

universally close to 1. Although Gutenberg and Richter³ recognized a curvature in the distribution for large magnitudes, this was thought to be due either to incompleteness of the early catalogue or, later, to magnitude saturation¹⁸. Having overcome these difficulties, we now see that there is a break in the slope. The *b* values of ~1 and 1.5 agree with Rundle's⁶ predictions.

That large and small earthquakes have different size distributions has important implications for earthquake hazard analysis, which often relies on predicting the former from extrapolation of the later. For an individual fault, we know that this difference results in large earthquakes occurring more frequently than expected from small earthquake activity^{19,20}. Here we have found, conversely, that for a system containing many faults, far fewer large events will occur than expected from extrapolating the distribution of small earthquakes. □

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Food-web analysis through field measurement of per capita interaction strength

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THE idea that the connections between species in ecological assemblages are characterized by a trait called 'interaction strength' has become a cornerstone of modern ecology. Since the classic paper of Watt¹, ecologists have acknowledged the importance of distinguishing pattern (static community features) from process (dynamically based mechanisms), which can determine the immediate observed details. Food webs display pathways of implied dynamics, and thus potentially unite pattern and process in a single framework^{2,3}. Most analyses^{4–8} have focused entirely on web topology and the derived descriptive properties. By contrast, attempts to generalize how natural communities are organized^{9,10} or summary statements about whole communities^{6,11–13} have emphasized critical processes. Elton's² insights and May's³ generalizations and analyses have stimulated current developments. In May's approach, the idea of interaction strength is precise, reflecting coefficients in a jacobian matrix associated with a community dynamics model. He found striking dependence of community stability both on web complexity and on the number and

strength of interactions. By contrast, empiricists have usually determined relative interaction strength from single-species removals analysed by multivariate statistics^{14,15}. I report here the first experimental study designed to estimate interaction strengths in a species-rich herbivore guild, documenting on a per capita basis mainly weak or positive interactions, and a few strong interactions, a pattern which has profound implications for community dynamics.

I sought a procedure for quantifying the magnitude of a consumer's influence on an entire assemblage, thus including direct and potentially indirect effects, that would be based on manipulation of single-species densities and that would permit direct comparison against some common standard or baseline condition. The most important interactions in a community context are those changing the density of a species which, in the absence of natural enemies or disturbance, would come to dominate the assemblage. Many marine examples exist in which monocultures formed by the local competitive dominant develop on shallow water, hard surfaces^{16,17}. The potential formation of a monoculture provides a common baseline and thus the means of calibrating the impact of individual species on an assemblage. A species capable of preventing the development of a monoculture, or destroying one already established, should be a strong interactor in the sense that its density and activities should have measurable consequences for the competitively superior prey, and thus indirectly for other members of the local assemblage. A consumer characterized by minimal effect on the dominant is apt to be of little direct significance to the whole assemblage, although its activities might influence some other prey. It would thus be a weakly interacting species. Here I describe a direct evaluation of interaction strength, one which permits unambiguous quantification and comparison. The derived metric is based on an estimate of per capita effect, distinguishes between biologically important in addition to statistically significant

