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FOOD WEBS: LINKAGE, INTERACTION STRENGTH AND COMMUNITY INFRASTRUCTURE

THE THIRD TANSLEY LECTURE

BY PROFESSOR R. T. PAINE

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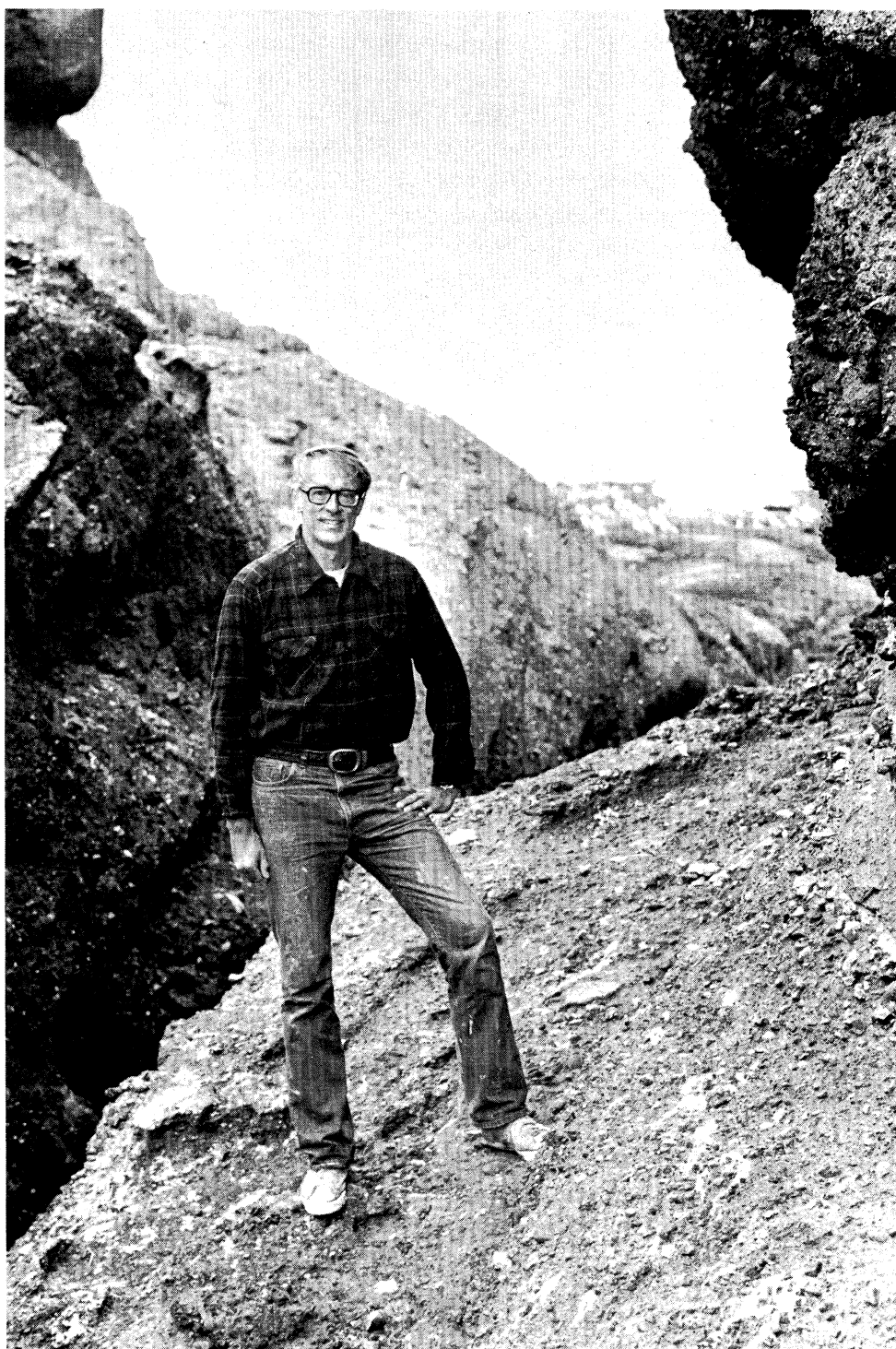
INTRODUCTION

It seems particularly opportune to discuss food webs and evolving views on their structure here for both their genesis and first modern treatment (Elton 1927) and much of their later development (May 1973; Pimm & Lawton 1978) has a decidedly British accent to it. The central significance of webs is derived from the fact that the links between species are often easily identified and the resultant trophic scaffolding provides a tempting descriptor of community structure. If this structure is in any fashion related to the persistence of natural communities or their stability, however defined, then we are dealing with issues of vital ecological importance.

