Trophic Control of Production in a Rocky Intertidal Community

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In the low intertidal zone at Tatoosh Island, Washington, United States, minimal estimates of primary production can vary from 0 to an average of 86 kilograms of wet mass per square meter per year when the grazing assemblage is manipulated. Highly productive annual kelps (Laminariales) replace less productive perennial species when macroscopic grazers are reduced or absent, resulting in monodominant assemblages of *Alaria marginata*. Experiments were repeated in seven consecutive years. Increased species richness makes no significant additional contribution to annual production. Rather, a competitively superior species is favored when its enemies are reduced, suggesting that terrestrial perspectives on the role of biodiversity that are developed without considering consumers may not be general.

Much contemporary ecology concerns the role of biodiversity in providing and even promoting ecosystem services such as primary production (*1*). Debate (*2*) with deep historical roots persists over the "individuality" and therefore the contribution of particular species (*3*, *4*), and uncertainty continues about how plants in multispecies mixtures coexist (*5*, *6*). Several field studies have reported a positive relationship between production and biodiversity (*7–11*). Detractors argue that these results are more an artifact than a result of experimentally varied biodiversity (*4*, *12*). With few exceptions, field experiments have emphasized terrestrial systems (*13*), neglecting or dismissing trophic interactions (*14*).

Here I examine the influence of consumers on production in a marine rocky intertidal assemblage at Tatoosh Island, Washington, United States (*15*). Marine benthic algae (kelps in the order Laminariales) were allowed to recruit at their natural rates to uniformly prepared rock surfaces rather than having species composition and recruitment density be predetermined factors. The sole treatment was reductions in the density of all macrograzers (urchins, chitons, and limpets). Thus, kelp diversity and its role are passive consequences of the experimental protocol rather than being directly manipulated, as in terrestrial studies. The research exploits well-established characteristics of marine intertidal assemblages: Interactions can be strong (*16*), grazers have the capacity to dominate all traits of the local algal assemblage (*17*), and monodominance within functional groups is commonplace (*16*). Kelps are major system components, often dominating lower shore levels when assessed by percent canopy cover or total biomass (*18*). Traditionally, they have been aggregated into a single functional group of "leathery macrophytes" (*19*) and they appear to be the most productive group on all shores. The geographic center of kelp diversification is the eastern Pacific (*20*): Of the 13 species (in 10 genera) potentially occupying the study locale (exposed shore, mid- to low intertidal), representatives (called species) of eight genera recruited to the experimental plots (*21*). Experiments were conducted in seven consecutive years (from 1994–1995 to 2000–2001); my more generalized observations and quantitative sampling of the biota began in 1968. The most significant change during this interval was the recovery of the population of sea otters (*Enhydra lutris*) (*22*).

Kelp presence and therefore annual production in urchin barrens, as reconstructed from photographs ($N = 9$) and direct sampling ($N = 5$), were nil (0 kg of wet mass m^{-2} year^{-1}). In the trophically intact (with otters) ecosystem, another state exists, expressed as vertically stratified, almost monospecific beds of *Hedophyllum* and *Laminaria*. *Hedophyllum* has been termed the dominant mid- to low intertidal brown alga on these and adjacent shores (*16*, *23–25*). It is a perennial species, and its multiblade morphology makes production estimates difficult. Such estimates are minimal because they ignore the leakage of dissolved organic carbon, the contribution of detrital materials (including spore production) because of the conveyor belt growth of kelps (*18*), and consumption by herbivores. First, I scraped sites and harvested the new growth a year later. No grazer manipulations were performed. Second, I simply harvested the standing crop, assuming that the wet weighed harvest was equivalent to one annual turnover (*26*). These production estimates are statistically indistinguishable [Table 1, analysis of variance (ANOVA), $P = 0.8$] and average 10.4 kg of wet mass m^{-2} year^{-1}. *Laminaria* also forms essentially monodominant stands in the absence of urchins beginning at about the −1.4-foot level. Most species in this genus are long-lived; their tendency to slough the previous year's growth permits annual production to be evaluated by harvesting above the meristem and wet weighing the new growth. Twenty-five plants were sampled from each of four stands in July 2001. Correction to a square meter basis generates an estimate of annual production. No effective grazer exclusions were possible at this lowest tidal level; the minimal production estimate is 12.6 (SE = 0.52) kg of wet mass m^{-2} year^{-1}.

