREE & FOUR SPECIES

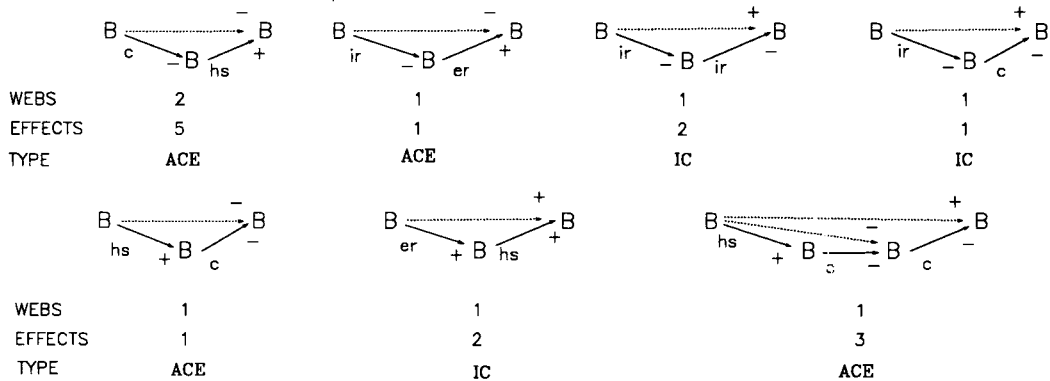


FIG. 17. Indirect effect sequences involving either >4 species and spanning two levels (top), or involving ≥3 species within the basal level (bottom), from experiments in which basal species were manipulated. See legends to Figs. 1 and 14 for additional codes.

sion was indicated by the results of the second panel from the right in the bottom row of Fig. 21: in the absence of both mussels and whelks, barnacles dominated space.

When barnacle recruitment was near zero, the outcome was independent of whelk or mussel abundance (Figs. 21 and 22). The community consisted only of the few barnacle individuals that did recruit and a few hungry whelks. Mussel colonization failed almost completely, because on these smooth surfaces mussels will recruit only if barnacles are present to facilitate mussel recruitment (Menge 1976; see also Petraitis 1990, Menge 1991b, web 13 in Appendix 1). This dependence of mussels on barnacles is not absolute: mussels settled on any surface irregularities, including rough rock surfaces, cracks and crevices, and around algal holdfasts (Menge 1976).

These results indicate that a surprisingly complex interaction occurred among these three species. In fact, the three-way interaction term (*Nucella* × *Semibalanus* × *Mytilus*) was highly significant (Table 7), indicating that the effect of each species depended on whether or not each of the other species was present (Fig. 22). Together, the significant interaction terms (Table 7)

suggest that indirect effects were important in this simple community.

In this analysis, assumptions of normality and independence of error terms were met, but Cochran's test (Winer et al. 1991) suggested variances were unequal. This inequality of variances seemed due to low sample sizes in three treatment combinations (2, 3, and 3; maximum sample size was 15) and the fact that prey abundance was zero in all replicates of several treatment combinations (Fig. 21). Adding "dummy" variance values (of low magnitude) to these combinations did not alter Cochran's test. Underwood (1981) suggests that in such cases, one option is to proceed with the analysis using a more stringent level of significance. Since the *P* values for all tests were extremely low (*P* ≤ 0.0001; Table 7), I proceeded with the analysis anyway, although the conclusions should be regarded with caution.

The indirect effects in this interaction are interpreted as shown in Fig. 23. First, *Nucella* had direct predatory effects on both the barnacle and mussel, but appeared to initially concentrate its efforts on mussels. By overgrowing and smothering barnacles, mussels had a direct negative effect on *Semibalanus*. Thus, as indicated by

TABLE 5. Summary of types of "classic" and new types, or "expanded" definition indirect effects identified in the 23 interaction webs. An entry of "..." indicates categories that are necessarily 0 by the definition of the type of indirect effect. For instance, basal species cannot produce keystone predation indirect effects. Code to subheadings: 3 spp., three-species indirect effect sequences; 4 spp., four-species sequences; 5 spp., five-species sequences; tot., total number of sequences;  $\geq 2$ Levels, sequences including two or more levels; 1Level, sequences entirely on a single level.

Type of indirect effect	Number of:	Group manipulated										
		Predators				Herbivores			Basal species			
		3 spp.	4 spp.	$\geq 5$ spp.	Tot.	3 spp.	4 spp.	Tot.	3 spp.	$\geq 4$ spp.	Tot.	1Level $\geq 3$ spp.
Keystone predation—classic	Webs	13	1	0	13	10	1	10	...	...	...	...
	Effects	115	6	0	121	40	8	48	...	...	...	...
Keystone predation—expanded	Webs	0	2	0	2	8	1	8	...	...	...	...
	Effects	0	9	0	9	17	1	18	...	...	...	...
Trophic cascade—classic	Webs	4	1	1	4	...	...	...	...	...	...	...
	Effects	9	4	17	30	...	...	...	...	...	...	...
Trophic cascade—expanded	Webs	1	2	0	3	...	...	...	...	...	...	...
	Effects	1	6	0	7	...	...	...	...	...	...	...
Exploitation competition—classic	Webs	5	0	0	5	2	0	2	...	...	...	...
	Effects	10	0	0	10	5	0	5	...	...	...	...
Exploitation competition—expanded	Webs	1	0	0	1	0	0	0	...	...	...	...
	Effects	1	0	0	1	0	0	0	...	...	...	...
Apparent competition—classic	Webs	0	0	0	0	1	0	1	11	3	11	...
	Effects	0	0	0	0	1	0	1	86	10	96	...
Apparent competition—expanded	Webs	0	0	0	0	2	0	2	5	2	5	4
	Effects	0	0	0	0	3	0	3	22	9	31	10
Indirect mutualism—classic	Webs	0	1	0	1	0	0	0	...	...	...	...
	Effects	0	13	0	13	0	0	0	...	...	...	...
Indirect mutualism—expanded	Webs	0	1	0	1	0	2	2	...	...	...	...
	Effects	0	22	0	22	0	5	5	...	...	...	...
Habitat facilitation	Webs	7	1	1	7	1	0	1	0	0	0	0
	Effects	10	15	15	40	2	0	2	0	0	0	0
Apparent predation	Webs	5	2	0	6	3	0	3	4	0	4	0
	Effects	10	12	0	22	4	0	4	15	0	15	0
Indirect commensalism—classic	Webs	0	0	0	0	0	1	1	0	0	0	0
	Effects	0	0	0	0	0	1	1	0	0	0	0
Indirect commensalism—expanded	Webs	2	0	0	2	0	0	0	5	0	5	2
	Effects	6	0	0	6	0	0	0	6	0	6	5
Indirect defense	Webs	0	0	0	0	3	0	3	10	0	10	0
	Effects	0	0	0	0	5	0	5	29	0	29	0
Total	Webs	16	5	1	16	15	5	16	17	3	17	4
	Effects	162	87	32	281	77	15	92	158	19	177	15
	Types	15	13	4	33	15	4	19	20	4	24	7

predator manipulations, whelks had an indirect positive effect on barnacles, and the indirect effect sequence was keystone predation (Fig. 23A).

Second, as a primary food source of whelks, *Mytilus* had a direct positive effect on *Nucella*. Since barnacles reached higher abundances in the absence than in the presence of whelks (right four panels in Fig. 21), predation had a negative effect on barnacles. Thus, by serving as the primary prey and thereby deflecting predation from the barnacle, the mussel had an indirect positive effect on the barnacle (Fig. 23B). This type of interaction would normally be termed apparent competition, a "trophic-linkage" indirect effect (Kerfoot and Miller 1987, Pennings 1994). In this case, however, the indirect effect of mussels through whelks on barnacles is positive not negative, evidently because the

whelks switched their attention to barnacles in the absence of mussels. This appears to be an example where modified behavior produced an indirect change opposite to that expected from straightforward trophic-linkage effects (e.g., Abrams 1992).

Finally, the barnacle enhanced mussel recruitment, thereby providing whelks a more abundant food source. The barnacle therefore had an indirect positive effect on the predator, an example of apparent predation (Fig. 23C).

What is the overall importance of these indirect effects? To evaluate this, I ran two analyses on the data set. The first, assumed to reflect the variance caused by direct interactions, estimated the percent of the community variance (final abundances of barnacles and mussels) explained by a statistical model including

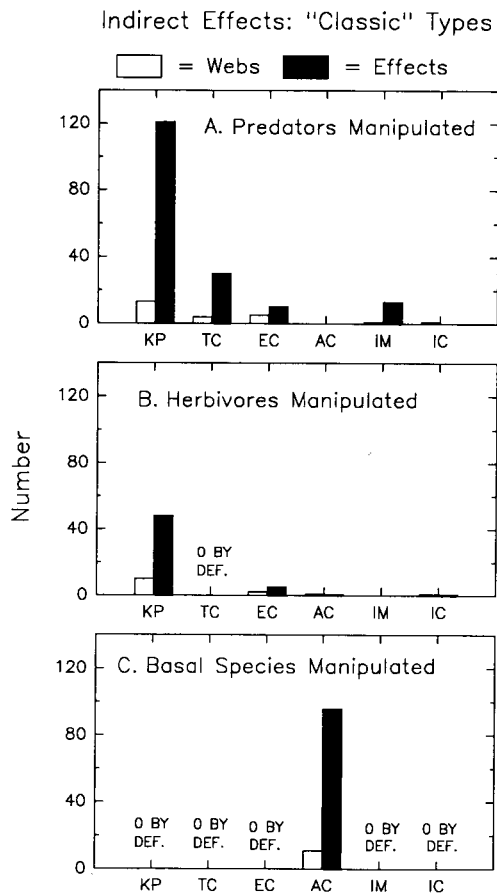


FIG. 18. Frequencies of "classic" types of indirect effect (solid bars) and number of webs in which each effect occurred (open bars), summed for all webs. Arranged by type of effect (code in Fig. 1) from experiments in which (A) predators, (B) herbivores, or (C) basal species were manipulated. "0 by def." indicates categories in which no effects could occur according to the definition of the effect.

only the main effects. The second, assumed to reflect variation due to both direct and indirect effects, estimated the variance explained by a statistical model including both main effects and interactions. The difference between the first and second analysis should suggest the importance of indirect effects to community variation.

As shown in Table 7, the full MANOVA model with interactions is highly significant, as is that without interactions. Estimates of the proportion of the variance of each prey species that is explained by the analysis are provided by the coefficient of determination ( $R^2$ ). With interactions, the full model accounts for 76 and 89% of the variance in final abundance of *Semibalanus* and *Mytilus*, respectively. Without interactions, only 48 and 40% of the variance of barnacles and mussels, respectively, was explained. These univariate results therefore suggest that 28 and 49% of the variance of barnacles and mussels, respectively, was due to statistical interactions among the independent variables. In other words, on average, direct and indirect effects each accounted for about half of the total variance explained for each prey species.

As noted above, however, community structure is multivariate in nature, since, for example, barnacles and mussels interact and both respond to other species such as whelks. Hence, for instance, some of the variation seen in univariate analyses may cancel out, and separate estimates of variance explained for each of the two prey populations does not provide a clear indication of the level of community variance explained by the experiment.

As in Table 4, I used the redundancy coefficient ( $R^2_{\text{yik}}$ ; Dillon and Goldstein 1984) to estimate community variance. The analysis involved running a MANOVA with and without interactions, and in each case generating canonical correlation coefficients and

TABLE 6. Summary of frequency (proportion of total indirect effects for the web) of types of indirect effect by web. "Classic" and "Expanded definition" indirect effects are lumped. Webs are listed (from top to bottom) by number, region, and tidal level/wave exposure. Code to regions: NE, New England, PNW, Pacific Northwest; SC, Southern California; GOC, Gulf of California; EA, Eastern Australia; GOP, Gulf of Panama; SA, South Africa West Coast; CH, Chile. Tidal levels: H, high

Type of indirect effect	Web										
	1 NE ME	2 NE HE	3 SC MI	4 NE HI	5 GOC MI	6 CR MI	7 PNW HE	8 EA MI	9 SC HP	10 GOP HI	11 PNW LI
Total indirect effects	0	1	3	8	7	1	5	23	8	14	7
No. types	0	1	2	5	6	1	4	6	1	6	4
No. species in web	3	3	4	4	4	5	6	8	8	8	8
No. levels in web	1	2	2	3	3	3	3	3	2	4	2
Keystone predation	...	...	0.67	0.38	0.14	...	0.20	0.22	1.0	0.21	0.58
Apparent competition	...	1.0	...	0.25	...	...	0.20	0.17	...	...	0.14
Habitat facilitation	...	...	...	...	0.14	1.0	...	0.13	...	...	...
Apparent predation	...	...	...	0.13	0.14	...	...	0.22	...	0.14	...
Indirect mutualism	...	...	...	...	0.29	...	...	...	...	...	...
Trophic cascade	...	...	...	...	...	...	0.40	0.09	...	0.14	...
Indirect defense	...	...	...	0.13	0.14	...	...	0.17	...	0.07	0.14
Indirect commensalism	...	...	0.33	...	0.14	...	0.20	...	...	0.29	0.14
Exploitation competition	...	...	...	0.13	...	...	...	...	...	0.14	...

canonical loadings for use in calculating redundancy coefficients. In each case, I assumed that redundancy coefficients provided an estimate of community variance accounted for by the model. Further, I also assumed that the difference between coefficients from analyses with and without interactions provided an estimate of community variance accounted for by interactions.

Without interactions 44% of the multivariate "variance" was explained, while with interactions 82% was explained (Table 8), so statistical interactions among independent variables accounted for 38% of community variance. Hence, the multivariate analysis also suggests that direct and indirect effects were each responsible for nearly half of the total community variation explained by this analysis.

Canonical loadings of the dependent variables with interactions separate the two canonical variates more clearly and sensibly than does the analysis without interactions. With interactions, variate 1 is clearly associated with *Mytilus* and variate 2 is clearly associated with *Semibalanus* (Table 8). The loadings with interactions also indicate more clearly the type of effect each independent variable has on each dependent variable. For variate 1, high mussel abundance (a significant positive loading; +0.997) is associated with low whelk abundance = low predation (a significant negative loading; -0.683) and high barnacle abundance = a good settlement surface (a significant positive loading; 0.764). For variate two, high barnacle abundance (a significant positive loading; 0.965) is associated with low mussel abundance = low interspecific competition (a significant negative loading; -0.952).

Without interactions, the analysis yields significant *Y* set mussel and barnacle loadings for both variates rather than a single significant loading for each variate (Table 8). Moreover, these loadings provide no sensible

Indirect Effects: Expanded Definitions

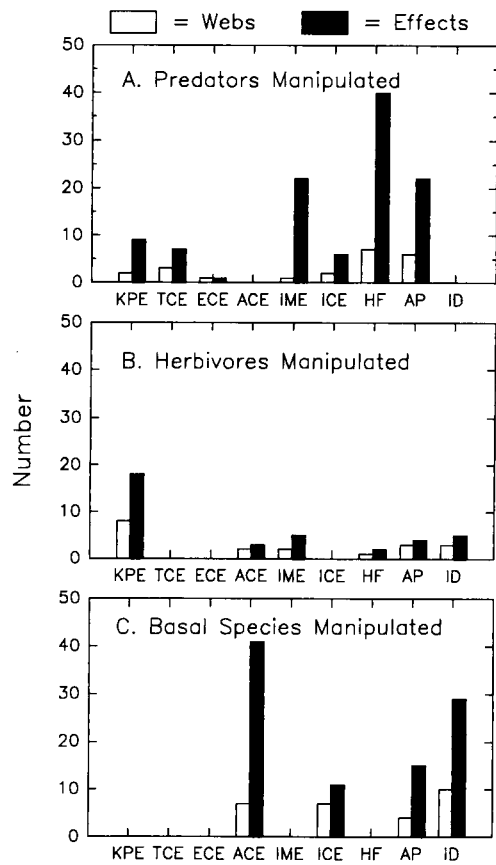


FIG. 19. Frequencies of "expanded" types of indirect effects. See legends to Figs. 11-14 for codes to types and Fig. 18 legend for further explanation.

zone; M, mid zone; L, low zone. Degree of wave exposure: E, exposed to high waves; I, intermediate exposure to waves; P, protected from high waves. Total indirect effects are from Appendix 2; no. species and no. levels in web are from Table 2. No. types are the total number of kinds of indirect effects in the web of the nine types listed below. Proportions are calculated as the number of each type/total indirect effects.