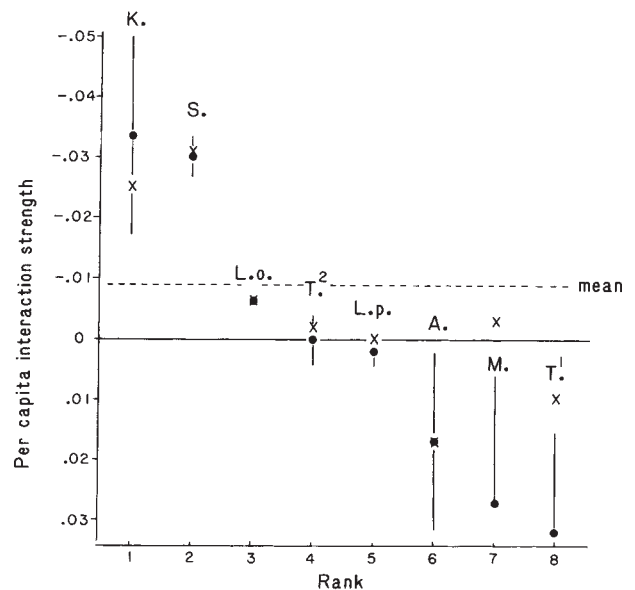


FIG. 1 Per capita interaction strength, measured as a grazer's capacity to influence the establishment of brown algal sporelings, ranked from negative to positive values. The bootstrap procedure calculated the index $E-C/Cd$, where d represents the density of the specific replicate, for as many times as that treatment was replicated. From these data a mean and s.e. were calculated. This procedure was then repeated 100 times; the means of these means and standard errors are given in Table 1 and graphed here (●, bootstrap means and their s.e.). The procedure mirrors the field experimental protocol and preserves the sensitivity of s.e. estimates to the number of replicates. Field experimental means (×) are also shown. S., *S. purpuratus*; K., *K. tunicata*; L.o., *L. ochraceus*; M., *M. hindsi*; L.p., *L. painei*; T., *T. lineata*; A., *A. mitra*. Exact values and sample details are given in Table 1. The dashed line is the mean of all species values, and is negative as expected in a predator-prey relationship.

TABLE 1 Measured and derived data on experimentally excluded grazers

Taxon/species	Treatment replicates	Natural density (number m ⁻²)	Range of experimental density (number m ⁻²)	Experimental per capita effect	Effect on % sporeling change	Bootstrapped per capita effect (±1 s.e.)
Sea urchin						
<i>Strongylocentrotus purpuratus</i>	5	25.4	15–44	-0.031	-78.7	-0.030(±0.003)
Chiton						
<i>Katharina tunicata</i>	4	28.0	8–30	-0.025	-70.0	-0.033(±0.016)
<i>Mopalia hindsii</i>	3	1.9	20–42	-0.003	-0.6	+0.027(±0.022)
<i>Tonicella lineata</i> /first series	6	12.3	30–83	+0.005	+6.2	+0.033(±0.022)
<i>Tonicella lineata</i> /second series	8	12.3	36–500	-0.002	-2.5	+0.000(±0.004)
Limpet						
<i>Acmaea mitra</i>	7	4.3	15–22	+0.017	+7.3	+0.017(±0.016)
<i>Lottia painei</i>	9	3.2	159–271	-0.001	-0.3	+0.002(±0.002)
<i>L. ochraceus</i>	1	0.1	115	-0.007	-0.1	-0.006
Grazer-free controls	41					

Total grazer enclosures, or exclosures, for individual species were made from rings or 'doughnut' of Sea Goin' Poxy Putty™ surrounding natural rock surfaces at about the 0.0 m tidal level. Once the putty had hardened, it was dried and painted with copper-based antifouling paint and all resident brown algae were removed from the surrounded surface. Whenever possible the area of the experimental arena was scaled to the needs and natural population density of the target species. This was not always possible, and thus for the smaller bodied or less common species, treatment densities tend to greatly exceed natural densities. The product of experimental per capita effect × natural density suggests the possible influence of each species on the early survival of a complex of brown algal sporelings, the reference state against which all impacts were judged. Details of the bootstrap procedure used to estimate mean (and s.e. of that mean) per capita effect are provided in the text and Fig. 1.

influences, and thus relates immediately to the important applied matter of whether a single species has the capacity to alter the structure of an entire assemblage.

Experiments were conducted at Tatoosh Island (48°24'N, 124°44'W) on the exposed outer coast of Washington State, United States. There, as at many comparable sites, the mid-low intertidal zones are dominated by stands of laminarialian brown algae¹⁸; traditional schemes of description have even characterized these low intertidal zones by their dominant species¹⁹. At Tatoosh the canopy-forming algae are *Hedophyllum sessile* in the presence of grazers¹⁸, and *Alaria* spp. when grazers are absent or experimentally excluded¹⁷. Under this canopy, space tends to be dominated by 10–15 species of coralline and numerous fleshy red algae. A phylogenetically diverse guild of grazers consume these plants, including crabs, sea urchins, chitons, limpets, a few fishes and an ecologically unknown set of mesograzers²⁰, mainly amphipods. These results concern only a subset of these grazers, but I believe they incorporate all but one of the ecologically important species. Treatments and number of replicates are listed in Table 1. The experiments were generally initiated in mid-August and terminated the following April. Control treatments ($N=41$) were not invaded by macrograzers, and suggest that elevated, painted surfaces were effective enclosures/exclosures for molluscan grazers. Similarly, the paint has little effect on the surrounding algae (L. Johnson, personal communication). To constrain sea urchins a wire barrier enclosed the painted surface. I used the density of brown algal sporelings <5 cm long that had appeared by April in control (grazer-free) treatments as the common reference state. Counts of sporeling numbers suggest domination by *Alaria* (March 1990, 93% of 1,026 plants; April 1990, 92% of 469 plants). The change relative to the mean control value was then determined for each replicate on a m² basis, and expressed as the ratio:

$$\frac{\text{Treatment density} - \text{Control density}}{\text{Control density}} \quad \text{or} \quad \frac{E - C}{C}$$

The ratio varies from -1.0 (total annihilation of sporelings) to 0 (no apparent effect) to some theoretically unlimited positive value in cases where brown algal recruitment or survival was enhanced. This value was then adjusted to a per capita basis by dividing by the grazer density characteristic of that specific replicate. Because the index embodies average values for control yet independently estimated values for grazer and algal density,

the full range of variation inherent in the experimental protocol is not adequately expressed by parametric statistical procedure. Instead, the entire data set was bootstrapped²¹ to recreate the field experiment so that there were paired experimentals and controls. Mean per capita effect on the basis of field data and means and standard errors on the basis of the bootstrap are given in Table 1 and Fig. 1.

Per capita influence on sporeling density showed both negative and positive values, with an average impact of -0.009 (or -0.9% m⁻² per 7.5 months). A net negative value should characterize a guild of consumers. The positive effects are explicable because these species consume crustose coralline algae, which in turn can inhibit algal spore recruitment^{22,23}. Although this data set does not include all members of the grazer guild, it is clear that the majority of the species (5 of 7) are relatively benign, and either have no significant negative influence on the

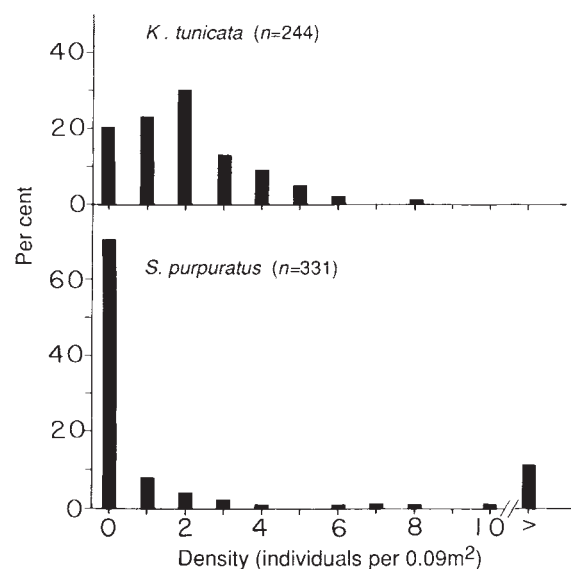


FIG. 2 Density estimates of the two invertebrate grazers characterized by strong trophic interactions at Tatoosh Island. Quadrat dimensions were 30 × 30 cm; n , number of samples taken 1988–1991. The chiton *Katharina* density is adequately described by a fit to a Poisson series ($\chi^2=13.7$, $P>0.05$). Urchin densities are extremely under-dispersed, indicating extensive aggregation.

reference state (*Lottia painei*; *Tonicella*, second series) or interact positively (*Acmaea mitra*; *Mopalia*; *Tonicella*, first series). The first series of *Tonicella* experiments, conducted at relatively low algal recruitment densities (510 m^{-2}), suggests recruitment enhancement, presumably because invadable substratum is generated by the grazers' foraging. At the much higher algal densities ($4,800\text{ m}^{-2}$) characteristic of the second series, the influence of this weakly rasping chiton was swamped, and no interaction effect is detectable.