Controlled manipulations were performed on the north-facing aspect of Tatoosh. A ring of nontoxic epoxy putty was formed to enclose a small, usually less than 500 cm^{2}, natural surface (*27*). In treatments identified as experimental, in which long-term grazer presence was eliminated or reduced, the resident grazers would be removed; the surface scraped; a commercial-grade oven cleaner sprayed on to kill residual algal fragments, spores, and the microscopic gametophytes; and the putty painted with a copper-based antifouling paint. Controls were identical, except that no paint was used. Both treatments were begun in late summer and maintained whenever possible during the winter months. Sporelings were counted in March/April, and the resident laminariallians were harvested in the June/July interval. 1994–1995 and 1995–1996 manipulations lack controls because they were part of a continuing study of interaction strength (*27*). In the five subsequent

Table 1. Net annual production (in kg of wet mass m^{-2} year^{-1}) by *Hedophyllum sessile*. Estimates (followed by SEs in parentheses) are based on mass harvested from 0.50-m^{2} plots and wet weighed in the field. All harvested and 1995–2001 samples were from Tatoosh. The 1977–1988 data combine earlier Tatoosh samples with others from Waadah Island. No significant differences exist: ANOVA, $P = 0.8$.

	Interval and condition						
	1979–1995 harvested	1977–1988 sampled	1995 sampled	1996 sampled	1998 sampled	2000 sampled	2001 sampled
N	12	15	4	12	14	19	12
Hedophyllum production	12.9 (1.43)	9.6 (0.75)	8.4 (1.25)	9.1 (1.93)	9.7 (2.68)	10.6 (2.26)	12.7 (2.78)

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years, controls were used to quantify grazer impacts as indicated by differences between treatments. Annual production estimates for each experimental plot were generated by harvesting, wet weighing, correcting to a square meter basis, and adjusting for the fraction of the year from initiation to harvest, yielding a measure of kilograms of wet mass m^{-2} $year^{-1}$. Two patterns are apparent. The most striking (Table 2, part A) is the influence that macrograzer exclusion has on estimated brown algal production: The 5-year comparison (from 1996 to 2001) shows an order of magnitude enhancement in the experimental plots (86.0 kg of wet mass m^{-2} $year^{-1}$) over control values (8.6 kg). Second, in grazer exclusion treatments, *Alaria* ranks first in production in all 7 years and *Nereocystis*, an annual but generally subtidal species, ranks second in 4 out of 7 years. Under experimental conditions, *Alaria* alone makes up 81% of production; combined with *Nereocystis*, it accounts for 93%. Based on production potential (*19*), when grazing pressure is reduced, this system collapses to one or perhaps two dominant species.

Frequency of recruitment provides another metric of potential ecological importance. Three species reliably invade the grazer exclusion plots: *Alaria*, 28 out of 29 plot-years; *Laminaria*, 21 out of 29 plot-years; and *Hedophyllum*, 11 out of 29 plot-years. The remaining guild members are infrequently present, though two of them, *Nereocystis* (4 out of 29 plot-years) and *Egregia* (1 out of 29 plot-years), can be highly productive and, on a plot-by-plot basis, comparable to *Alaria*. By contrast, in the 17 control plots, no species dominated in sporeling presence, with three species occurring about half the time (*Laminaria*, 9 out of 17 plot-years; *Alaria*, 7 out of 17; *Hedophyllum*, 8 out of 17). The remaining five kelps were essentially absent, reflecting the powerful grazer influence. The shift in assemblage composition favors the less productive but perennial *Hedophyllum* and *Laminaria* when grazers are present at normal densities. Conversely, *Alaria* and *Nereocystis* predominate when grazing intensity is substantially reduced.