Web														Total	%
12 SC LI	13 NE MI	14 SA LMP	15 SC LE	16 SC LP	17 NE LP	18 SA LME	19 CH MI	20 NE MP	21 CH MI	22 GOP LI	23 PNW LI				
17	36	5	8	18	24	8	23	74	36	50	189	565	...		
4	6	2	1	2	4	4	3	5	5	3	8	83	...		
9	9	10	10	10	10	12	13	14	18	21	23	...	...		
2	3	2	3	2	3	3	3	3	3	4	3	...	...		
0.35	0.17	...	1.0	0.89	0.71	0.25	0.22	0.39	0.50	0.52	0.19	196	34.7		
0.29	0.42	0.80	...	...	0.13	0.25	0.65	0.43	0.22	...	0.25	141	25.0		
...	0.06	...	...	...	0.08	...	...	0.03	...	...	0.16	42	7.4		
...	0.14	...	...	...	...	...	...	0.08	...	0.22	0.05	41	7.3		
...	...	...	...	...	...	...	0.13	...	...	...	0.19	40	7.1		
...	...	...	...	...	...	...	...	...	...	0.26	0.10	37	6.5		
0.29	0.17	...	...	...	0.08	0.25	...	0.07	0.06	...	0.03	34	6.0		
0.18	0.06	0.20	...	...	...	0.25	...	...	0.06	...	...	18	3.2		
...	...	...	...	0.11	...	...	...	...	0.17	...	0.03	16	2.8		

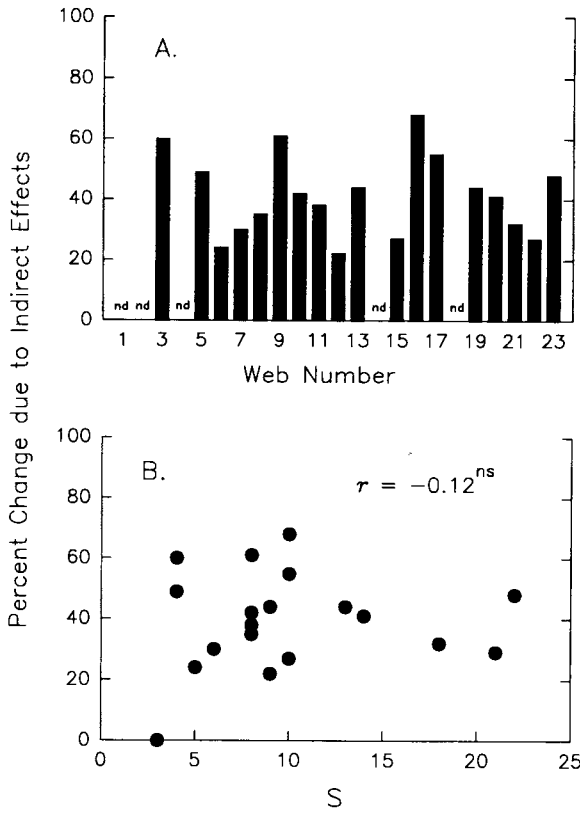


FIG. 20. Percent change of abundances of organisms caused by indirect effects by (A) web number (Appendix 1) and by (B) number of species per web. ND = no data.

resolution of the nature of the associations between *Y* set and *X* set variates (Table 8). Without interactions, variate one suggests high barnacle abundance and moderate mussel abundance (*Y* set) results from low predation and high barnacles (*X* set). Variate two suggests low mussel abundance and high barnacle abundance (*Y* set) results from low mussels (*X* set). It seems clear that these interpretations make little sense.

DISCUSSION

The conclusions of this analysis of 23 rocky intertidal interaction webs fall into three main categories: general patterns of indirect effects in relation to web structure, frequencies of both classic and new types of indirect effects, and the importance of indirect vs. direct effects. Before exploring the implications of these results, however, I consider the limitations of the data.

Potential artifacts and biases

First, the data set, i.e., the interaction webs, could have been impaired by several potential biases. For example, as noted by others (Fairweather 1990, Penning 1994), the mechanisms underlying indirect effects are rarely determined experimentally. Rather, indirect effects and their underlying causes are generally inferred from the results of studies testing for the influence of direct interactions. While interpretations are generally based on direct observation of events after manipulations, and usually have a strong natural history basis, only a few studies have been designed to test for indirect effects (e.g., Dungan 1987, Schmitt 1987, Wootton 1994), and even these excellent studies did not perform all possible tests.

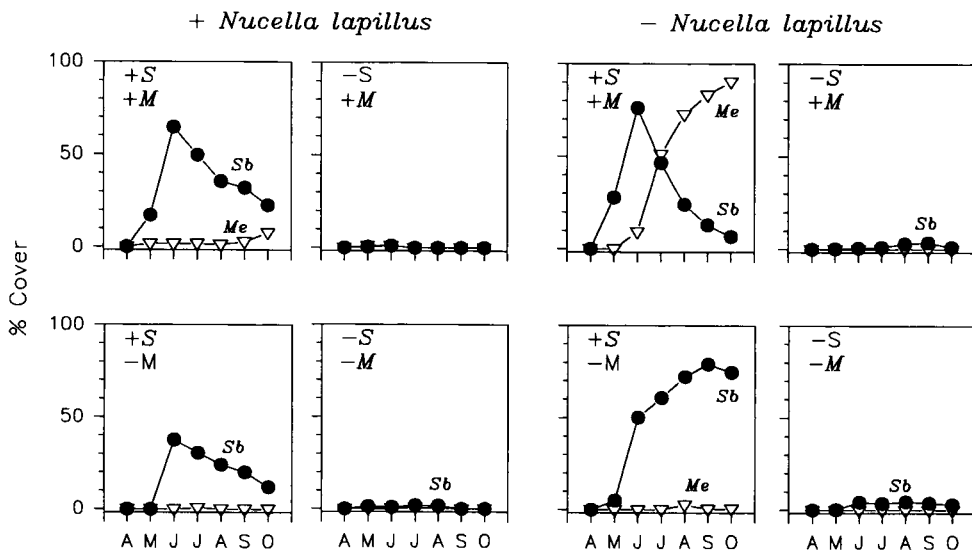


FIG. 21. Results of the Grindstone Neck, Maine experiments on the interactions between *Nucella*, *Semibalanus*, and *Mytilus*. Panels on the left are treatments with *Nucella* present, panels on the right are treatments with *Nucella* absent. The treatment for each panel is coded as presence (+) or absence (-) of *Semibalanus* (S) or *Mytilus* (M). The smaller Sb and Me symbols indicate the temporal changes in abundance in each treatment of the barnacle and mussel, respectively.

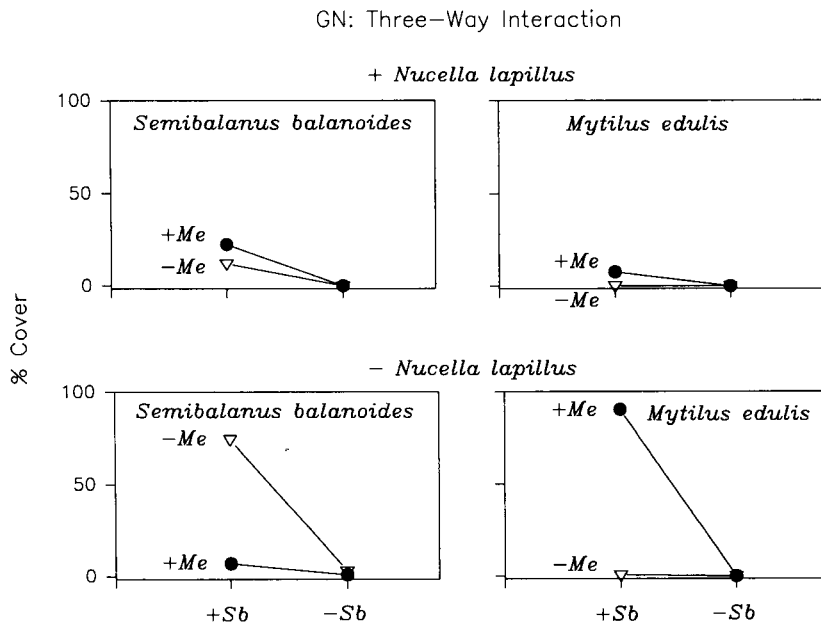


FIG. 22. Interpretation of the significant three-way interaction term of the analysis in Table 6. Data are the final (i.e., in October) mean percent covers of mussels (the two panels on the right) and barnacles (the two panels on the left). Treatments were *Nucella* present (top panels) and absent (bottom panels), *Semibalanus* present (left symbols in each panel) and absent (right symbols in each panel), and *Mytilus* present (●) and absent (▽). GN = Grindstone Neck.

Thus, the 23 interaction webs presented here necessarily include both potential errors in interpretation and mistaken inferences. However, as noted earlier, I made a serious effort to make conservative decisions in assembling the webs. The occurrences of both direct and indirect effects was checked for each web several times to weed out errors and eliminate overinterpretations. While others might construct somewhat dif-

ferent webs, I had some webs checked by those whose work I had used to make the web. In all cases, the corrections suggested by these experts were minor. Further, in one case (two webs), other workers (G. M. Branch and R. Bustamante, University of Capetown, South Africa) were able to follow my protocol and construct webs that I used with only a few revisions (see above, *Methods: Rocky intertidal interaction*

TABLE 7. Multivariate analysis of variance of community regulation at Grindstone Neck, Maine. Community structure (i.e., the dependent variables) was quantified as the final percent cover (arcsine transformed) of the mussel *Mytilus edulis* (Me) and the barnacle *Semibalanus balanoides* (Sb) in experiments conducted on canopy-free rock surfaces. The factors tested were presence or absence of *Nucella lapillus* (Nl), *S. balanoides*, and *M. edulis*. \*\*\*,  $P < 0.001$ .

Variables	Without interactions					With interactions				
	Multivariate analysis				Univariate analysis	Multivariate analysis				Univariate analysis
	Wilks' lambda	F	df	P	R <sup>2</sup>	Wilks' lambda	F	df	P	R <sup>2</sup>
Full model	0.237	17.9	6, 102	≤0.0001	%Sb = 48.3 %Me = 39.9	0.029	32.8	14, 94	≤0.0001	%Sb = 75.7 %Me = 88.5
Main effects										
<i>Nucella lapillus</i>	0.543	21.5	2, 51	≤0.0001	...	0.549	19.3	2, 47	≤0.0001	...
<i>Semibalanus balanoides</i>	0.497	25.8	2, 51	≤0.0001	...	0.352	43.3	2, 47	≤0.0001	...
<i>Mytilus edulis</i>	0.702	10.8	2, 51	0.0001	...	0.470	26.5	2, 47	≤0.0001	...
Interactions										
Nl × Sb	...	...	...	...	...	0.575	17.4	2, 47	≤0.0001	...
Nl × Me	...	...	...	...	...	0.537	20.3	2, 47	≤0.0001	...
Sb × Me	...	...	...	...	...	0.474	26.1	2, 47	≤0.0001	...
Nl × Sb × Me	...	...	...	...	...	0.547	19.4	2, 47	≤0.0001	...

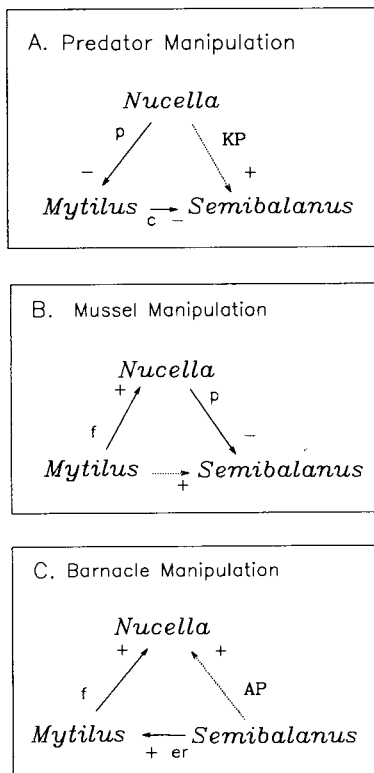


FIG. 23. The interaction webs represented by the experiments summarized in Tables 7 and 8 and Figs. 21 and 22.

*webs: assembly*). I therefore argue that, on the basis of present knowledge, these webs represent a rigorously constructed and reliable data set.

Second, these webs might include a bias resulting from the research focus of the investigators performing the original studies. For instance, the high frequency of keystone predation and the low frequency of exploitation competition might be simple artifacts of an emphasis on predator-prey interactions and a lack of interest in studying interactions between species on the same level high in the food web. Alternatively, these results could be due to a preponderance of basal species in the webs.

There was clearly a bias toward manipulation of consumers in these webs. Of 32 predators, 42 herbivores, and 146 basal species involved in strong interactions over all 23 webs, 90.6% (29) of the predators, 81% (34) of the herbivores, but only 26% (38) of the basal species were manipulated. This emphasis on the role of the consumers undoubtedly underlies the high frequencies of indirect effects involving linkages between levels, and may underlie the prevalence of keystone predation (Table 6). On the other hand, apparent competition, involving indirect effects of one prey on another through their common predator, was nearly as common as keystone predation (Table 6) despite being an effect most often detected by manipulating basal species. Moreover, trophic cascades, detected by removing top predators,

appeared uncommon among these webs (Table 6). Hence, despite a bias toward manipulation of predators, some predator-initiated indirect effects were uncommon while some basal-species-initiated indirect effects were common.

While the low frequency of exploitation competition is likely due in part to biases in research focus, I argue that, at least among these webs, the frequency of this indirect effect would increase only marginally were there more studies done within consumer levels. First, 14 of the 21 manipulated webs had 0–1 predator(s) at level 3 or 4 (Appendix 1). Assuming that other predators in the food webs from which these interaction webs were constructed did not, in fact, interact strongly with the prey of the predators included in these interaction webs, no exploitation competition would be possible in these cases. Second, most webs involved predator manipulations and thus exploitation competition would be suggested if a second predator increased in the absence of the first. Since in most cases the investigators monitored their experiments regularly, I assume such responses would generally be obvious and at least mentioned if not quantified by the author. I therefore suggest that the relatively low occurrence of exploitation competition in these webs is real, although the actual frequency is likely to be higher than 2.6% of all cases and this effect is likely to occur in a greater proportion of the webs.

Third, if just those webs that have been relatively more intensively studied (webs 5, 7, 8, 12, 13, 17, 20, 21, 22, 23) are examined, similar patterns of occurrence of indirect effects are seen: keystone predation and apparent competition are common and exploitation com-

TABLE 8. Canonical correlation analysis of the Grindstone Neck, Maine experiment (see Table 7). Values in boldface are significant at the 5% level with a critical correlation coefficient value of 0.379 ( $k = 3$  independent variables, 54 df).

Variables	Canonical variates	
	1	2
<i>Y<sub>i</sub></i> Community structure (final % cover)		
With interactions		
<i>Mytilus edulis</i>	<b>0.997</b>	0.085
<i>Semibalanus balanoides</i>	-0.262	<b>0.965</b>
Without interactions		
<i>Mytilus edulis</i>	<b>0.553</b>	<b>-0.833</b>
<i>Semibalanus balanoides</i>	<b>0.721</b>	<b>0.693</b>
<i>X<sub>i</sub></i> Factors manipulated (present vs. absent)		
<i>Nucella lapillus</i>	<b>-0.683</b>	-0.026
<i>Mytilus edulis</i>	0.147	<b>-0.952</b>
<i>Semibalanus balanoides</i>	<b>0.764</b>	0.193
Canonical correlations		
With interactions	<b>0.941</b>	<b>0.864</b>
Without interactions	<b>0.819</b>	<b>0.529</b>
Redundancy coefficient ( $R^2_{\text{tr}}$ )		
With interactions		82.0%
Without interactions		44.1%

petition is rare (Table 6). Most of these cases also have a greater variety of types of indirect effects than do the less intensively studied cases. Hence, although the proportions of different types of indirect effects may vary with increased experimentation, especially at the basal levels and within higher levels, the general patterns of indirect effects in marine intertidal interaction webs seem likely to remain similar to those seen in this analysis.

Fourth, biases might have been introduced by variation among the studies in either the intensity of experimentation or the level of taxonomic resolution. As indicated in Figs. 6–8, however, such biases appeared to have minimal influence on the general patterns of indirect effects. Nonetheless, it seems likely that for specific webs, more extensive experimentation may alter some patterns. For example, in view of the wide variety of types of indirect effect occurring in most webs (Table 6), it is likely that further work will show that, in fact, webs 2, 6, 9, and 15 have more than the one general type of indirect effect with which they are currently credited (although simpler webs such as web 2 will undoubtedly still have relatively few interaction chains).

Fifth, I dealt almost exclusively with trophic-linkage indirect effects, primarily because information on other types of indirect effects is minimal at best. Thus, it is possible that, for example, behavioral indirect effects may complicate the interpretations I made based on changes in abundance. An example of this possibility was seen in the analysis of the New England interaction web (Fig. 23). Unfortunately, essentially no information is available on behavioral indirect effects in these webs. Recently, however, the field studies of Wootton (1992, 1993, 1994) on the outer coast of Washington indicated behavioral modification of interaction links were common, as suggested by Abrams (1987, 1992). Interestingly, however, and in contrast to theoretical expectation, Wootton's (1994) analysis showed that despite a possibly high frequency of behaviorally mediated indirect effects, indirect effects were still predictable using path analysis on abundance data. It thus seems possible that many behaviorally mediated indirect effects occurred in my data set but were indistinguishable from abundance-mediated indirect effects. While uncertainties remain, I believe that the present analysis advances our understanding of the patterns and importance of indirect effects in this set of relatively well-studied communities. Moreover, the patterns documented here suggest several interesting hypotheses that could be tested in future studies. I address these below.