The two strongly negative species (*Katharina* and *Strongylocentrotus purpuratus*) are statistically indistinguishable (analysis of variance; $F=0.41$, $P>0.5$). Their effects are not additive because urchins at densities greater than about 30 m^{-2} exclude *Katharina* (by eating them or driving them away). Hence these strong interactors do not coexist at their average (Table 1) densities although sparsely mixed populations are commonplace. Sea urchins in particular are widely acknowledged to suppress development of brown algal canopies, in the process producing 'barrens'²³. Calculations based on average Tatoosh densities in the low intertidal (25.4 m^{-2}) and the experimentally estimated per capita effect (-0.031) predict that some brown algae should be able to recruit successfully. But urchins are not haphazardly distributed (Fig. 2), existing in aggregations in which local density often exceeds 200 m^{-2} . Under such conditions, no fleshy algae survive, implying that factors spatially concentrating a strong individual effect will make a significant contribution to community organization, as in insects^{24,25}. By contrast, *Katharina* is randomly or haphazardly distributed (Fig. 2). Calculation of local effect indicates that about 70% of the algae ($28\text{ m}^{-2} \times -0.025$) will be consumed during the sporeling stage. The surviving density is more than sufficient to produce a 100% brown algal canopy, even in the presence of numerous weakly interacting grazers.

I chose to work with a guild of invertebrates generally considered to be 'grazers'. The presence of interactions of both signs significantly departing from zero (no effect) (Fig. 1) in closely related taxa (for example in both chitons and limpets) warns against the assumption of simple additivity, that is, that all guild members will have the same sign to their impact on the community, and implies that compensatory interactions could be commonplace. Equally, the exaggerated density of some grazers (Table 1) suggests that the effects are probably real. If a negative effect cannot be detected at 2–900 times the natural density, there are probably no circumstances under which it might exist.

I have thus presented an approach to quantifying per capita interaction strength in ecological communities that is practical, that allows statistical inference while distinguishing biological importance, and that summarizes and even predicts the capacity of a single species to alter the structure of an entire assemblage. When applied to a rocky intertidal community, 5 of 7 consumer species interact weakly or even positively with a competitively dominant prey. If communities are generally typified by such patterns of a few strong interactions embedded in a majority of negligible effects, the implications for community stability and organization are substantial. Significantly, none of this information can be obtained without experimental manipulation, regardless of how convenient or appealing it might be to infer the intensity and consequences of interspecific interactions from observation alone. Alternative but promising experimental approaches²⁶ to identifying whether particular predator–prey interactions are strong or weak, in the context of community-wide influence, have yet to proceed beyond single-species evaluations. The strong skew of interaction strengths (Table 1) bears important implications for the management and conservation of natural assemblages. When combined with estimates of density and tendencies toward aggregation, the relative importance and potential involvement of a species in chains of indirect effects can be identified. Management, conservation and even reconstruction of natural assemblages will require such information. □

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Peripheral nerve injury triggers central sprouting of myelinated afferents

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THE central terminals of primary afferent neurons are topographically highly ordered in the spinal cord¹. Peripheral receptor sensitivity is reflected by dorsal horn laminar location: low-threshold mechanoreceptors terminate in laminae III and IV (refs 2, 3) and high-threshold nociceptors in laminae I, II and V (refs 4, 5). Unmyelinated C fibres, most of which are nociceptors⁶, terminate predominantly in lamina II (refs 5, 7). There is therefore an anatomical framework for the transfer of specific inputs to localized subsets of dorsal horn neurons. This specificity must contribute to the relationship between a low-intensity stimulus and an innocuous sensation and a noxious stimulus and pain. We now show that after peripheral nerve injury the central terminals of axotomized myelinated afferents, including the large A β fibres, sprout into lamina II. This structural reorganization in the adult central nervous system may contribute to the development of the pain mediated by A-fibres that can follow nerve lesions in humans^{8,9}.

Peripheral nerve injury in humans is associated with decreased or abnormal sensations, including pain^{8–12}. Here we examined whether structural changes in the central terminals of the axotomized primary afferent neurons have a particular role in the development of these sensory disorders. Our rationale for this is the finding that after peripheral nerve injury the expression of the developmentally regulated phosphoprotein GAP-43, which is associated with or is a marker of axonal growth¹³, is increased in small and large dorsal root ganglion cells^{14–16} and is distributed not only to the damaged axonal tip in the