Bootstrapping ($N = 2000$ resamples) confirms these results (Table 2, part B). When mean production estimates in the controls are subtracted from those of the grazer reduction plots, *Hedophyllum* and *Laminaria* are the only species with negative values. In addition, the pattern of site domination by *Alaria* (87% of total production) is repeated.

This experimentally generated shift in dominance can be explained by the interaction of two distinctive processes. First, other experiments (Table 3) identify *Katharina* as the most likely cause of change in kelp species composition when sea urchin impact is minimal. When *Katharina* is present, *Alaria* is rare and *Hedophyllum* comprises the majority of identifiable sporelings. When *Katharina* is removed, 76% of the sporelings are *Alaria*, suggesting substantially enhanced survivorship in grazer-free space. Thus, *Alaria* seems differentially susceptible to the grazer; no differences in *Hedophyllum* densities were apparent when *Katharina* was present or absent (Wilcoxon rank-sign test, $P = 0.33$). Second, *Alaria* canopy cover is positively related to the recruitment success of its sporelings (Fig. 1). Because *Alaria* is a short-distance disperser (*28*), increases in *Alaria* sporeling density and therefore in reproductive adults should be enhanced by the continued absence of *Katharina*, a self-augmenting feedback. Such shifts in canopy dominance can be maintained if *Katharina* is stringently removed, and they result in persistent monodominant stands (*16*).

Despite their small area ($\bar{x}$ = 370 cm^2; range, 248 to 576 cm^2), the experimental and

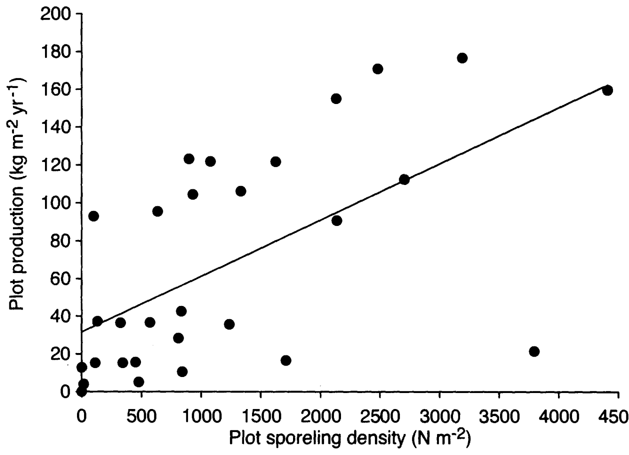


Fig. 1. In grazer exclusion plots ($N = 29$ plots, 1995–2001), higher density of *Alaria marginata* sporelings, sampled in April/May, correlates positively with production estimates in June/July (linear regression, $r^2 = 0.39$, $P < 0.01$).

Table 2. Part A: Site production data, omitting *Pleurophycus* and *Lessoniopsis*, which occurred in trace amounts. Units are kg of wet mass m^{-2} $year^{-1}$ (followed by SEs in parentheses). The experimental procedure effectively reduced entry by benthic macrograzers, especially chitons and limpets. It was ineffectual against mobile mesograzers (such as amphipods and crabs). The 1994–1995 and 1995–1996 treatments were comparable grazer removals in an extension of (*27*). Part B: Bootstrapped mean values for 1996–1997 through 2000–2001 for experimental sites ($N = 21$) and controls ($N = 17$). Values are production estimates in experimental treatments minus those of controls, for each species, based on $N = 2000$ resamples.