#### *Web structure and indirect effects*

The analysis suggested that each species interacts strongly with an increasing number of species as species richness increases (Fig. 2A) and that these interactions produced more indirect effects and more sequences per species in larger webs (Figs. 2B and 3A). In other words, the number of strong interactions per species is greater

in more diverse webs. Further, the number of indirect effects and pathways or series of interactions producing these effects also increases with web diversity. These relationships suggest that for any rocky intertidal community at least, number of indirect effects, or number per species, can be predicted by knowing the number of species involved in strong interactions. While determining which interactions in a previously unstudied food web are strong would still involve time-consuming experimentation, the effort involved would still be less than what would be required if tests for indirect effects also had to be carried out. Moreover, indirect effect structure appeared independent of both the proportion of species manipulated (Fig. 7) and the proportion of biological species (vs. trophic species; Fig. 8). This suggests that investigators were able to identify and first manipulate those species responsible for most indirect effects. If so, it may be possible to characterize the interaction structure of a community in a relatively brief time using a few, carefully designed experiments on a few key species. Wootton's (1994) study provides a successful example of this approach in a study combining path analysis and field experimentation. Still more savings in time, effort, and cost might be possible if future analyses reveal nonintrusive methods of identifying that subset of species in a food web which are involved in strong interactions. I emphasize, however, that such methods are presently unavailable. Construction of interaction webs still depends on field experimentation.

The extent to which these predictive relationships can be extended beyond marine intertidal habitats is unclear. Community dynamics in freshwater communities possess some similarities to dynamics seen in marine communities, particularly with respect to the strong effect of predation on community structure (e.g., Hall et al. 1970, Paine 1977, Carpenter et al. 1985, Menge 1992, Power 1992a, Menge et al. 1994), so some aspects of the present analyses may extend to freshwater communities. Relatively little experimental work is available from freshwater benthic habitats, however, so detailed comparisons may be premature. Because of fundamental differences in physical environments (e.g., Denny 1990, Liem 1990), terrestrial communities may have fundamentally different dynamics from aquatic communities (Strong 1992). Nonetheless, some analyses (Schoener 1989, 1993) suggest many similarities between terrestrial and most aquatic communities.

Parenthetically, it is appropriate to comment on the relationship between the present results and certain results from analyses of food webs. A fundamental result of early food web analyses was that connectance, the proportion of the total number of trophic links observed out of the total number possible in a food web, decreases with increasing species richness (e.g., May 1973, Pimm 1982). Stated another way, this relationship was termed the "link-species scaling law," which states that the number of links per species ( $L/S$ ) is independent of species richness and is  $\approx 2$ , or that  $L = 2S$ . Recent workers

have questioned these conclusions, arguing on the basis of more rigorously constructed food webs that connectance either was constant (Martinez 1992) or increasing (Winemiller 1989) with increasing species richness. For instance, Martinez (1992) proposed that links scale to species as  $L = kS^2$ , where  $k$  is a constant, and found that his food web set could not refute this hypothesis.

In my analysis, strong interactions (D) scaled with species richness (S) as  $D = 0.92S^{1.69}$  (Table 3), the exponent of which is close to the value (1.54) calculated by Martinez (1992) for a large set of 175 food webs (see also Schoener 1989). This regression for the 23 intertidal interaction webs is thus intermediate between the link-species scaling relationship ( $L = 2S$ ) and the constant connectance relationship ( $L = kS^2$ ). This means that connectance is still inversely related to species richness but that D/S is not constant with increasing S but increases. J. Bengtsson (*personal communication*) speculates that the exponent of  $\approx 1.5$  has real significance, as it means that each species interacts with more species as web size increases, but that for each species added, the increase in numbers of strong interactions is smaller and smaller.

The ecological significance of this relationship is unclear, however, because my analysis is fundamentally different from analyses of food webs. Interaction webs include only strong interactors, and D includes all strong interactions, not just trophic interactions. Hence, the generality of the relationships documented in Table 3 cannot be ascertained until a similar analysis is done with interaction webs from other habitats. Nonetheless, it is intriguing that the relationships I have documented are in the same ballpark as those based on analyses of food webs. This may suggest that the controversial set of food webs used in the earlier analyses (Schoener 1989, Cohen et al. 1990, Martinez 1991, Polis 1991) somehow captured much of the structure, or at least paralleled the structure of their included interaction webs. Resolution of this issue awaits further analysis.

#### *Basal species vs. sessile herbivores*

The detailed analysis suggests that keystone predation and apparent competition were the most common indirect effects in these webs, while exploitation competition was least common (Table 6). Curiously, a type of indirect effect that appears quite common in freshwater communities, trophic cascades, was also relatively uncommon in these webs. This raises the question of if, despite appearances, trophic cascades are actually rare in most aquatic communities, or alternatively, if trophic cascades in some sense replace keystone predation as the dominant indirect effect in freshwater communities.

I suggest that keystone predation and trophic cascades represent qualitatively different versions of the same type of interaction. The distinction hinges on the alternative concepts of "basal species" vs. "sessile herbivores." As noted earlier, if interaction webs are based on the mechanisms of resource utilization, then plants

and sessile filter-feeders are placed on the same "basal" level. Predation on sessile animals frees plants from competition and thereby indirectly maintains high plant abundance, which is the classic form of keystone predation. Since plants and sessile animals are considered to be on the same level in the web, such indirect effects involve two levels.

If, on the other hand, plants and sessile filter-feeders are categorized trophically, then the above two-level system becomes a three-level system, with sessile filter-feeders on the second, herbivore level. In this web arrangement, the identical interaction (predation holds sessile animal abundance low allowing plant abundance to be high) is exactly comparable to a trophic cascade, except that the direct interaction between sessile animals and benthic macrophytes is interference competition, not herbivory. These considerations, and many of the expanded definition sequences of trophic cascades and keystone predation documented above (Figs. 18 and 19, Table 5), suggest that these two types of indirect effects may be, in some cases at least, topologically and dynamically if not mechanistically comparable.

Does this mean that freshwater and marine biota have fundamentally different, unique characteristics or that the distinction between trophic cascades and keystone predation is dependent on some other feature? I argue in favor of the latter: trophic cascades seem more typical of pelagic communities, where sessile herbivores (and sessile plants) cannot, by definition, occur, while keystone predation typifies benthic communities. Like benthic marine habitats, benthic freshwater communities have both sessile plants and sessile animals. Interaction webs in these habitats appear poorly known, however, although the recent spectacular invasion of zebra mussels to the U.S. Great Lakes (Griffiths et al. 1991, Schloesser et al. 1991) may help alter this situation.

#### *On predicting the importance of indirect effects*

Both types of analysis of the importance of indirect effects suggest that 40–50% of the change seen after perturbations in these intertidal communities is due to indirect effects (e.g., Fig. 20, Tables 7 and 8). Importantly, this conclusion appears independent of the species richness of the interaction web. Assuming interaction web size is correlated with food web size, the proportion of change in the community accounted for by indirect effects may also be relatively constant as well. Thus, to the extent that such results can be generalized, we might predict that when strong interactions occur within a community, about half of the change resulting from perturbations involving these interactions will be due to indirect effects. As with frequencies of indirect effects, such a predictive capacity should at least reduce the intensity of study needed to determine the general impact of alterations of the abundance of strongly interacting species in a community. This is because the design of experiments needed to quantify indirect

effects becomes unwieldy rapidly as the number of species in the system increases (e.g., Yodzis 1988, Loehle 1990, Pennings 1994). As noted earlier, another important issue relating to predicting the importance of indirect effects, the influence of experiment duration on the detection and strength of indirect effects relative to direct effects (Bender et al. 1984, Pennings 1994), will be addressed elsewhere (B. A. Menge, *unpublished manuscript*). Briefly, analyses suggest that in this data set at least, most experiments were run well beyond an approximate state of a new, postmanipulation equilibrium, and therefore that few additional indirect effects remained to be discovered.

Questions remain, however. First, how predictable are specific changes resulting from indirect effects? Second, how extensively must we test for direct effects to predict even general levels of change due to indirect effects? Third, can these results from marine rocky intertidal habitats be generalized to other habitats? Fourth, why are the relative contributions of direct and indirect effects to change in community structure roughly similar and what are the causes of variation around this level?

1) Present knowledge seems insufficient to allow a truly general statement regarding the extent to which the indirect effects of direct interactions can be predicted in a novel system. In marine communities, however, we have developed over the past three decades a large wealth of ecological and natural history knowledge, which may permit considerable insight into the regulation of little-studied communities. For example, Jane Lubchenco and I predicted with some accuracy the general interaction dynamics of the rocky intertidal community on the Pacific coast of the Bay of Panama (web 22, Appendix 1) on the basis of a month of observations made 3 yr prior to beginning our experimental studies. Key observations were the low abundances of foliose algae and benthic sessile invertebrates, high abundances and/or large sizes of both invertebrate and vertebrate predators, and signs of strong grazing and predation such as fish graze marks on encrusting algae and recently crushed barnacles and bivalves. The main feature we missed during our preliminary expedition was the very low rates of recruitment of sessile organisms into this habitat (e.g., Menge 1991a). Wootton's (1994) application of path analysis to interaction webs in an intertidal community on the outer Washington coast is consistent with the view that the interaction web approach offers much promise in predicting community regulation.

I thus assert that with our current state of knowledge, experienced marine ecologists should be capable of predicting at least some aspects of community dynamics in unstudied marine communities on the basis of experiments and observations in comparable types of well-studied communities. Similar claims could also be made for freshwater communities, as an extensive body of experiment-based insight into community dynamics in such habitats has accumulated (e.g., review in Carpenter 1988, see also Power 1990, 1992b, Wootton and Power

1993). At the same time, there will also be surprises due to novel linkages, or different effects of familiar types of linkages, and unexpected causes of familiar types of pattern (e.g., Leibold and Wilbur 1992). At issue is the extent to which a priori knowledge allows prediction of the  $\approx 50\%$  of community dynamics that this paper suggests might be attributable to indirect (and direct) effects.

2) As argued earlier, the intensity of study of direct effects needed to predict the level of change due to indirect effects may be less than had been previously thought. Together, the observation that indirect effect structure was independent of the fraction of species manipulated (Fig. 6B) and the independence of the level of change from web species richness (Fig. 20B) suggest that most change due to indirect effects can be identified with minimal but properly designed experimentation. At the same time, it is undoubtedly too early to adopt this minimalist approach. As argued by Fairweather (1990) and Pennings (1994), additional detailed studies like those of Schmitt (1987) and Dungan (1987) are needed to explicitly test for the presence and importance of indirect effects. Further, almost no empirical information is available regarding the patterns, importance, and predictability of behavioral indirect effects. In view of Abrams' (1987, 1992) theoretical arguments predicting low predictability of such effects, there is an urgent need for field studies incorporating such effects as well as studies investigating indirect effects of other factors such as nutrients. Accumulation of such knowledge should allow rigorous evaluation of the patterns implicit in the present analysis.

3) As suggested earlier, it seems likely that the patterns revealed in this analysis of marine intertidal webs may apply to other aquatic habitats, especially benthic marine and freshwater communities. This speculation should be testable for freshwater communities at least, given the extensive knowledge we have for such systems. Due to the shortage of comparable studies from terrestrial communities, the applicability of the present results to terrestrial habitats cannot be determined at present. Although the community dynamics revealed by studies like those of Spiller and Schoener (1990a, b) and Brown et al. (1986) demonstrated many parallels with results from aquatic systems, we need to amass many more such studies before initial judgements can be made.

4) The apparent constancy of the level of change due to indirect effects in these webs is intriguing. Why should the amount of change due to indirect effects be approximately equal to that due to direct effects? I suggest that this pattern is due largely to two factors: in most of the webs, (1) strongly interacting omnivores (consumers of both plants and animals) were absent, and (2) changes due to direct effects were usually inverse and similar in magnitude to those due to indirect effects.

First, in most of these studies, the dominant consumers included carnivores and/or herbivores. Thus, if con-

sumption of, for example, sessile animals by a predator led to increased cover of plants, and herbivory was not strong enough to compensate and depress plant abundance, then the relative magnitudes of the changes in cover of sessile animals and plants should be similar. Since the former was due to a direct effect and the latter was due to an indirect effect, each accounts for about half of the induced change. Of course, in most such cases, the experiment inducing such a result actually produced an increase in cover of sessile animals and a decrease in cover of plants after removal of predators, since the natural pattern (with predators) was commonly high plant abundance and low sessile animal abundance. Hence, when consumers are "specialized" to the extent that they are strictly carnivorous or herbivorous, we might expect that change due to direct and indirect effects would be similar.

Second, the changes summarized in the above paragraph depend on reciprocal, relatively rapid changes in covers of plants and sessile animals. These reciprocal changes can be due to interference competition or inhibition of recruitment, both of which were common in these webs (Figs. 11–17). The scenario outlined here is also most likely when total cover of sessile animals + foliaceous plants is high, which is commonly the case in these webs (e.g., Menge and Farrell 1989).

What is the cause of variation above or below the average level of  $\approx 40\text{--}50\%$  change due to indirect effects? One important cause is changes in mobile consumers (herbivores, predators), which would not be accounted for under the above scenario. Another is changes in epiphytic ephemeral algae, which can attach to either the sessile animals or plants and can occur as both short- and long-term indirect changes. Both of these changes might be expected to increase the total change in community structure above the mean of 40–50%.

Strong omnivory might be expected to hold the magnitude of indirect change in community structure to levels below the general mean of 40–50%. For example, in Panama, the dominant consumers were omnivorous (Menge and Lubchenco 1981, Menge et al. 1986a, b), and included large fishes and crabs. The consequence of this was that strong trophic links occurred between consumers and both sessile animals and foliose algae. This was in strong contrast to the case in certain temperate communities (e.g., Paine 1966, 1974, Menge 1976, Lubchenco and Menge 1978, Dethier and Duggins 1984), where strong trophic links were focused either on sessile animals or on foliose algae. Thus, in Panama, consumers simultaneously kept the abundances of plants and animals to low levels. Moreover, predation on both mobile invertebrate grazers and ephemeral seaweeds was also consistently high (Menge et al. 1986a, b), so that indirect change in these groups was minimized as well.

I therefore suggest that when omnivory is strong, indirect effects may contribute minimally to community structure. Insofar as change is due to species interactions

in a given community, most patterns, and change in pattern, in such communities should be due to direct effects. Alternatively, however, as the number of omnivores increases, indirect effects may increase in importance due to direct and indirect effects of interactions among omnivores (e.g., exploitation competition may increase; J. Bengtsson, *personal communication*). Investigation of the importance of omnivory thus appears to be an important issue, and intensive study of this problem is badly needed. I recognize, however, that factors other than species interactions, including rates of recruitment and productivity (e.g., Connell 1985, Gaines and Roughgarden 1985, Sutherland 1990, Menge 1991a, 1992, Wootton and Power 1993), can also have major effects on community structure. Evaluation of the relative importance of these factors and species interactions in controlling community structure is an important issue and will be a major focus of future research.

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APPENDIX 1

Direct interaction web matrices and indirect effect sequences. Each species is coded as a predator ( $P_i$ ; numeric code, 1), a herbivore ( $H_i$ ; 2), a competitively dominant basal species ( $D_i$ ; 3), a competitively intermediate species ( $I_i$ ; 4), or a competitively subordinate species ( $S_i$ ; 5), where  $i = 1$  to  $n$  species of that type of species in the web. Species causing the (direct) effect are in columns and species affected are in rows. “ $\times$ ” refers to intraspecific effects when they are unknown. Types of effects are positive (+), negative (–), or none (0). The identity of each member of each web (**Web components**) is listed beside the interaction matrix, with the manipulated species shown in boldface. Indirect effect categorization involved first identifying each **Indirect effect sequence**, using results from studies listed for each web. In indirect effect sequences, the species initiating the effect is to the left, the species receiving the effect is to the right. Direct effects are not in parentheses; indirect effects are in parentheses following the species receiving the indirect effect. For instance, in web 2,  $D_1$  (a barnacle) had a positive effect (provided shelter) on  $H_1$  (a grazing snail), which had a negative effect on (reduced the abundance of)  $S_1$  (microalgae); the indirect effect of  $D_1$  on  $S_1$  was thus negative (by providing shelter, the barnacle allowed the grazers to control the abundance of the microalgae). Subscripts in boldface indicate cases where several equivalent species were grouped. Each indirect effect sequence was then given: a **Numeric code**, using the numbering system given above; an **Interaction code**, using the lettering system listed above but dropping the species number subscript and indicating the species indirectly affected in underlined boldface (thus, interaction codes such as “**HBB**” are read as “a herbivore directly affected a basal species [B] and indirectly affected another basal species through a direct interaction between the basal species); an **Effect sequence**, which lists the sign of the effects (+ or – for direct and  $p$  [positive] or  $n$  [negative] for indirect effects); and a **Direct interaction sequence**, which lists the specific direct effects ( $p$ , predation;  $c$ , competition;  $ir$ , inhibition of recruitment;  $hs$ , provision of habitat or shelter;  $f$ , food;  $er$ , enhancement of recruitment;  $if$ , inhibition of feeding; see *Definitions* and Table 1) in each interaction chain. Indirect effects are then summarized in three ways. The first and broadest category, **Types of indirect effects**, refers to each unique combination of **Interaction code**, **Effect sequence**, and **Direct interaction sequence**. The second category, **Sequences/type**, refers to the total number of direct interaction pathways in each **Indirect effect sequence**. The third category, **Total number**, refers to the actual number of **NEW** indirect effects produced by each **Indirect effect sequence**. “New” indirect effects are those not included in indirect effect sequences earlier in each subtable for each web. Ecologically similar species are grouped in indirect effect sequences where more than one species is involved in producing or receiving an effect and the effect of or on each species is the same. For example, in web 13, whelks reduce mussel abundance and mussels inhibit grazing by two littorine snail species (sequence code 132), so whelks have two positive indirect effects on littorines. See *Definitions* for further details. Note that the display of data changes after web 6. For webs 1–6, indirect effects are printed below the direct effect matrix; for webs 7–23, indirect effects appear on the facing page, opposite the direct effect matrix. The final page of the Appendix continues the indirect effect list for web 23.

Web 1: New England Mid Exposed (Little Brewster Point, Massachusetts) (Menge 1976)

Direct interaction matrix				Web components			
$D_1$	$I_1$	$S_1$					
$D_1$	$\times$	+	0	$D_1$ , <i>Mytilus edulis</i>			
$I_1$	–	$\times$	0	$I_1$ , <i>Semibalanus balanoides</i>			
$S_1$	–	–	$\times$	$S_1$ , ephemeral algae			
Indirect effect sequence				Indirect effects			
	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Types	Sequences/type	Total number
None							

Web 2: New England High Exposed (Pemaquid Point, Maine) (B. A. Menge 1976, *personal observations*)

Direct interaction matrix				Web components			
$H_1$	$D_1$	$S_1$					
$H_1$	$\times$	+	+	$H_1$ , <i>Littorina saxatilis</i>			
$D_1$	0	$\times$	0	$D_1$ , <i>Semibalanus balanoides</i>			
$S_1$	–	0	$\times$	$S_1$ , microalgae			
Indirect effect sequence				Indirect effects			
	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Types	Sequences/type	Total number
$D_1 + H_1 - S_1 (-)$	325	<b>HBB</b>	+ – $n$	hs/p	1	1	1

APPENDIX 1. Continued.

Web 3: Southern California Boulder Field Mid Zone Intermediate (Montecito, California) (Van Tamelen 1987)

Direct interaction matrix					Web components						
H <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>								
H <sub>1</sub>	-	-	+	+	<b>H<sub>1</sub>, <i>Lottia pelta</i></b> <b>S<sub>1</sub>, <i>Chthamalus</i> spp.</b> S <sub>2</sub> , ulvoids S <sub>3</sub> , microalgae						
S <sub>1</sub>	0	×	-	-							
S <sub>2</sub>	-	0	×	0							
S <sub>3</sub>	-	0	0	×							
Indirect effect sequence					Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
									Types	Sequences/ type	Total number
H <sub>1</sub> -S <sub>2</sub> -S <sub>1</sub> (+)					255	HBB	--p	p/ir	1	2	1
H <sub>1</sub> -S <sub>1</sub> -S <sub>2</sub> (+)-H <sub>1</sub> (-)					2552	HBBH	--p-n	p/ir/ir	1	1	1
S <sub>1</sub> -H <sub>1</sub> -S <sub>2</sub> (+)					525	HBB	--p	if/p	1	1	1
Total									3	4	3

Web 4: New England High Intermediate (Grindstone Neck, Maine) (Menge 1976; B. A. Menge and J. Lubchenco, *personal observations*)

Direct interaction matrix					Web components						
P <sub>1</sub>	H <sub>1</sub>	D <sub>1</sub>	S <sub>1</sub>								
P <sub>1</sub>	×	0	+	0	<b>P<sub>1</sub>, <i>Nucella lapillus</i></b> H <sub>1</sub> , <i>L. saxatilis</i> D <sub>1</sub> , <i>S. balanoides</i> S <sub>1</sub> , <i>Ulothrix</i> sp./ <i>Urospora</i> sp.						
H <sub>1</sub>	0	×	+	+							
D <sub>1</sub>	-	0	-	-							
S <sub>1</sub>	0	-	-	×							
Indirect effect sequence					Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
									Types	Sequences/ type	Total number
P <sub>1</sub> -D <sub>1</sub> +P <sub>1</sub> (-)					131	PBP	++n	p/f	1	1	1
P <sub>1</sub> -D <sub>1</sub> +H <sub>1</sub> (-)					132	PBH	++n	p/hs	1	1	1
P <sub>1</sub> -D <sub>1</sub> -S <sub>1</sub> (+)					135	PBB	--p	p/c	1	1	1
H <sub>1</sub> -S <sub>1</sub> -D <sub>1</sub> (+)					253	HBB	--p	p/c	1	1	1
H <sub>1</sub> -S <sub>1</sub> -D <sub>1</sub> (+)					253	HBB	--p	p/ir	1	1	0
D <sub>1</sub> +P <sub>1</sub> -D <sub>1</sub> (-)					313	PBP	++n	f/p	1	1	1
D <sub>1</sub> +H <sub>1</sub> -S <sub>1</sub> (-)					325	HBB	++n	hs/p	1	1	1
S <sub>1</sub> -D <sub>1</sub> +H <sub>1</sub> (-)					532	BBH	++n	ir/hs	1	1	1
Total									8	8	7

Web 5: Northern Gulf of California Mid Intertidal Intermediate (Dungan 1986, 1987)

Direct interaction matrix					Web components						
P <sub>1</sub>	H <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>								
P <sub>1</sub>	×	0	+	0	<b>P<sub>1</sub>, <i>Acanthina angelica</i></b> <b>H<sub>1</sub>, <i>Lottia strongiana</i></b> <b>S<sub>1</sub>, <i>Chthamalus anisopoma</i></b> S <sub>2</sub> , <i>Ralfsia</i> sp.						
H <sub>1</sub>	0	×	-	+							
S <sub>1</sub>	-	0	×	-							
S <sub>2</sub>	0	-	-	×							
Indirect effect sequence					Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
									Types	Sequences/ type	Total number
P <sub>1</sub> -S <sub>1</sub> -H <sub>1</sub> (+)					152	PBH	--p	p/ir	1	1	1
P <sub>1</sub> -S <sub>1</sub> -S <sub>2</sub> (+)					155	PBB	--p	p/c	1	1	1
H <sub>1</sub> -S <sub>1</sub> -S <sub>2</sub> (+)+P <sub>1</sub> (+)					2551	HBBP	--p+p	p/c/f	1	1	2
S <sub>1</sub> -H <sub>1</sub> -S <sub>2</sub> (+)					525	HBB	--p	if/p	1	1	1
S <sub>2</sub> -S <sub>1</sub> -H <sub>1</sub> (+)					552	BBH	--p	c/ir	1	1	1
S <sub>2</sub> -S <sub>1</sub> +P <sub>1</sub> (-)					551	PBP	++n	c/f	1	1	1
Total									6	6	7

Web 6: Pacific Coast, Costa Rica, Mid Intertidal Intermediate (Ortega 1985, Sutherland and Ortega 1986, Sutherland 1990)

Direct interaction matrix					Web components						
P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>							
P <sub>1</sub>	×	0	0	+	0	<b>P<sub>1</sub>, <i>Acanthina brevidentata</i></b> <b>H<sub>1</sub>, <i>Fissurella virescens</i></b> <b>H<sub>2</sub>, <i>Siphonaria gigas</i></b> <b>S<sub>1</sub>, <i>Chthamalus fissus</i></b> S <sub>2</sub> , microalgae					
H <sub>1</sub>	0	-	0	0	+						
H <sub>2</sub>	0	0	-	-	+						
S <sub>1</sub>	-	0	0	×	0						
S <sub>2</sub>	0	-	-	0	×						
Indirect effect sequence					Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
									Types	Sequences/ type	Total number
P <sub>1</sub> -S <sub>1</sub> -H <sub>2</sub> (+)					152	PBH	--p	p/ir	1	1	1

## APPENDIX 1. Continued.

Direct interaction matrix										Web components
Web 7: Oregon High Intertidal Intermediate (Boiler Bay) (Marsh 1986a, b, Farrell 1988, 1991)										
	P <sub>1</sub>	H <sub>1</sub>	D <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>				
P <sub>1</sub>	×	+	0	0	0	0				P <sub>1</sub> , <i>Arenaria melanocephala</i>
H <sub>1</sub>	-	×	+	-	0	+				H <sub>1</sub> , <i>Lottia digitalis</i> / <i>L. strigatella</i>
D <sub>1</sub>	0	-	×	+	0	0				D <sub>1</sub> , <i>Pelvetiopsis limitata</i> <i>Endocladia muricata</i>
S <sub>1</sub>	0	-	-	×	0	0				S <sub>1</sub> , <i>Balanus glandula</i>
S <sub>2</sub>	0	0	0	-	×	0				S <sub>2</sub> , <i>Chthamalus dalli</i>
S <sub>3</sub>	0	-	0	0	0	×				S <sub>3</sub> , microalgae
Web 8: Cape Banks, Sydney, Australia Mid Intertidal Intermediate (Underwood and Jernakoff 1981, 1984, Creese 1982, Jernakoff 1983, Underwood et al. 1983, Fairweather 1985, 1990, Fletcher and Creese 1985)										
	P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	H <sub>3</sub>	D <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>		
P <sub>1</sub>	×	0	+	+	0	+	+	+		P <sub>1</sub> , <i>Morula marginalba</i>
H <sub>1</sub>	0	-	0	0	±	-	-	+		H <sub>1</sub> , <i>Cellana tramoserica</i>
H <sub>2</sub>	-	-	×	0	±	+	0	+		H <sub>2</sub> , <i>Patelloida latistrigata</i>
H <sub>3</sub>	-	0	0	-	+	+	0	+		H <sub>3</sub> , <i>Littorina unifasciata</i>
D <sub>1</sub>	0	-	-	-	×	-	0	0		D <sub>1</sub> , <i>ulvoids</i>
S <sub>1</sub>	-	-	0	0	-	-	-	-		S <sub>1</sub> , <i>Tesseropora rosea</i>
S <sub>2</sub>	-	0	0	0	-	-	-	-		S <sub>2</sub> , <i>Chamaesipho columna</i>
S <sub>3</sub>	0	-	-	-	0	0	0	×		S <sub>3</sub> , microalgae
Web 9: Southern California Upper Shore (Santa Catalina Island) (Robles 1987)										
	P <sub>1</sub>	D <sub>1</sub>	I <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>		
P <sub>1</sub>	×	+	+	+	0	0	0	0		P <sub>1</sub> , <i>Panulirus interruptus</i>
D <sub>1</sub>	-	×	0	0	+	+	+	+		D <sub>1</sub> , <i>Mytilus californianus</i>
I <sub>1</sub>	-	0	×	0	+	+	+	+		I <sub>1</sub> , <i>Mytilus edulis</i>
S <sub>1</sub>	0	0	0	×	+	+	+	+		S <sub>1</sub> , <i>Brachidontes adamsianus</i>
S <sub>2</sub>	0	-	-	0	×	0	0	0		S <sub>2</sub> , <i>Gigartina canaliculata</i>
S <sub>3</sub>	0	-	-	0	0	×	0	0		S <sub>3</sub> , <i>Pterocladia capillacea</i>
S <sub>4</sub>	0	-	-	0	0	0	×	0		S <sub>4</sub> , <i>Laurencia pacifica</i>
S <sub>5</sub>	0	-	-	0	0	0	0	×		S <sub>5</sub> , <i>Rhodoglossum affine</i>
Web 10: Pacific Coast, Panama, High Intertidal Intermediate (Taboguilla Island) (Garrity and Levings 1981, Lubchenco et al. 1984)										
	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	H <sub>1</sub>	H <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>		
P <sub>1</sub>	×	0	0	+	+	0	0	0		P <sub>1</sub> , <i>Arothron meleagris</i>
P <sub>2</sub>	0	×	0	+	+	0	0	0		P <sub>2</sub> , <i>Diodon hystrix</i>
P <sub>3</sub>	-	-	×	0	+	0	0	0		P <sub>3</sub> , <i>Purpura pansa</i>
P <sub>4</sub>	-	-	0	×	0	0	0	+		P <sub>4</sub> , <i>Acanthina brevidentata</i>
H <sub>1</sub>	-	-	-	0	×	0	+	0		H <sub>1</sub> , <i>Nerita scabricosta</i>
H <sub>2</sub>	0	0	0	0	-	×	+	0		H <sub>2</sub> , <i>Littorina modesta</i>
S <sub>1</sub>	0	0	0	0	-	-	×	0		S <sub>1</sub> , microalgae
S <sub>2</sub>	0	0	0	-	-	0	0	×		S <sub>2</sub> , <i>Chthamalus fissus</i>
Web 11: San Jan Island (Pile Point) Washington, Mid/Low Intermediate (Dethier and Duggins 1984, 1988, Duggins and Dethier 1985)										
	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	D <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>		
H <sub>1</sub>	×	0	+	+	+	+	+	+		H <sub>1</sub> , <i>Katharina tunicata</i>
H <sub>2</sub>	0	×	+	+	+	0	0	0		H <sub>2</sub> , <i>Lottia</i> spp.
D <sub>1</sub>	-	0	×	-	0	0	0	0		D <sub>1</sub> , <i>Hedophyllum sessile</i>
D <sub>2</sub>	-	0	0	×	0	0	0	0		D <sub>2</sub> , large brown algae
S <sub>1</sub>	-	-	-	-	×	-	-	-		S <sub>1</sub> , microalgae
S <sub>2</sub>	-	0	-	-	0	×	0	0		S <sub>2</sub> , thin bladed algae
S <sub>3</sub>	-	0	-	-	0	0	×	0		S <sub>3</sub> , finely branched algae
S <sub>4</sub>	-	0	-	-	0	0	0	×		S <sub>4</sub> , corticated algae
Web 12: Southern California Boulderfield Low Intermediate (Santa Barbara, California) (Sousa 1979)										
	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	I <sub>1</sub>	I <sub>2</sub>	I <sub>3</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	
H <sub>1</sub>	×	0	+	0	0	0	0	0	0	H <sub>1</sub> , <i>Pachygrapsus crassipes</i>
H <sub>2</sub>	0	×	+	-	0	0	0	0	0	H <sub>2</sub> , <i>Lottia</i> spp.
D <sub>1</sub>	-	-	×	-	-	-	0	0	0	D <sub>1</sub> , <i>Ulva</i> spp.
I <sub>1</sub>	0	0	-	-	-	-	0	0	0	I <sub>1</sub> , <i>Gigartina canaliculata</i>
I <sub>2</sub>	0	0	-	-	×	-	0	0	-	I <sub>2</sub> , <i>Gelidium coulteri</i>
I <sub>3</sub>	0	0	-	-	-	×	0	0	0	I <sub>3</sub> , <i>Gigartina leptorhynchus</i>
S <sub>1</sub>	0	0	-	-	-	-	×	0	0	S <sub>1</sub> , <i>Chthamalus fissus</i>
S <sub>2</sub>	0	0	-	-	-	-	-	×	0	S <sub>2</sub> , <i>Rhodoglossum affine</i>
S <sub>3</sub>	0	0	-	0	0	0	0	×	0	S <sub>3</sub> , bluegreen algae
Web 13: New England Mid Intermediate (Grindstone Neck, Maine) (Menge 1976, 1991a, b; Lubchenco 1983, 1986; B. A. Menge and J. Lubchenco, unpublished data)										
	P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	I <sub>1</sub>	I <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	
P <sub>1</sub>	×	0	0	+	+	+	0	0	0	P <sub>1</sub> , <i>Nucella lapillus</i>
										H <sub>1</sub> , <i>Littorina littorea</i>
										H <sub>2</sub> , <i>L. obtusata</i>

APPENDIX 1. Continued.