Year	Treatment	*n*	Total production	*Alaria*	*Nereocystis*	*Costaria*	*Egregia*	*Laminaria*	*Hedophyllum*	*Alaria* (% total)	*Alaria* + *Nereocystis* (% total)
						Part A					
1994–95	Experimental	4	129.4 (11.4)	91.5 (19.2)	30.5 (30.5)	1.7 (1.0)	0.0 (0.0)	3.0 (1.0)	2.7 (0.9)	70.7	94.3
1995–96	Experimental	4	28.1 (2.67)	21.8 (8.8)	4.7 (4.7)	0.3 (0.3)	0.0 (0.0)	0.7 (0.3)	0.2 (0.2)	77.8	94.5
1996–97	Control	3	8.9 (0.93)	7.5 (4.8)	0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.3 (0.9)	0.0 (0.0)	85.1	85.1
1996–97	Experimental	6	36.8 (4.33)	34.9 (15.3)	0 (0.0)	1.1 (0.9)	0.0 (0.0)	0.9 (0.3)	0.0 (0.0)	94.7	94.7
1997–98	Control	2	18.4 (1.55)	12.7 (6.6)	0 (0.0)	2.6 (2.6)	0.0 (0.0)	3.1 (0.4)	0.0 (0.0)	69.3	69.3
1997–98	Experimental	4	57.6 (4.28)	31.2 (20.7)	0 (0.0)	2.9 (1.8)	21.3 (21.3)	2.2 (0.6)	0.0 (0.0)	54.2	54.2
1998–99	Control	4	14.4 (0.98)	7.1 (7.1)	0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.4 (2.3)	4.9 (2.1)	49.6	49.6
1998–99	Experimental	4	117.4 (13.4)	108.2 (35.4)	7.5 (7.5)	1.2 (1.1)	0.0 (0.0)	0.2 (0.0)	0.4 (0.1)	92.1	98.6
1999–2000	Control	4	0 (0)	0 (0.0)	0 (0.0)	0.0 (0.0)	0.0 (0.0)	<0.1 (0.0)	<0.1 (0.0)	0.0	0.0
1999–2000	Experimental	3	102.4 (9.14)	70.6 (30.9)	31.7 (31.7)	0.0 (0.0)	0.0 (0.0)	<0.1 (0.0)	<0.1 (0.0)	69.0	100.0
2000–2001	Control	4	1.1 (0.12)	0 (0.0)	0 (0.0)	1.0 (0.7)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.0	0.0
2000–2001	Experimental	4	115.6 (14.5)	115.6 (35.0)	0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	100.0	100.0
						Part B					
1996–97 to 2000–2001			78.3 (15.4)	67.9 (13.5)	7.5 (5.8)	0.8 (0.6)	4.0 (4.0)	−0.5 (0.6)	−1.3 (0.7)	86.7	95.8

control plots were invaded by 8 of the 10 possible kelp genera: Only *Pterygophora* and *Cymathere* were not sampled, and both of these are predominantly subtidal in occurrence. During the 1996–2001 interval, the exclusion plots on average contained significantly more species than did the control plots (Fig. 2; two-way ANOVA: both treatment and year were highly significant, $P < 0.05$; the interaction term was 0.08). The pattern reflects the higher probability of even infrequent recruitment and survival by rare species in the reduction of grazing influences. Increased richness does not contribute significantly to plot production values when *Alaria* is subtracted from the site total (Fig. 3; 1994–2001; $P = 0.57$, raw data; $P = 0.72$, log-transformed data). Thus, production estimates for individual plots are dominated by *Alaria*, and there is no pattern of positive augmentation by other kelps. Idiosyncratic influences vary with kelp identity, recruitment ability, and maximal growth potential. The herbivore-mediated trade-off between plant defense and grazer impact favors *Alaria* in the grazer reduction plots (Tables 2 and 3) (*16*). It is unknown whether dominance is expressed by superior acquisition of holdfast, space, dense sporeling recruitment and the resultant resource preemption, or shading by a dense canopy.