Indirect effect sequence	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
					Types	Sequences/ type	Total number
<b>Web 7:</b>							
$P_1 - H_1 - D_1(+)$	123	<u>PHB</u>	--p	p/p	1	1	1
$P_1 - H_1 - S_1(+)$	125	<u>PHB</u>	--p	p/ir	1	1	1
$H_1 - S_1 - S_2(+)$	255	<u>HBB</u>	--p	ir/c	1	1	1
$S_1 - H_1 - D_1(+)$	523	<u>BHB</u>	--p	if/p	1	1	1
$S_1 + H_1 - S_1(-)$	525	<u>BHB</u>	+ -n	f/ir	1	1	1
Total					5	5	5
<b>Web 8:</b>							
$P_1 - H_{2,3} - D_1(+)$	123	<u>PHB</u>	--p	p/p	1	2	2
$P_1 - S_1 - H_1(+)$	152	<u>PBH</u>	--p	p/ir	1	1	1
$P_1 - S_1 + H_{2,3}(-) - D_1(+)$	1523	<u>PBHB</u>	+ -n -p	p/hs/p	1	2	4
$P_1 - S_1 - S_2(+)$	1553	<u>PBBB</u>	--p -n	p/ir/c	1	1	2
$H_1 - H_2 + P_1(-)$	221	<u>HHP</u>	+ -n	c/f	1	1	1
$H_1 - S_1 + P_1(-)$	251	<u>HPB</u>	+ -n	ir/f	1	1	1
$H_1 - D_1 - H_2(+)$	232	<u>HBB</u>	--p	ir/ir	1	1	1
$H_1 - S_1 - H_1(+)$	252	<u>HBB</u>	--p	ir/ir	1	1	1
$H_1 - S_1 + H_{2,3}(-)$	252	<u>HBB</u>	+ -n	ir/hs	1	2	2
$H_1 - S_1 - S_2(+)$	255	<u>HBB</u>	--p	ir/c	1	1	1
$H_1 - D_1 - S_1(+)$	235	<u>HBB</u>	--p	p/ir	1	1	1
$H_1 - S_1 - S_2(+)$	255	<u>HBB</u>	--p	p/ir	1	1	1
$H_2 + P_1 - S_1(-)$	215	<u>HPB</u>	+ -n	f/p	1	1	1
$H_2 + P_1 - H_2(-)$	212	<u>HPB</u>	+ -n	f/p	1	1	1
$D_1 - S_1 + P_1(-)$	351	<u>BPP</u>	+ -n	c/f	1	1	1
$S_1 + P_1 - H_2(-)$	512	<u>BPB</u>	+ -n	f/p	1	1	1
$S_1 + P_1 - S_2(+)$	515	<u>BPB</u>	+ -n	f/p	1	1	1
Total					15	20	23
<b>Web 9:</b>							
$P_1 - D_1 - S_2 \epsilon(+)$	135	<u>PBB</u>	--p	p/c	1	4	4
$P_1 - I_1 - S_2 \epsilon(+)$	145	<u>PBB</u>	--p	p/c	1	4	4
Total					1	8	8
<b>Web 10:</b>							
$P_{1,2} - P_1 - H_1(+)$	112	<u>PPH</u>	--p	p/p	1	2	2
$P_{1,2} - P_1 - S_2(+)$	115	<u>PPB</u>	--p	p/p	1	2	2
$P_{1,2} - H_1 + P_1(-)$	121	<u>PHB</u>	+ -n	p/f	1	2	2
$P_{1,3} - H_1 - H_2(+)$	122	<u>PHB</u>	--p	p/c	1	3	3
$P_2 - H_1 - S_2(+)$	1251	<u>PHBP</u>	+ -n +p	p/ir/f	1	1	2
$H_1 - S_2 + P_2(-)$	251	<u>HBP</u>	+ -n	ir/f	1	1	1
$S_2 + P_2 + P_{1,2}(+)$	511	<u>BPP</u>	+ +p	f/f	1	2	2
Total					7	13	14
<b>Web 11:</b>							
$H_1 - D_{1,2} + H_2(-)$	232	<u>HBB</u>	+ -n	p/hs	1	2	1
$H_1 - D_{1,2} - S_{1,4}(+)$	235	<u>HBB</u>	--p	p/c	1	8	4
$D_1 - S_1 + H_2(-)$	352	<u>BHB</u>	+ -n	c/f	1	1	1
$H_1 - D_1 - S_1(+)$	2352	<u>HBBH</u>	+ -n +p	p/c/f	1	1	1
Total					4	12	7
<b>Web 12:</b>							
$H_1 - D_1 - I_{1,3}(+)$	234	<u>HBB</u>	--p	p/ir	1	3	3
$H_1 - D_1 - S_{2,4}(+)$	235	<u>HBB</u>	--p	p/ir	1	2	2
$H_2 - D_1 - S_1(+)$	235	<u>HBB</u>	--p	p/ir	1	1	1
$D_1 + H_{1,2} - D_1(-)$	323	<u>BHB</u>	+ -n	f/p	1	2	2
$D_1 - I_1 - I_{1,2}(+)$	344	<u>BBB</u>	--p	ir/ir	1	2	2
$I_{1,4} - D_1 + H_1(-)$	432	<u>BHB</u>	+ -n	c/f	1	3	3
$I_1 - D_1 - I_1(+)$	434	<u>BBB</u>	--p	ir/c	1	1	1
$I_2 + S_1 - I_2(-) - I_{1,3}(+)$	4544	<u>BBBB</u>	+ -n -p	hs/c/c	1	2	3
Total					6	16	17
<b>Web 13:</b>							
$P_1 - D_1 - H_{1,2}(+)$	132	<u>PBH</u>	--p	p/ir	1	2	2
$P_1 - D_1 - I_1(+)$	134	<u>PBB</u>	--p	p/c	1	1	1
$P_1 - D_1 - S_{1,3}(+)$	135	<u>PBB</u>	--p	p/c	1	2	2

## APPENDIX 1. Continued.

Direct interaction matrix										Web components	
Web 13: Continued											
	P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	I <sub>1</sub>	I <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>		
H <sub>1</sub>	0	×	0	-	+	+	0	+	+	D <sub>1</sub> , <i>Mytilus edulis</i>	
H <sub>2</sub>	0	0	×	-	0	+	0	+	+	I <sub>1</sub> , <i>Semibalanus balanoides</i>	
D <sub>1</sub>	-	0	0	-	+	0	0	0	0	I <sub>2</sub> , <i>Fucus vesiculosus</i>	
I <sub>1</sub>	-	0	0	-	×	-	0	0	-	S <sub>1</sub> , algal crusts	
I <sub>2</sub>	0	-	0	-	+	×	0	-	-	S <sub>2</sub> , epiphytes	
S <sub>1</sub>	0	0	0	-	-	+	×	0	-	S <sub>3</sub> , ephemeral algae	
S <sub>2</sub>	0	-	-	0	0	+	0	×	0		
S <sub>3</sub>	0	-	-	-	0	-	0	0	×		
Web 14: South Africa West Coast Mid/Low Protected (Granatina Bay, Groenriver) (R. Bustamante and G. M. Branch, personal communication; Day et al. 1991)											
	H <sub>1</sub>	H <sub>2</sub>	H <sub>3</sub>	I <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>	S <sub>6</sub>	
H <sub>1</sub>	×	0	0	-	0	0	0	0	+	+	H <sub>1</sub> , <i>Patella granatina</i>
H <sub>2</sub>	0	×	0	-	0	0	0	0	+	0	H <sub>2</sub> , <i>P. granularis</i>
H <sub>3</sub>	0	0	×	-	0	0	0	0	+	0	H <sub>3</sub> , <i>Oxystele</i> spp.
I <sub>1</sub>	-	0	0	×	0	0	0	0	0	0	I <sub>1</sub> , <i>Gunnarea capensis</i>
S <sub>1</sub>	-	-	0	0	×	0	0	0	0	0	S <sub>1</sub> , ephemeral algae ( <i>Porphyra capensis</i> , <i>Ulva</i> sp.)
S <sub>2</sub>	-	-	0	0	0	×	0	0	0	0	S <sub>2</sub> , foliose algae ( <i>Iridaea capensis</i> , <i>Gigartina</i> spp.)
S <sub>3</sub>	-	-	0	0	0	0	×	0	0	0	S <sub>3</sub> , <i>Aeodes</i> sp.
S <sub>4</sub>	-	-	0	0	0	0	0	×	0	0	S <sub>4</sub> , <i>Caulacanthus ustulatus</i>
S <sub>5</sub>	-	-	-	0	0	0	0	0	×	0	S <sub>5</sub> , microalgae
S <sub>6</sub>	0	0	0	0	0	0	0	0	0	×	S <sub>6</sub> , drift kelp (an external source)
Web 15: Southern California Low Intertidal Exposed (Santa Catalina Island) (Robles and Robb 1993)											
	P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	I <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>	
P <sub>1</sub>	×	+	+	+	+	+	0	0	0	0	P <sub>1</sub> , <i>Panulirus interruptus</i>
H <sub>1</sub>	0	×	0	0	0	0	+	+	+	+	H <sub>1</sub> , limpets
H <sub>2</sub>	-	0	×	0	0	0	+	+	+	+	H <sub>2</sub> , chitons
D <sub>1</sub>	-	0	0	×	0	0	±	±	±	±	D <sub>1</sub> , <i>Mytilus californianus</i>
I <sub>1</sub>	-	0	0	-	×	0	+	+	+	+	I <sub>1</sub> , <i>Mytilus edulis</i>
S <sub>1</sub>	-	0	0	-	0	×	+	+	+	+	S <sub>1</sub> , <i>Brachidontes adamsianus</i>
S <sub>2</sub>	0	0	0	±	-	0	×	0	0	0	S <sub>2</sub> , <i>Corallina officinalis</i>
S <sub>3</sub>	0	0	0	±	-	0	0	×	0	0	S <sub>3</sub> , <i>Gigartina canaliculata</i>
S <sub>4</sub>	0	0	0	±	-	0	0	0	×	0	S <sub>4</sub> , <i>Laurencia pacifica</i>
S <sub>5</sub>	0	0	0	±	-	0	0	0	0	×	S <sub>5</sub> , <i>Gelidium coulteri</i>
Web 16: Southern California Low Intertidal Protected (Santa Catalina Island) (Robles and Robb 1993)											
	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	D <sub>1</sub>	I <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>	
P <sub>1</sub>	×	0	0	+	+	+	0	0	0	0	P <sub>1</sub> , <i>Panulirus interruptus</i>
P <sub>2</sub>	0	×	0	+	+	+	0	0	0	0	P <sub>2</sub> , labrid fishes
P <sub>3</sub>	0	0	×	+	+	+	0	0	0	0	P <sub>3</sub> , <i>Ceratostoma nuttalli</i>
D <sub>1</sub>	-	-	0	×	0	0	+	+	+	+	D <sub>1</sub> , <i>Mytilus californianus</i>
I <sub>1</sub>	-	-	0	-	×	0	+	+	+	+	I <sub>1</sub> , <i>Mytilus edulis</i>
S <sub>1</sub>	-	-	0	-	0	×	+	+	+	+	S <sub>1</sub> , <i>Brachidontes adamsianus</i>
S <sub>2</sub>	0	0	0	-	-	0	×	0	0	0	S <sub>2</sub> , <i>Corallina officinalis</i>
S <sub>3</sub>	0	0	0	-	-	0	0	×	0	0	S <sub>3</sub> , <i>Gigartina canaliculata</i>
S <sub>4</sub>	0	0	0	-	-	0	0	0	×	0	S <sub>4</sub> , <i>Laurencia pacifica</i>
S <sub>5</sub>	0	0	0	-	-	0	0	0	0	×	S <sub>5</sub> , <i>Gelidium coulteri</i>
Web 17: New England Low Protected (Canoe Beach Cove, Nahant, Massachusetts) (Lubchenco and Menge 1978, Lubchenco 1980, 1983)											
	P <sub>1</sub>	P <sub>2</sub>	H <sub>1</sub>	D <sub>1</sub>	I <sub>1</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>	
P <sub>1</sub>	×	0	0	+	+	0	0	0	0	0	P <sub>1</sub> , <i>Asterias</i> spp.
P <sub>2</sub>	0	×	+	+	+	0	0	0	0	0	P <sub>2</sub> , <i>Carcinus maenas</i>
H <sub>1</sub>	0	-	×	+	+	+	0	0	+	+	H <sub>1</sub> , <i>Littorina littorea</i>
D <sub>1</sub>	-	-	0	×	+	+	0	0	0	0	D <sub>1</sub> , <i>Mytilus edulis</i>
I <sub>1</sub>	-	-	0	-	×	-	0	0	0	0	I <sub>1</sub> , <i>Semibalanus balanoides</i>
S <sub>1</sub>	0	0	0	-	-	×	-	0	0	0	S <sub>1</sub> , <i>Chondrus crispus</i>
S <sub>2</sub>	0	0	-	-	±	+	×	0	0	0	S <sub>2</sub> , ephemeral algae
S <sub>3</sub>	0	0	0	-	-	-	-	×	0	0	S <sub>3</sub> , fleshy red encrusting algae
S <sub>4</sub>	0	0	0	-	-	-	-	0	×	0	S <sub>4</sub> , encrusting coralline algae
S <sub>5</sub>	0	0	0	-	-	-	-	0	0	×	S <sub>5</sub> , <i>Ralfsia</i> sp.

APPENDIX 1. Continued.

Indirect effect sequence	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
					Types	Sequences/ type	Total number
Web 13:							
$P_2 - I_1 + I_2(-)$	144	<b>PBB</b>	$- + n$	p/hs	1	1	1
$H_1 - I_2 - I_1(+)$	244	<b>HBB</b>	$-- p$	p/c	1	1	1
$H_{1,2} - S_2 - I_2(+)$	254	<b>HBB</b>	$-- p$	p/c		2	1
$H_1 - S_1 - S_1(+)$	255	<b>HBB</b>	$-- p$	p/c		1	1
$D_1 + P_1 - D_1(-)$	313	<b>BPB</b>	$+ + n$	f/p	1	1	1
$D_1 + P_1 - I_1(-)$	314	<b>BPB</b>	$+ + n$	f/p		1	1
$D_1 - I_1 + H_1(-)$	342	<b>BBH</b>	$- + n$	c/hs	1	1	1
$D_1 - I_2 + H_{1,2}(-)$	342	<b>BBH</b>	$- + n$	c/f	1	2	2
$D_1 - I_1 + S_2(-)$	345	<b>BBS</b>	$- + n$	c/hs	1	1	1
$I_1 + H_1 - I_2(-)$	424	<b>BHB</b>	$+ + n$	ct/p	1	1	1
$I_1 + H_1 - S_1(-)$	425	<b>BHB</b>	$+ + n$	ct/p		1	1
$I_1 + I_2 + H_{1,2}(+)$	442	<b>BBH</b>	$+ + p$	hs/f	1	2	2
$I_1 + I_2 + S_{1,2}(+)$	445	<b>BBS</b>	$+ + p$	ct/hs	1	2	2
$I_2 + P_1 - D_1(-)$	413	<b>BPB</b>	$+ + n$	hs/p	1	1	1
$I_2 + P_1 - I_1(-)$	414	<b>BPB</b>	$+ + n$	hs/p		1	1
$I_2 + H_{1,2} - S_2(-)$	425	<b>BBS</b>	$+ + n$	hs/p	1	2	1
$I_2 + H_{1,2} - S_2(-) - I_2(+)$	4254 <sup>c</sup>	<b>BHBS</b>	$+ + n - p$	hs/p/c	1	2	1
$I_2 + H_{1,2} - S_2(-) - I_2(+)$	4254	<b>BHBS</b>	$+ + n - p$	hs/p/ir	1	2	2
$I_2 - I_1 + P_1(-)$	441	<b>BBP</b>	$- + n$	ir/f	1	1	1
$I_2 + S_2 + H_{1,2}(+)$	452	<b>BBH</b>	$+ + p$	ct/hs	1	2	2
$S_2 + H_{1,2} - S_1(-)$	525	<b>BHB</b>	$+ + n$	f/p	1	2	2
$S_2 + H_{1,2} - S_2(-)$	525	<b>BHB</b>	$+ + n$	f/p		2	2
$S_2 + H_1 - S_1(-) - S_1(+)$	5255	<b>BHBS</b>	$+ + n - p$	f/p/c	1	1	2
Total					19	38	36
Web 14:							
$S_2 + H_{1,2} - S_1(-)$	525	<b>BHB</b>	$+ + n$	f/p	1	2	1
$S_6 + H_1 - S_{2,3}(-)$	525	<b>BHB</b>	$+ + n$	f/p		2	2
$I_1 - H_{1,2} - S_1(+)$	425	<b>BHB</b>	$-- p$	c/p	1	2	1
$S_2 + H_1 - I_1(-)$	425	<b>BHB</b>	$+ + n$	f/c	1	1	1
Total					3	7	5
Web 15:							
$P_1 - D_1 - S_{2,3}(+)$	135	<b>PBB</b>	$-- p$	p/c	1	1	4
$P_1 - I_1 - S_{2,3}(+)$	145	<b>PBB</b>	$-- p$	p/c		1	4
Total					1	2	8
Web 16:							
$P_1 - D_1 + P_3(-)$	131	<b>PBP</b>	$- + n$	p/f	1	1	1
$P_1 - I_1 + P_3(-)$	141	<b>PBP</b>	$- + n$	p/f		1	1
$P_{1,2} - D_1 - S_{2,3}(+)$	135	<b>PBB</b>	$-- p$	p/c	1	8	8
$P_{1,2} - I_1 - S_{2,3}(+)$	145	<b>PBB</b>	$-- p$	p/c		8	8
Total					2	18	18
Web 17:							
$P_{1,2} - D_1 - H_1(+)$	132	<b>PBH</b>	$-- p$	p/if	1	2	2
$P_{1,2} - D_1 - I_1(+)$	134	<b>PBB</b>	$-- p$	p/c	1	2	2
$P_{1,2} - D_1 - S_{1,2}(+)$	135	<b>PBB</b>	$-- p$	p/c		10	10
$P_1 - I_1 - S_{2,3}(+)$	145	<b>PBB</b>	$-- p$	p/c		4	0
$H_1 - S_2 - I_1(+)$	254	<b>HBB</b>	$-- p$	p/ir	1	1	1
$H_1 - S_2 - S_{1,2,3}(+)$	255	<b>HBB</b>	$-- p$	p/c	1	4	4
$D_1 + P_1 - D_1(-)$	313	<b>BPB</b>	$+ + n$	f/p	1	1	1
$D_1 + P_1 - I_1(-)$	314	<b>BPB</b>	$+ + n$	f/p		1	1
$I_1 + P_1 - D_1(-)$	413	<b>BPB</b>	$+ + n$	f/p		1	1
$D_1 - S_1 + H_1(-)$	352	<b>BBH</b>	$- + n$	c/hs	1	1	1
$D_1 - S_2 + H_1(-)$	352	<b>BBH</b>	$- + n$	c/f	1	1	1
Total					7	28	24

APPENDIX 1. Continued.

Direct interaction matrix													Web components	
Web 18: South African West Coast Mid/Low Exposed (Island Point, Groenriver) (R. Bustamante and G. M. Branch, <i>personal communication</i> ; Bosman et al., 1987, Griffiths and Hockey 1987, Bosman and Hockey 1988a, b, Branch and Griffiths 1988, Day et al. 1991, Griffiths et al. 1992, Hockey and van Schurink 1992)														
P <sub>1</sub>	P <sub>2</sub>	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	I <sub>1</sub>	I <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>			
P <sub>1</sub>	×	0	0	0	+	0	0	0	0	0	0	0	P <sub>1</sub> , <i>Nucella cingulata</i>	
P <sub>2</sub>	0	×	0	0	+	0	0	0	0	0	0	0	P <sub>2</sub> , <i>N. dubia</i>	
H <sub>1</sub>	0	0	×	0	-	0	0	0	0	0	+	0	H <sub>1</sub> , <i>Patella argenvillei</i>	
H <sub>2</sub>	0	0	0	×	0	0	0	0	0	0	+	0	H <sub>2</sub> , <i>P. granularis</i>	
D <sub>1</sub>	0	0	0	-	0	×	0	0	0	0	0	0	D <sub>1</sub> , <i>Mytilus galloprovincialis</i>	
I <sub>1</sub>	0	0	0	0	-	×	0	0	0	0	0	0	I <sub>1</sub> , <i>Gunnarea capensis</i>	
I <sub>2</sub>	0	0	0	0	-	0	0	×	0	0	0	0	I <sub>2</sub> , <i>Champia lumbricalis</i>	
S <sub>1</sub>	0	0	0	-	0	0	0	×	0	0	0	0	S <sub>1</sub> , ephemeral algae ( <i>Porphyra capensis</i> , <i>Ulva</i> sp.)	
S <sub>2</sub>	0	0	0	-	0	0	-	-	×	0	0	0	S <sub>2</sub> , foliose algae ( <i>Iridaea capensis</i> , <i>Gigartina</i> spp.)	
S <sub>3</sub>	0	0	0	0	-	0	-	-	-	×	0	0	S <sub>3</sub> , coralline crusts ( <i>Spongite</i> spp., <i>Phymatolithon acervatum</i> , <i>Leptophyton ferox</i> , <i>Mesophyllum</i> spp.)	
S <sub>4</sub>	0	0	0	0	+	0	0	0	0	0	0	×	S <sub>4</sub> , microalgae	
S <sub>5</sub>	0	0	0	0	0	0	0	0	0	0	0	×	S <sub>5</sub> , <i>Bunodactis raynaudi</i>	
Web 19: Southern Chile, Low/Mid Intertidal Intermediate (Moreno and Jaramillo 1983, Jara and Moreno 1984, Moreno et al. 1984, 1986, Godoy and Moreno 1989)														
P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	H <sub>3</sub>	D <sub>1</sub>	D <sub>2</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>	S <sub>6</sub>	S <sub>7</sub>	S <sub>8</sub>	
P <sub>1</sub>	×	0	0	0	+	0	+	+	0	0	0	0	0	P <sub>1</sub> , <i>Concholepas concholepas</i>
H <sub>1</sub>	0	×	0	0	0	+	0	0	+	+	+	0	+	H <sub>1</sub> , <i>Fissurella picta</i>
H <sub>2</sub>	0	0	×	0	0	+	0	0	0	0	0	0	0	H <sub>2</sub> , <i>Siphonaria lessona</i>
H <sub>3</sub>	0	0	0	×	0	0	0	0	0	0	0	0	+	H <sub>3</sub> , <i>Lottia</i> spp.
D <sub>1</sub>	-	0	0	0	×	0	0	0	0	0	0	0	0	D <sub>1</sub> , <i>Perumytilus purpuratus</i>
D <sub>2</sub>	0	-	0	0	0	×	0	0	0	0	0	0	0	D <sub>2</sub> , <i>Iridaea laminarioides</i>
S <sub>1</sub>	-	0	0	0	-	-	×	0	0	0	0	0	0	S <sub>1</sub> , <i>Jehlium cirratum</i>
S <sub>2</sub>	-	0	0	0	-	-	0	×	0	0	0	0	0	S <sub>2</sub> , <i>Chthamalus scabrosus</i>
S <sub>3</sub>	0	-	0	0	0	-	0	0	×	0	0	0	0	S <sub>3</sub> , <i>Gymnogongrus furcellatus</i>
S <sub>4</sub>	0	-	0	0	0	-	0	0	0	×	0	0	0	S <sub>4</sub> , <i>Ulva rigida</i>
S <sub>5</sub>	0	-	0	0	0	-	0	0	0	0	×	0	0	S <sub>5</sub> , <i>Porphyra columbina</i>
S <sub>6</sub>	0	0	0	0	0	-	0	0	0	-	0	×	0	S <sub>6</sub> , encrusting coralline algae
S <sub>7</sub>	0	-	0	0	0	-	0	0	0	0	0	0	×	S <sub>7</sub> , microalgae
S <sub>8</sub>	0	0	0	0	-	-	0	0	0	0	0	0	×	S <sub>8</sub> , <i>Phymactis clematis</i>
Web 20: New England Mid Protected (Canoe Beach Cove, Nahant, Massachusetts) (Lubchenco Menge 1975, Menge 1976, 1991a, Lubchenco 1983, 1986, B. A. Menge and J. Lubchenco, <i>unpublished data</i> )														
P <sub>1</sub>	H <sub>1</sub>	H <sub>2</sub>	D <sub>1</sub>	I <sub>1</sub>	I <sub>2</sub>	I <sub>3</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>3</sub>	S <sub>4</sub>	S <sub>5</sub>	S <sub>6</sub>	S <sub>7</sub>	
P <sub>1</sub>	×	0	0	+	+	+	+	0	0	0	0	0	0	P <sub>1</sub> , <i>Nucella lapillus</i>
H <sub>1</sub>	0	×	0	-	+	+	+	0	0	+	0	+	0	H <sub>1</sub> , <i>Littorina littorea</i>
H <sub>2</sub>	0	0	×	-	0	+	+	0	0	+	0	0	0	H <sub>2</sub> , <i>L. obtusata</i>
D <sub>1</sub>	-	0	0	×	+	0	0	0	0	0	0	0	0	D <sub>1</sub> , <i>Mytilus edulis</i>
I <sub>1</sub>	-	0	0	-	×	-	-	0	0	0	0	0	0	I <sub>1</sub> , <i>Semibalanus balanoides</i>
I <sub>2</sub>	0	0	0	-	+	×	0	0	0	-	-	0	0	I <sub>2</sub> , <i>Ascophyllum nodosum</i>
I <sub>3</sub>	0	0	0	-	+	-	×	0	0	-	0	0	0	I <sub>3</sub> , <i>Fucus vesiculosus</i>
S <sub>1</sub>	0	0	0	-	-	+	+	×	0	0	0	-	0	S <sub>1</sub> , encrusting coralline algae
S <sub>2</sub>	0	0	0	-	-	+	+	0	×	0	0	-	0	S <sub>2</sub> , <i>Hildenbrandia</i> sp.
S <sub>3</sub>	0	0	0	-	-	+	+	0	0	×	0	0	0	S <sub>3</sub> , epiphytic algae
S <sub>4</sub>	0	0	0	-	-	0	0	+	0	0	×	0	0	S <sub>4</sub> , <i>Polysiphonia lanosa</i>
S <sub>5</sub>	0	0	0	0	0	+	+	0	0	-	×	0	0	S <sub>5</sub> , ephemeral algae
S <sub>6</sub>	0	0	0	-	-	0	0	±	-	0	0	0	×	S <sub>6</sub> , <i>Serularia</i> sp.
S <sub>7</sub>	0	0	0	-	0	+	+	0	0	0	0	0	×	S <sub>7</sub> , encrusting bryozoans

APPENDIX 1. Continued.

Indirect effect sequence	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
					Types	Sequences/ type	Total number
Web 18:							
$H_1 - I_2 - S_2(+)$	245	<b>HBB</b>	--p	p/c	1	1	1
$H_1 - S_1 - S_2(+)$	255	<b>HBB</b>	--p	p/c	1	1	1
$H_1 - D_1 + P_1(-)$	231	<b>HBP</b>	+-n	c/f	1	1	1
$H_1 - D_1 + P_2(-)$	231	<b>HBP</b>	+-n	c/hs	1	1	1
$D_1 - H_1 - S_1(+)$	325	<b>BHB</b>	--p	c/p	1	1	1
$D_1 - H_1 - I_2(+)$	324	<b>BHB</b>	--p	c/p	1	1	1
$S_4 + H_1 - S_1(-)$	525	<b>BHB</b>	+-n	f/p	1	1	1
$S_4 + H_2 - S_1(-)$	525	<b>BHB</b>	+-n	f/p	1	1	1
Total					5	8	8
Web 19:							
$P_1 - D_1 - S_{1,2,3}(+)$	135	<b>PBB</b>	--p	p/c	1	3	3
$H_1 - D_2 - S_{1,2}(+) + P_1(+)$	2351	<b>HBBP</b>	--p+p	p/c/f	1	2	3
$H_1 - D_2 - S_{6,8}(+)$	235	<b>HBB</b>	--p	p/c	1	2	2
$D_2 + P_1 - D_1(-)$	313	<b>BPB</b>	+-n	f/p	1	1	1
$S_{1,2} + P_1 - S_{1,2}(-)$	515	<b>BPB</b>	+-n	f/p	1	4	2
$D_2 + H_1 - S_{2,3,4,7}(-)$	325	<b>BHB</b>	+-n	f/p	1	4	4
$S_4 + H_1 - S_{6,7}(-)$	525	<b>BHB</b>	+-n	f/p	1	2	2
$S_4 + H_1 - D_2(-) - S_{1,2,6}(+)$	5235	<b>BHBB</b>	+-n-p	f/p/c	1	3	4
$S_4 + H_1 - D_2(-) - S_{1,2}(+)$	5235	<b>BHBB</b>	+-n-p	f/p/c	1	2	2
Total					6	23	23
Web 20:							
$P_1 - D_1 - H_{1,2}(+)$	132	<b>PBH</b>	--p	p/if	1	2	2
$P_1 - I_1 + H_1(-)$	142	<b>PBH</b>	+-n	p/er	1	1	1
$P_1 - D_1 - I_{2,3}(+)$	134	<b>PBB</b>	--p	p/c	1	2	2
$P_1 - D_1 - S_{1,2,5,7}(+)$	135	<b>PBB</b>	--p	p/c	1	5	5
$P_1 - I_1 + I_2(-)$	144	<b>PBB</b>	+-n	p/er	1	1	1
$P_1 - D_1 - I_1(+)+S_1,7(+)$	1345	<b>PBBB</b>	--p+p	p/ir/hs	1	7	7
$H_1 - I_1 - I_2(+)$	244	<b>HBB</b>	--p	p/ir	1	1	1
$H_{1,2} - S_1 - I_1(+)$	254	<b>HBB</b>	--p	p/c	1	2	2
$H_{1,2} - S_1 - S_2(+)$	255	<b>HBB</b>	--p	p/c	1	2	2
$H_1 - S_1 - S_{1,2}(+)$	255	<b>HBB</b>	--p	p/c	1	2	2
$H_1 - S_1 - S_1(+)$	255	<b>HBB</b>	--p	p/c	1	1	0
$H_{1,2} - S_1 - I_2(+)+S_{6,7}(+)$	2545	<b>HBBB</b>	--p+p	p/c/hs	1	4	8
$D_1 + P_1 - D_1(-)$	313	<b>BPB</b>	+-n	f/p	1	1	1
$D_1 + P_1 - I_1(-)$	314	<b>BPB</b>	+-n	f/p	1	1	1
$I_{2,3} + P_1 - D_1(-)$	413	<b>BPB</b>	+-n	hs/p	1	2	2
$I_{2,3} + P_1 - I_1(-)$	414	<b>BPB</b>	+-n	hs/p	1	2	2
$I_1 + H_1 - I_1(-)$	424	<b>BHB</b>	+-n	er/p	1	1	1
$I_1 + H_1 - S_{1,5}(-)$	425	<b>BHB</b>	+-n	er/p	1	2	2
$I_2 + H_1 - S_1(-)$	425	<b>BHB</b>	+-n	hs/p	1	1	1
$I_3 + H_{1,2} - S_5(-)$	425	<b>BHB</b>	+-n	hs/p	1	2	2
$I_1 + H_2 - S_1(-)$	425	<b>BHB</b>	+-n	hs/p	1	1	1
$I_1 + H_1 - S_{1,5}(-)$	425	<b>BHB</b>	+-n	hs/p	1	2	2
$S_4 + H_1 - I_2(-)$	524	<b>BHB</b>	+-n	f/p	1	1	1
$S_4 + H_{1,2} - S_5(-)$	525	<b>BHB</b>	+-n	f/p	1	2	2
$S_4 + H_1 - S_1(-)$	525	<b>BHB</b>	+-n	f/p	1	1	1
$I_1 + H_1 - S_1(-) - S_{1,2}(+)$	4255	<b>BHBB</b>	+-n-p	er/p/c	1	2	2
$I_{2,3} + H_1 - S_5(-) - S_{1,2}(+)$	4255	<b>BHBB</b>	+-n-p	hs/p/c	1	2	2
$I_{2,3} + H_2 - S_1(-) - S_4(+)$	4255	<b>BHBB</b>	+-n-p	hs/p/c	1	2	1
$I_1 + H_1 - S_1(-) - S_4(+)$	4255	<b>BHBB</b>	+-n-p	hs/p/c	1	1	1
$S_4 + H_1 - S_1(-) - S_{1,2}(+)$	5255	<b>BHBB</b>	+-n-p	f/p/c	1	2	2
$I_{2,3} - I_1 + P_1(-)$	441	<b>BBP</b>	+-n	ir/f	1	2	1
$D_1 - I_1 + H_{1,2}(-)$	342	<b>BBH</b>	+-n	c/er	1	2	2
$D_1 - I_{2,3} + H_{1,2}(-)$	342	<b>BBH</b>	+-n	c/hs	1	4	2
$I_1 + I_1 + H_{1,2}(+)$	442	<b>BBH</b>	++p	er/hs	1	2	2
$I_{2,3} + S_1 + H_{1,2}(+)$	452	<b>BBH</b>	++p	hs/f	1	4	2
$D_1 - I_{2,3} + S_{3,4,6,7}(-)$	345	<b>BBB</b>	+-n	c/hs	1	8	4
$I_2 - I_1 + I_1(-)$	444	<b>BBB</b>	+-n	ir/er	1	1	1
Total					23	81	74



APPENDIX 1. Continued.