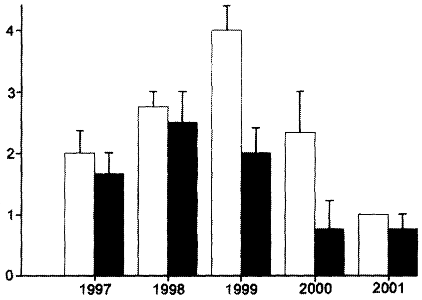


Fig. 2. Mean kelp species richness (error bars indicate SE) by year in plots with uninhibited grazer entry (solid bars) and those with restricted access (open bars). The latter treatment consistently has more species (ANOVA, $P < 0.01$).

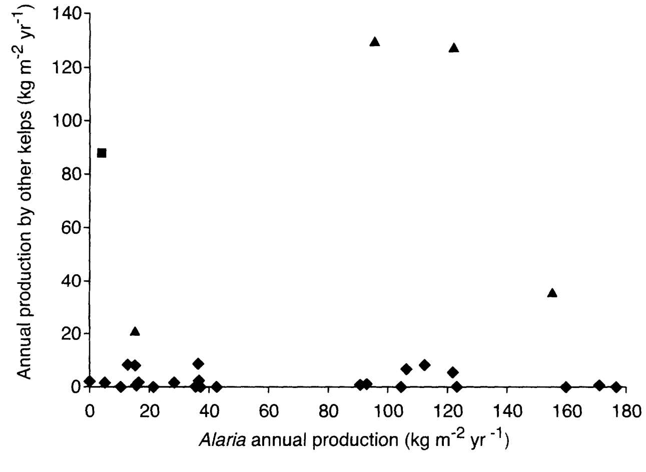
Ecological assemblages characterized by single-species dominance are commonplace in many ecosystems. Tropical hardwoods can occupy more than 50% of the canopy and sometimes 90 to 100%, with some stands covering several thousand square kilometers (*29*, *30*); mussel beds, mangrove stands, subtidal marine meadows, boreal forests, and salt marshes provide other well-documented examples. If these monodominant species add dimensionality to a system, species richness dependent on habitat structure is almost certain to increase (*31*). On Washington's outer coast, the most diverse assemblage is the "natural" world, and assessment of richness is dependent on the number of trophic levels included and, within levels, one's choice of functional groupings.

Terrestrial plant systems appear to be additive (*10*): The presence of more species confers a benefit, measured as higher organic production, though the ecological mechanisms maintaining coexistence remain poorly understood, and the extrinsic influences of grazing (or disease) have generally been ignored. My results identify a different pattern. Laminariallian production is essentially unmeasurable in the presence of sea urchins, although capable of attaining average levels of 80 to 90 kg of wet mass m^{-2} year^{-1} when they and other grazers are removed. When otters are present, the system is trophically intact, and mid- to low-shore production is about 10 to 13 kg of wet mass m^{-2} year^{-1}. In the experimentally reduced presence of all major grazers, the dynamics become substitutive, and a competitively dominant species (*Alaria*) overwhelms and replaces perennial, less productive species. The fundamental ecological questions relate entirely to spatially localized, short-term processes (*32*): Do consumers have important roles to play? Will trade-offs favor competitively superior, highly productive plants when their enemies are absent? On this marine shore, the answer to both questions is yes, suggesting that interpretations of system services (*1*) made without considering grazing impacts may not be general.

Table 3. Density (in N m^{-2}) of brown algal sporelings ($\bar{x}$, SE) at two sites with and four sites without *Katharina*. *Hedophyllum* density is independent of the presence or absence of *Katharina* (Wilcoxon rank-sum test, $P = 0.33$); *Alaria* density is highly dependent on *Katharina* (Wilcoxon test, $P < 0.01$).

Manipulation	n	*Hedophyllum*	*Alaria*	Comment
Katharina present	17	159	6	96% *Hedophyllum*
Katharina absent	33	106	330	76% *Alaria*

Fig. 3. Annual production in grazer exclusion plots ($N = 29$ plots, 1995–2001). Per plot production by *Alaria marginata* is highly variable; the contribution of other kelp species (diamonds) does not augment production (linear regression, $r^2 = 0.01$, $P = 0.57$). The idiosyncratic contributions of *Nereocystis* (triangles) and *Egregia* (square) as conspicuous outliers are identified.



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21. The kelp species are *Laminaria setchellii*, *Pleurophycus gardneri*, *Costaria costata*, *Hedophyllum sessile*, *Nereocystis luetkeana*, *Lessoniopsis littoralis*, *Alaria marginata*, and *Egregia menziesii*.
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No Major Schizophrenia Locus Detected on Chromosome 1q in a Large Multicenter Sample

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Reports of substantial evidence for genetic linkage of schizophrenia to chromosome 1q were evaluated by genotyping 16 DNA markers across 107 centimorgans of this chromosome in a multicenter sample of 779 informative schizophrenia pedigrees. No significant evidence was observed for such linkage, nor for heterogeneity in allele sharing among the eight individual samples. Separate analyses of European-origin families, recessive models of inheritance, and families with larger numbers of affected cases also failed to produce significant evidence for linkage. If schizophrenia susceptibility genes are present on chromosome 1q, their population-wide genetic effects are likely to be small.

Schizophrenia causes severe morbidity in 0.2 to 1% of the world's population, with a heritability of 0.70 to 0.85 attributable to complex inheritance (*1*). No specific genetic variation has been convincingly associated with susceptibility. Some genome-wide scans have produced significant evidence for linkage, but no result has been consistently replicable (*2*). In small genome scans of complex disorders, the largest estimated genetic effects often reflect a substantial upward bias, requiring evaluation in independent, larger samples (*3*). The present multicenter pedigree sample was assembled to determine the degree of support for schizophrenia candidate regions (*4*, *5*).

Several recent reports have suggested schizophrenia susceptibility loci of major effect on chromosome 1q. Brzustowicz *et al.* (*6*) reported a significant multipoint lod score (logarithm of the odds ratio for linkage) of 6.50 between markers D1S1653 and D1S1679 [162 to 163 cM from the p terminus (*7*)] in 22 Canadian-Celtic families. Nearby, Gurling *et al.* (*8*) reported a multipoint lod score of 3.2 (176.6 cM) in 13 British and Icelandic pedigrees. More distally, Ekelund *et al.* (*9*) reported lod scores of 3.2 (240.4 cM) in 168 Finnish nuclear families, and of 2.30 (222 cM) in 53 families from an isolated subpopulation. Finally, the Disrupted in Schizophrenia (DISC) genes *DISC-1* and *DISC-2* (*10*) (238.5 cM) are disrupted by a balanced (1;11) (q42.1;q14.3) translocation that segregates with schizophrenia and mood disorders in a Scottish pedigree (*11*).

To evaluate these findings, we genotyped 16 microsatellite markers (*12*) on chromosome 1q in 779 informative pedigrees containing 984 affected sibling pairs (ASPs) and 1918 genotyped individuals with schizophrenia or schizoaffective disorder, from eight independently collected samples (*13*) [Web tables 1 and 2 (*14*)]. The chromosome 1q findings were reported after formation of the multicenter sample (i.e., there was no selection bias). Primary statistical analyses included multipoint ASP (*15*) and nonparametric linkage (NPL) analyses (*16*) and logistic regression analysis (*17*) to test for intersample heterogeneity of sharing in ASPs and for linkage while taking intersample heterogeneity into account (*18*). Results are shown in Fig. 1 [for details, see Web table 3 (*14*)]. Only one of the individual samples [National Institute of Mental Health (NIMH)] produced a nominally significant result ($P = 0.049$) near the Finnish isolate peak (*9*). We observed no other significant results in individual samples or in the combined sample.

There are several possible explanations for the absence of support for linkage in this large sample, aside from the possibility of undetected genotyping errors or differences in diagnostic practice. Ethnicity could be a factor (*19*). However, many families in the University of Wales College of Medicine (Cardiff) and Virginia Commonwealth University (VCU)/Ireland samples had ethnic backgrounds (Scottish,

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