Indirect effect sequence	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
					Types	Sequences/ type	Total number
Web 21:							
$P_1 - D_1 + P_{1,2}(-)$	131	PBP	$- + n$	p/f	1	2	2
$P_1 - D_1 - H_{1,2}(+)$	132	PBH	$-- p$	p/c	1	2	2
$P_1 - D_1 - S_{1,12}(+)$	135	PBB	$-- p$	p/c	1	12	12
$P_2 - D_1 - S_{1,2}(+)$	135	PBB	$-- p$	p/c	1	2	2
$H_{1,2} - S_{3,6,9,10,12} + H_{1,2}(-)$	252	HBH	$- + n$	p/f	1	28	4
$H_{1,2} - S_{3,6,9,10,12} - S_{7,8}(+)$	255	HBH	$-- p$	p/c	1	28	4
$D_1 - S_{3,12} + H_{1,2}(\leq 5)$	352	BHH	$- + n$	c/f	1	20	2
$D_2 + P_1 - D_1(-)$	313	BPB	$+ - n$	f/p	1	1	1
$S_{3,12} + H_{1,2} - S_{3,12}(-)$	525	BHB	$+ - n$	f/p	1	126	7
					8	221	36
Web 22:							
$P_{1,2,4} - H_{4,5} - S_{3,4}(+)$	125	PHB	$-- p$	p/p	1	12	2
$P_6 - H_5 - S_{3,5}(+)$	125	PBH	$-- p$	p/p	1	3	3
$P_{1,2} - D_1 - S_6 \text{ } \rho(+)$	135	PBB	$-- p$	p/c	1	8	4
$P_{1,2} - S_1 - S_{3,4,6} \text{ } \rho(+)$	155	PBB	$-- p$	p/c	1	12	6
$P_{2,3} - S_{3,4} - S_6 \text{ } \rho(+)$	155	PBB	$-- p$	p/c	1	12	4
$P_3 - S_1 + D_1(-)$	153	PBB	$- + n$	p/er	1	1	1
$P_1 - S_1 - S_1 + S_{3,4}(-) - S_6 \text{ } \rho(+)$	1555	PBBB	$- + n - p$	p/hs/c	1	32	8
$P_5 - H_2 - S_{3,5}(+) + D_1(+)$	1253	PHBB	$-- p + p$	p/p/er	1	3	4
$P_5 - H_{4,5} - S_6(+)-S_{7,9}(-)$	1253	PHBB	$-- p - n$	p/p/c	1	6	4
$H_{1,4} - S_1 + D_1(-)$	253	HBH	$- + n$	p/er	1	2	1
$H_1 - S_{4,5} + D_1(-)$	253	HBH	$- + n$	p/er	1	2	1
$H_{1,3} - S_{3,4} - S_6 \text{ } \rho(+)$	255	HBH	$-- p$	p/c	1	24	4
$H_1 - S_{3,5} - S_6(+)$	255	HBH	$-- p$	p/c	1	3	1
$H_4 - S_6 - S_7 \text{ } \rho(+)$	255	HBH	$-- p$	p/c	1	3	3
$H_5 - S_5 - S_6 \text{ } \rho(+)$	255	HBH	$-- p$	p/c	1	4	4
Total					8	127	50
Web 23:							
$P_1 - H_1 - I_1(+)+H_2(+)+P_1(+)$	12421	PHBHP	$-- p + p + p$	p/p/f/f	1	1	3
$P_1 - H_1 - S_{8,10}(+)+H_{2,3}(+)+P_1(+)$	12521	PHBHP	$-- p + p + p$	p/p/f/f	1	6	6
$P_1 - H_1 - S_{8,10}(+)+H_1(+)+P_2(+)$	12521	PHBHP	$-- p + p + p$	p/p/f/f	1	3	1
$P_1 - H_1 - S_6(+)$	125	PHB	$-- p$	p/p	1	1	1
$P_3 - H_2 - I_1(+)+H_1 \text{ } 2(+)+P_1(+)$	12421	PHBHP	$-- p + p + p$	p/p/f/f	1	2	2
$P_3 - H_2 - S_{8,10}(+)+H_1 \text{ } 3(+)+P_1(+)$	12521	PHBHP	$-- p + p + p$	p/p/f/f	1	9	4
$P_1 - H_1 - S_{8,10}(+)+H_1(+)+P_2(+)$	12521	PHBHP	$-- p + p + p$	p/p/f/f	1	3	1
$P_1 - D_1 + P_3(-)$	131	PBP	$- + n$	p/f	1	1	1
$P_1 - S_{1,2} + P_{2,4}(-)$	151	PBP	$- + n$	p/f	1	4	2
$P_1 - I_2 - H_1(+)$	142	PBH	$-- p$	p/f	1	1	1
$P_1 - D_1 - H_{1,3}(+)+P_1(+)$	1321	PBHP	$-- p + p$	p/f/f	1	2	3
$P_1 - D_1 - H_4(+)+P_1(+)$	1321	PBHP	$-- p + p$	p/f/f	1	1	2
$P_1 - D_1 - H_{1,4}(+)-I_1(-)$	1324	PBBH	$-- p - n$	p/f/p	1	2	3
$P_1 - D_1 - H_{1,3,4}(+)-S_{8,10}(-)$	1325	PBBH	$-- p - n$	p/f/p	1	9	4
$P_1 - D_1 - H_3(+)-S_{3,6}(-)$	1325	PBBH	$-- p - n$	p/f/p	1	2	2
$P_1 - D_1 - H_4(+)-S_{6,7}(-)$	1325	PBBH	$-- p - n$	p/f/p	1	2	1
$P_1 - D_1 - H_3(+)-I_1(-)+P_{1,2}(-)$	13241	PBBHP	$-- p - n + n$	p/f/f/f	1	2	3
$P_1 - D_1 - H_3(+)-S_{1,2}(-)+P_{1,2}(-)$	13251	PBBHP	$-- p - n + n$	p/f/f/f	1	4	4
$P_1 - D_1 - H_4(+)-I_1(-)-I_1(+)$	13244	PBBBH	$-- p - n - p$	p/f/p/c	1	1	2
$P_1 - D_1 - H_1(+)-S_1(-)-S_5(+)$	13255	PBBBH	$-- p - n - p$	p/f/p/c	1	1	1
$P_1 - D_1 - H_1(+)-I_1(-)+H_2(-)+P_1(-)$	132421	PBBBHP	$-- p - n + n + n$	p/f/f/p/f/f	1	1	2
$P_1 - D_1 - H_1(+)-S_{8,10}(-)+H_3(-)+P_1(-)$	132521	PBBBHP	$-- p - n + n + n$	p/f/f/p/f/f	1	3	3
$P_1 - D_1 - S_1 \text{ } 10(+)$	135	PBB	$-- p$	p/c	1	10	10
$P_{1,4} - S_1 - S_2(+)$	155	PBB	$-- p$	p/c	1	2	1
$P_1 - I_2 - I_1(+)$	144	PBB	$-- p$	p/c	1	1	1
$P_1 - I_{1,2} - S_{1,3,7,10}(+)$	145	PBB	$-- p$	p/c	1	14	7
$P_4 - I_1 - S_{1,2,7,10}(+)$	145	PBB	$-- p$	p/c	1	6	6
$P_1 - D_1 + S_{3,4}(-)$	135	PBB	$- + n$	p/hs	1	2	2
$P_{1,4} - I_1 + S_1(-)$	145	PBB	$- + n$	p/hs	1	2	2
$P_4 - S_1 + S_1(-)$	155	PBB	$- + n$	p/hs	1	1	1
$P_1 - D_1 + S_2(-)$	135	PBB	$- + n$	p/f	1	1	1
$P_1 - D_1 - I_1(+)+P_{1,2,4}(+)$	1341	PBBP	$-- p + p$	p/c/f	1	3	4
$P_1 - D_1 - I_2(+)+P_1(+)$	1341	PBBP	$-- p + p$	p/c/f	1	1	2
$P_1 - D_1 - S_{1,2}(+)+P_{1,2,4}(+)$	1351	PBBP	$-- p + p$	p/c/f	1	6	5

APPENDIX 1. Continued.

Indirect effect sequence	Numeric code	Interaction code	Effect sequence	Direct interaction sequence	Indirect effects		
					Types	Sequences/ type	Total number
Web 23 Continued:							
$P_1 - I_1 - S_{1,2}(+) + P_{1,2,4}(+)$	1451	PBBP	--p+p	p/c/f		6	2
$P_1 - D_1 - I_3(+) + H_{1,2,4}(+)$	1342	PBBH	--p+p	p/c/f	1	3	4
$P_1 - D_1 - S_{3,6}(+) + H_3(+)$	1352	PBBH	--p+p	p/c/f		2	3
$P_1 - D_1 - S_{6,7}(+) + H_3(+)$	1352	PBBH	--p+p	p/c/f		2	2
$P_1 - D_1 - S_{8,10}(+) + H_{1,4}(+)$	1352	PBBH	--p+p	p/c/f		12	7
$P_1 - I_1 - S_{8,10}(+) + H_{1,4}(+)$	1452	PBBH	--p+p	p/c/f		12	3
$P_1 - I_1 - S_{3,6}(+) + H_3(+)$	1452	PBBH	--p+p	p/c/f		2	2
$P_1 - I_1 - S_{6,7}(+) + H_3(+)$	1452	PBBH	--p+p	p/c/f		2	1
$P_1 - D_1 - I_1(+) + S_{6,9}(+)$	1345	PBBB	--p+p	p/c/hs	1	2	2
$P_1 - D_1 - S_1(+) + S_3(+)$	1355	PBBB	--p+p	p/c/hs		1	1
$P_1 - I_1 - S_1(+) + S_3(+)$	1455	PBBB	--p+p	p/c/hs		1	1
$P_1 - D_1 - I_1(+) - S_{8,10}(-)$	1345	PBBB	--p-n	p/c/c	1	2	2
$H_1 - S_{8,10} + H_3(-)$	252	HBH	+n	p/f	1	3	1
$H_{3,4} - S_{8,10} - S_{6,7}(+)$	255	HBH	--p	p/c	1	12	2
$H_1 - I_1 - S_{1,2}(+)$	245	HBH	--p	ir/c	1	2	2
$H_1 - S_1 - S_2(+)$	255	HBH	--p	ir/c		1	1
$H_4 - I_1 + S_6(-)$	245	HBH	+n	p/hs	1	1	1
$D_1 + P_1 - H_{1,2}(-)$	312	BPB	+n	f/p	1	2	2
$D_1 + P_1 - I_{1,2}(-)$	314	BPB	+n	f/p	1	2	2
$D_1 + P_2 - I_1(-)$	314	BPB	+n	f/p		1	1
$D_1 + P_{1,4} - S_{1,2}(-)$	315	BPB	+n	f/p		4	2
$I_{1,2} + P_1 - D_1(-)$	413	BPB	+n	f/p		2	1
$I_1 + P_1 - I_1(-)$	414	BPB	+n	f/p		1	1
$I_2 + P_1 - I_1(-)$	414	BPB	+n	f/p		1	1
$I_{1,2} + P_1 - S_{1,2}(-)$	415	BPB	+n	f/p		4	2
$I_1 + P_2 - D_1(-)$	413	BPB	+n	f/p		1	1
$I_1 + P_4 - S_{1,2}(-)$	415	BPB	+n	f/p		2	2
$S_{1,2} + P_{1,4} - D_1(-)$	513	BPB	+n	f/p		4	2
$S_{1,2} + P_{1,4} - I_1(-)$	514	BPB	+n	f/p		4	2
$S_{1,2} + P_1 - I_1(-)$	514	BPB	+n	f/p		2	2
$S_{1,2} + P_{1,4} - S_{1,2}(-)$	515	BPB	+n	f/p		8	2
$I_1 + H_{1,2,4} - S_{8,10}(-)$	425	BHH	+n	f/p	1	9	3
$S_6 + H_1 - S_{7,10}(-)$	525	BHH	+n	f/p		4	4
$S_8 + H_{3,4} - S_{6,7,9,10}(-)$	525	BHH	+n	f/p		8	4
$S_9 + H_{3,4} - S_{6,8,10}(-)$	525	BHH	+n	f/p		8	4
$S_{10} + H_{3,4} - S_{6,8}(-)$	525	BHH	+n	f/p		8	4
$S_8 + H_{1,2} - S_{9,10}(-)$	525	BHH	+n	f/p		4	2
$S_9 + H_{1,2} - S_{8,10}(-)$	525	BHH	+n	f/p		4	2
$S_{10} + H_{1,2} - S_{8,9}(-)$	525	BHH	+n	f/p		4	2
$I_1 + S_6 + H_{3,4}(+)$	455	BBH	++p	hs/f	1	2	2
$I_1 + S_9 + H_{1,4}(+)$	455	BBH	++p	hs/f		4	2
$I_1 - S_{8,10} + H_{1,4}(-)$	455	BBH	+n	c/f	1	8	4
$I_1 + S_6 - S_7(-)$	455	BBH	+n	hs/c	1	1	1
Total					27	278	188





APPENDIX 2. Continued.

Subtype of interaction			Web number																				No. of webs with each subtype	Type			
			Region, tidal height, and wave exposure																								
			NE	NE	SC	NE	GOC	CR	PNW	EA	SC	GOP	PNW	SC	NE	SA	SC	SC	NE	SA	CH	NE			CH	GOP	PNW
Interaction code	Effect seq.	Direct inter. seq.	Indirect effects	ME	HE	MI	HI	MI	MI	HE	MI	HP	HI	LI	LI	MI	LMP	LE	LP	LP	LME	MI	MP	MI	LI	LI	
Three-species subtotals			Subtypes	0	0	1	2	0	0	1	8	0	1	2	1	1	0	0	0	2	3	1	2	2	2	4	15
			No. seq.	0	0	2	2	0	0	1	11	0	1	10	6	4	0	0	0	5	4	2	8	56	38	19	169
			No. eff.	0	0	1	2	0	0	1	11	0	1	5	6	3	0	0	0	5	4	2	7	8	14	7	77
Four-species chains																											
<b>HBBP</b>	--p+p	p/c/f	No. seq.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3	2
			No. eff.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	5
<b>HBBB</b>	--p+p	p/c/hs	No. seq.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	4	1
			No. eff.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	8
<b>HBBH</b>	--p-n	p/ir/ir	No. seq.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
			No. eff.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<b>HBBH</b>	--p+p	p/c/f	No. seq.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
			No. eff.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Four-species subtotals			Subtypes	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	4
			No. seq.	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	4	0	0	0	0	9
			No. eff.	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0	0	0	3	8	0	0	0	0	15
Herbivore manipulation subtot.			subtypes	0	0	2	2	1	0	1	8	0	1	3	1	1	0	0	0	2	3	2	3	2	2	4	19
			No. seq.	0	0	3	2	1	0	1	11	0	1	11	6	4	0	0	0	5	4	4	12	56	38	19	178
			No. eff.	0	0	2	2	2	0	1	11	0	1	6	6	3	0	0	0	5	4	5	15	8	14	7	92
Basal species manipulations																											
Three-species chains																											
<b>BHB</b>	+ - n	f/p	No. seq.	0	0	0	0	0	0	0	0	0	0	2	4	4	0	0	0	2	6	4	126	0	49	197	
			No. eff.	0	0	0	0	0	0	0	0	0	0	2	4	3	0	0	0	2	6	4	7	0	26	54	
<b>BHB</b>	+ - n	er/p	No. seq.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0	0	0	0	5	
			No. eff.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0	0	0	0	0	5	
<b>BHB</b>	+ - n	f/ir	No. seq.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
			No. eff.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<b>BHB</b>	+ - n	hs/p	No. seq.	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	6	0	0	0	0	10	
			No. eff.	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	6	0	0	0	0	0	9	
<b>BHB</b>	--p	c/p	No. seq.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	4	
			No. eff.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	3	
<b>BHB</b>	--p	if/p	No. seq.	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
			No. eff.	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
<b>BHB</b>	+ - n	f/c	No. seq.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
			No. eff.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
<b>BPH</b>	+ - n	f/p	No. seq.	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	5	
			No. eff.	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	5	
<b>BPB</b>	+ - n	f/p	No. seq.	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	3	0	5	2	1	0	36	49	
			No. eff.	0	0	1	0	0	0	1	0	0	0	0	0	0	0	3	0	3	2	1	0	21	32		
<b>BPB</b>	+ - n	hs/p	No. seq.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	4	0	0	0	0	0	6	
			No. eff.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	4	0	0	0	0	0	6	
<b>BBP</b>	- + n	c/f	No. seq.	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
			No. eff.	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<b>BBP</b>	- + n	ir/f	No. seq.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	3	
			No. eff.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	
<b>BPP</b>	+ + p	f/f	No. seq.	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
			No. eff.	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<b>BBH</b>	- + n	c/f	No. seq.	0	0	0	0	0	0	0	0	0	1	3	2	0	0	0	1	0	0	0	20	0	8	35	
			No. eff.	0	0	0	0	0	0	0	0	0	1	3	2	0	0	0	1	0	0	0	2	0	4	13	
<b>BBH</b>	- + n	c/hs	No. seq.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	4	0	0	0	6	
			No. eff.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0	4	
<b>BBH</b>	- + n	c/er	No. seq.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	
			No. eff.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	
<b>BBH</b>	- + n	ir/hs	No. seq.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
			No. eff.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<b>BBH</b>	--p	c/if	No. seq.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
			No. eff.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<b>BBH</b>	+ + p	er/hs	No. seq.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	4	
			No. eff.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	4	
<b>BBH</b>	+ + p	hs/f	No. seq.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	4	0	0	0	6	12		
			No. eff.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	4	8		
Three-species subtotals			Subtypes	0	1	1	3	3	0	2	3	0	1	2	10	3	0	0	3	2	10	3	0	5	20		
			No. seq.	0	1	1	3	3	0	2	3	0	2	1	5	20	7	0	0	5	4	11	33	147	0	101	
			No. eff.	0	1	1	3	3	0	2	3	0	2	1	5	19	5	0	0	5	4	9	28	10	0	57	
Four-species chains																											
<b>BHBB</b>	+ - n - p	hs/p/c	No. seq.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	5	0	0	0	7		
			No. eff.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	5		



APPENDIX 3

Estimates of relative impacts of direct and indirect effects in rocky intertidal interaction webs. Change measurements are percent cover for sessile organisms (i.e., species codes D, I, and S) and percent of maximum density for mobile organisms (i.e., species codes P and H). See Appendix 1 for web codes and species webs. Change in density or percent cover of each species (code in italics) due to direct and indirect effects are shown in boldface. "Total change" is the sum of the absolute values of changes due to direct and indirect effects. In the "Species manip." column, - and + indicate that the species abundance was either decreased or increased, respectively.

Web	Species code	Species manip.	Resulting magnitude of change		Total change	% due to indir. effect			
			Direct effect	Indirect effect					
1	D <sub>1</sub>	-D <sub>1</sub>	<b>78I<sub>1</sub></b>	none	78	0			
	I <sub>1</sub>	...	...	...					
	S <sub>1</sub>	...	...	...					
3	H <sub>1</sub>	-H <sub>1</sub>	<b>65S<sub>2</sub></b>	<b>71S<sub>1</sub>, 25S<sub>2</sub></b>	161	60			
	S <sub>1</sub>	-S <sub>1</sub>	...	...					
	S <sub>2,3</sub>	...	...	...					
5	P <sub>1</sub>	-P <sub>1</sub>	<b>45S<sub>1</sub></b>	<b>45S<sub>2</sub>, 80H<sub>1</sub></b>	426	49			
	H <sub>1</sub>	-H <sub>1</sub>	<b>48S<sub>2</sub></b>	<b>25S<sub>1</sub></b>					
	S <sub>1</sub>	-S <sub>1</sub>	<b>83H<sub>1</sub>, 13S<sub>2</sub></b>	<b>58S<sub>2</sub></b>					
	S <sub>2</sub>	-S <sub>2</sub>	<b>29S<sub>1</sub></b>	...					
6	P <sub>1</sub>	-P <sub>1</sub>	<b>65S<sub>1</sub></b>	<b>29H<sub>2</sub></b>	123	24			
	H <sub>1</sub>	±H <sub>1</sub>	...	...					
	H <sub>2</sub>	±H <sub>2</sub>	...	...					
	S <sub>1</sub>	-S <sub>1</sub>	<b>29H<sub>2</sub></b>	...					
7	P <sub>1</sub>	-P <sub>1</sub>	<b>80H<sub>1</sub></b>	<b>50D<sub>1</sub>, 25S<sub>1</sub></b>	511	30			
	H <sub>1</sub>	-H <sub>1</sub>	<b>50D<sub>1</sub>, 25S<sub>1</sub>, 35S<sub>3</sub></b>	<b>30S<sub>2</sub></b>					
	D <sub>1</sub>	-D <sub>1</sub>	<b>5S<sub>1</sub></b>	...					
	S <sub>1</sub>	-S <sub>1</sub>	<b>71S<sub>2</sub>, 50D<sub>1</sub>, 40H<sub>1</sub></b>	<b>50D<sub>1</sub></b>					
	S <sub>2</sub>	-S <sub>2</sub>	...	...					
	S <sub>3</sub>	...	...	...					
	8	P <sub>1</sub>	-P <sub>1</sub>	<b>90H<sub>2</sub>, 53S<sub>1</sub>, 91H<sub>3</sub></b>			<b>52D<sub>1</sub>, 83H<sub>1</sub></b>	1190*	34*
		H <sub>1</sub>	-H <sub>1</sub>	<b>70D<sub>1</sub></b>			<b>90S<sub>1</sub>, 40H<sub>2</sub>*, 100H<sub>2</sub>†</b>		
H <sub>2</sub>		-H <sub>2</sub>	<b>40D<sub>1</sub></b>	<b>47S<sub>1</sub>, 55H<sub>1</sub>*, 20H<sub>2</sub>*, 30H<sub>1</sub>†, 30H<sub>2</sub>†</b>					
H <sub>3</sub>		-H <sub>3</sub>	<b>40D<sub>1</sub></b>	...					
D <sub>1</sub>		...	<b>+100H<sub>1</sub>, -100H<sub>1</sub></b>	...					
S <sub>1</sub>		-S <sub>1</sub>	<b>49H<sub>2</sub>, 91H<sub>1</sub></b>	<b>18H<sub>2</sub></b>					
S <sub>2</sub>		-S <sub>2</sub>	<b>61H<sub>1</sub></b>	...					
S <sub>3</sub>		...	...	...					
9		P <sub>1</sub>	-P <sub>1</sub>	<b>21D<sub>1</sub>/I<sub>1</sub></b>	<b>33S<sub>2,5</sub></b>	54	61		
	D <sub>1</sub> /I <sub>1</sub>	...	...	...					
	S <sub>1,5</sub>	...	...	...					
10	P <sub>1,2</sub>	-P <sub>1,2</sub>	<b>80H<sub>1</sub></b>	<b>20S<sub>2</sub></b>	351	42			
	P <sub>3</sub>	-P <sub>3</sub>	<b>91H<sub>1</sub></b>	<b>31S<sub>2</sub>, 98H<sub>2</sub></b>					
	P <sub>4</sub>	-P <sub>4</sub>	...	...					
	H <sub>1</sub>	-H <sub>1</sub>	<b>31S<sub>2</sub></b>	...					
	H <sub>2</sub>	...	...	...					
	S <sub>1,2</sub>	...	...	...					
11	H <sub>1</sub>	-H <sub>1</sub> , +H <sub>1</sub>	<b>111D<sub>1</sub>, 5S<sub>2</sub>, 5S<sub>3</sub>, 10S<sub>4</sub></b>	<b>100H<sub>2</sub>, 20S<sub>1</sub></b>	313	38			
	H <sub>2</sub>	...	...	...					
	D <sub>1</sub>	-D <sub>1</sub>	<b>20S<sub>1</sub>, 10S<sub>2</sub>, 16S<sub>3</sub>, 16S<sub>4</sub></b>	...					
	D <sub>2</sub>	-D <sub>2</sub>	...	...					
	S <sub>1,4</sub>	...	...	...					
	12	H <sub>1</sub>	-H <sub>1</sub>	<b>79D<sub>1</sub></b>			<b>23I<sub>1</sub></b>	447	22
H <sub>2</sub>		-H <sub>2</sub>	<b>10D<sub>1</sub></b>	<b>7I<sub>1</sub>, 67S<sub>1</sub>, 35S<sub>2</sub></b>					
D <sub>1</sub>		-D <sub>1</sub>	<b>93I<sub>1</sub></b>	...					
I <sub>1</sub>		-I <sub>1</sub>	...	...					
I <sub>2</sub>		-I <sub>2</sub>	<b>80D<sub>1</sub>, 18I<sub>1</sub>, 16I<sub>3</sub></b>	...					
I <sub>3</sub>		-I <sub>3</sub>	<b>17I<sub>1</sub>, 7I<sub>2</sub>, 27D<sub>1</sub></b>	...					
S <sub>1,3</sub>		...	...	...					
13		P <sub>1</sub>	-P <sub>1</sub>	<b>100D<sub>1</sub>, 72I<sub>1</sub></b>	<b>38S<sub>1</sub>, 100H<sub>1</sub>, 100H<sub>2</sub>, 78I<sub>2</sub></b>	1034	44		
	H <sub>1</sub>	-H <sub>1</sub>	<b>9I<sub>2</sub>, 100S<sub>3</sub></b>	<b>2I<sub>1</sub>, 26I<sub>2</sub>, 38S<sub>1</sub></b>					
	H <sub>2</sub>	-H <sub>2</sub>	...	...					
	D <sub>1</sub>	-D <sub>1</sub>	...	...					
	I <sub>1</sub>	-I <sub>1</sub>	...	...					
	I <sub>2</sub>	-I <sub>2</sub>	<b>125S<sub>1</sub>, 44S<sub>1</sub>, 21S<sub>2</sub></b>	...					
	S <sub>1,2</sub>	...	...	...					
	S <sub>3</sub>	-S <sub>3</sub>	...	...					
15	P <sub>1</sub>	-P <sub>1</sub>	<b>91D<sub>1</sub>/I<sub>1</sub>, 77H<sub>1</sub>/H<sub>2</sub></b>	<b>91S<sub>2,5</sub></b>	334	27			
	H <sub>1,2</sub>	...	...	...					
	D <sub>1</sub>	...	...	...					
	I <sub>1</sub>	...	...	...					
	S <sub>1,5</sub>	...	...	...					
16	P <sub>1</sub>	-P <sub>1</sub>	1. <b>16D<sub>1</sub>/I<sub>1</sub>‡</b>	<b>10S<sub>1,4</sub>‡, 6S<sub>2</sub>‡, 85P<sub>3</sub>‡</b>	117‡	86‡			
	P <sub>2</sub>	-P <sub>2</sub>	2. <b>35D<sub>1</sub>/I<sub>1</sub>‡</b>	<b>17S<sub>1,4</sub>‡, 18S<sub>2</sub>‡</b>					
	P <sub>3</sub>	-P <sub>3</sub>	...	...					
	D <sub>1</sub> /I <sub>1</sub>	...	...	...					
	S <sub>1,5</sub>	...	...	...					

## APPENDIX 3. Continued.

Web	Species code	Species manip.	Resulting magnitude of change		Total change	% due to indir. effect
			Direct effect	Indirect effect		
17	P <sub>1,2</sub>	-P <sub>1,2</sub>	100D <sub>1</sub> , 28I <sub>1</sub>	87S <sub>1</sub> , 100H <sub>1</sub> , 33S <sub>1</sub> , 40S <sub>4,5</sub>	686	55
	H <sub>1</sub>	-H <sub>1</sub>	70S <sub>2</sub>	85S <sub>1</sub> , 33S <sub>3</sub>		
	D <sub>1</sub>	-D <sub>1</sub>	...	...		
	I <sub>1</sub>	-I <sub>1</sub>	...	...		
	S <sub>1</sub>	-S <sub>1</sub>	10S <sub>2</sub>	...		
	S <sub>2</sub>	...	...	...		
	S <sub>3,4</sub>	-S <sub>3,4</sub>	100S <sub>5</sub>	...		
	S <sub>5</sub>	...	...	...		
19	P <sub>1</sub>	+P <sub>1</sub>	51D <sub>1</sub> , 22S <sub>1,2</sub>	...	395	44
	H <sub>1,3</sub>	-H <sub>1,3</sub>	90D <sub>2</sub>	43H <sub>2</sub> , 72S <sub>1,2</sub> , 60S <sub>6</sub>		
	D <sub>1</sub>	...	...	...		
	D <sub>2</sub>	-D <sub>2</sub>	40S <sub>4</sub> , 17S <sub>5</sub>	...		
	S <sub>1-8</sub>	...	...	...		
	S <sub>1-8</sub>	...	...	...		
20	P <sub>1</sub>	-P <sub>1</sub>	100D <sub>1</sub> , 58I <sub>1</sub>	100H <sub>1</sub> , 100H <sub>2</sub> , 88I <sub>2</sub> , 5I <sub>3</sub> , 4S <sub>3</sub> , 5S <sub>6</sub> , 21S <sub>1</sub> , 14S <sub>2</sub>	1099	41
	H <sub>1</sub>	-H <sub>1</sub>	12I <sub>1</sub> , 85S <sub>5</sub> , 40S <sub>1</sub>	33I <sub>2</sub>		
	H <sub>2</sub>	-H <sub>2</sub>	21S <sub>1</sub>	...		
	D <sub>1</sub>	-D <sub>1</sub>	...	...		
	I <sub>1</sub>	-I <sub>1</sub>	...	...		
	I <sub>2,3</sub>	-I <sub>2,3</sub>	17I <sub>2</sub> , 70I <sub>3</sub> , 21S <sub>1</sub> , 14S <sub>2</sub> , 4S <sub>3</sub> , 5S <sub>6</sub> , 99H <sub>1</sub> , 100H <sub>2</sub>	83P <sub>1</sub>		
	S <sub>1-7</sub>	...	...	...		
	S <sub>1-7</sub>	...	...	...		
21	P <sub>1</sub>	+P <sub>1</sub>	95D <sub>1</sub>	50S <sub>1,2</sub> , 80S <sub>1,2</sub>	609	32
	P <sub>2</sub>	-P <sub>2</sub>	17D <sub>1</sub>	22S <sub>1,2</sub>		
	H <sub>1,2</sub>	+H <sub>1,2</sub>	45S <sub>1,2</sub>	...		
	D <sub>1</sub>	...	...	...		
	D <sub>2</sub>	-D <sub>2</sub>	100D <sub>2</sub>	...		
	S <sub>1-3</sub>	...	...	...		
	S <sub>4-12</sub>	...	100H <sub>1</sub> , 100H <sub>2</sub>	45S <sub>3-12</sub>		
22	P <sub>1-6</sub>	-P <sub>1-6</sub>	70P <sub>3,6</sub> , 80H <sub>4</sub> , 78D <sub>1</sub> , 25S <sub>1</sub> , 64H <sub>4,5</sub>	20S <sub>3</sub> , 44S <sub>4</sub> , 70S <sub>6</sub> , 2S <sub>7</sub> , 5S <sub>2</sub> , 15S <sub>9</sub>	642	29
	H <sub>1</sub>	-H <sub>1</sub>	...	...		
	H <sub>2,3</sub>	-H <sub>2,3</sub>	25S <sub>2</sub>	...		
	H <sub>4</sub>	-H <sub>4</sub>	32S <sub>6</sub> , 44S <sub>4</sub> , 40S <sub>5</sub>	4S <sub>7</sub> , 4S <sub>8</sub> , 20S <sub>9</sub>		
	H <sub>5</sub>	-H <sub>5</sub>	...	...		
	D <sub>1</sub>	...	...	...		
	S <sub>1-9</sub>	...	...	...		
	S <sub>1-9</sub>	...	...	...		
23	P <sub>1</sub>	-P <sub>1</sub>	99D <sub>1</sub> , 4I <sub>2</sub> , 25H <sub>2</sub>	100H <sub>1</sub> , 100H <sub>3</sub> , 11I <sub>1</sub> , 1I <sub>2</sub> , 10I <sub>3</sub> , 19S <sub>1</sub> , 22S <sub>2</sub> , 9S <sub>1</sub> , 1S <sub>4</sub> , 5S <sub>5</sub> , 17S <sub>6</sub> , 4S <sub>7</sub> , 60S <sub>8</sub>	1168	48
	P <sub>2,3</sub>	...	...	...		
	P <sub>4</sub>	-P <sub>4</sub>	53S <sub>1</sub>	...		
	H <sub>1</sub>	-H <sub>1</sub>	60S <sub>8</sub>	65H <sub>3</sub> , 70I <sub>3</sub>		
	H <sub>2</sub>	...	...	...		
	H <sub>3</sub>	-H <sub>3</sub>	...	72S <sub>6</sub>		
	H <sub>4</sub>	-H <sub>4</sub>	100S <sub>8</sub> , 40I <sub>5</sub>	...		
	D <sub>1</sub>	...	...	...		
	I <sub>1,2</sub>	...	...	...		
	I <sub>3</sub>	-I <sub>3</sub>	61H <sub>1</sub> , 80S <sub>8</sub> , 80S <sub>9</sub>	...		
	S <sub>1-10</sub>	...	...	...		
	S <sub>1-10</sub>	...	...	...		
	S <sub>1-10</sub>	...	...	...		
	S <sub>1-10</sub>	...	...	...		

\* Results from Fletcher and Creese 1985.

† Results from Creese 1982.

‡ Two separate experiments in this web (referred to by "1." and "2." in direct effect column) yielded two separate estimates of total change and percentage due to indirect effects.