Elton's views have admirably withstood the tests of time. They were especially useful to field biologists, and encouraged the assembly and organization of feeding data into networks of trophically bonded species or higher taxa. The early emphasis was on connectedness *per se*. Perhaps the first significant deviation from this theme was the development of the trophic dynamic viewpoint of Lindeman (1942) and all subsequent efforts to describe energy transfer and material flow through communities. A second departure, and one I believe to be conceptually richer, was the formalization of the view that web structure and community stability were related (MacArthur 1955). May (1973) in another landmark publication questioned this relationship and called attention to four primary web features: the number of species involved, the nature of their interconnections, the number of connections per species, and the intensity of interaction between web members. This focus has stimulated application to agroecosystems (Southwood & Way 1970), new interpretations of the number of trophic levels (Pimm & Lawton 1977), and a resurgence of interest in the significance of mutualism (Vance 1978). It has not been characterized by stunning breakthroughs, ecological stability remains a frustrating issue, and to a field ecologist, the ties between model and reality at times appear remote. All but ignored in these recent developments is an insightful recognition that trophic pathways might contribute little to ecosystem stability, and that the answers lie in the spatial patterning of the environment (Smith 1972). I wish to return to the basic observations on food webs as a naturalist and experimentalist, and employing an approach advocated by Sir Arthur Tansley (Godwin 1977), ask whether we are modelling their correct properties, and if not, what modifications might be made.

TERMINOLOGY

The assumed importance of predator-prey or consumer-resource relationships, their relative ease of observation, and an attractive, simple graphical format have accelerated the interest of ecologist and mathematician alike on web structure and organization



Professor R. T. Paine

(Cohen 1978; MacDonald 1979). I have found the following terms useful, and apply most of them in their common-sense, conventional ways.

Food chains and webs. The concept was apparently Elton's (1927). A hierarchy of monophagous consumers would constitute a chain: collection of these into broader units incorporating polyphagous consumers generates a web (or food cycle). In many respects, these differ little from Darwin's (1859, p. 59) view that plants and animals 'are bound together by a web of complex relations.' Interacting species may be related through trophic links, and the number of such links per consumer measures its connectedness or connectance (May 1973). Unfortunately, there is currently no prescription for how much grouping by taxa or guild might be permissible when determining trophic connections. Cohen (1978) has discussed the point and his and other analyses (for instance, MacDonald 1979; Pimm & Lawton 1978) suggested that some taxonomic lumping introduces little apparent bias.

Trophic levels. The term is one of convenience but assignment to a level often cannot be made. Elton (1927) both recognized and paid particular attention to the obscuring influences of body size, and gave numerous examples of omnivores. Lindeman (1942) identified specific levels, but clearly stated that they became less precise as one moves up the food chain. Darnell (1961), amongst many, has argued for the prevalence of rampant trophic opportunism: consumer nutrition is often derived from numerous prey categories which themselves cannot be assigned to any single level. Although many species are more eclectic in their dietary choices, nonetheless it is impossible to defend the sanctity of the trophic level concept.

Cross-linkage. Alteration of a predator's density bears immediate potential significance for its prey. If space or other resources are limiting, changes resulting from competitive interactions are apt to be induced within the prey guild. I refer to these lateral connections between competitors within the community nexus as cross-links. I believe it essential that they be distinguished from trophic links.

Linkage strength. The strength or importance of a trophic relationship cannot be assumed equivalent for all web members. A consumer will be a strong interactor if, in its absence, pronounced changes ensue (MacArthur 1972). Removal of a weakly interacting species will yield no or slight change. The emphasis is on the functional role occupied by species within food webs as determined by experimental alterations of their abundances. The relative strength of interaction is in part due to the consumer's density, in part to limitation to the predation process imposed by prey size (Paine 1976). Predator food preference is an essential ingredient, and an effect is especially likely when the prey is competitively superior (Harper 1969; Paine 1969). In some senses 'strength' is an abstraction, for under some circumstances a potentially significant interaction may not be realized. Conversely, it is difficult to envision conditions which would reveal the outcome of a fundamentally weak interaction. A graphical description of linkage strength and other symbolisms are shown in Fig. 1.

Modules. Strong trophic interactions can produce predictable, persistent patterns in the resource guilds. Species that seem dependent on these resources, give evidence for evolved modification for use of, or association with, these resources, and that disappear upon the removal of a strongly interacting species (or appear with its addition) will be said to belong to a module. A module thus includes both a resource set and their specific

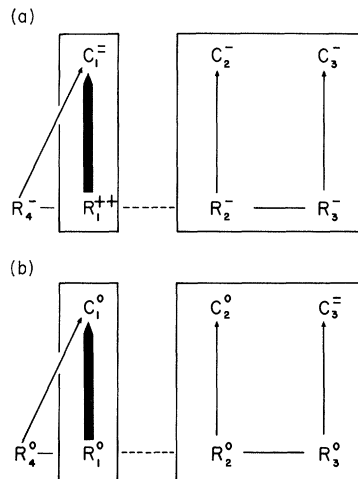


FIG. 1. A graphical model of interaction strength. (a) Strong interaction (b) weak interaction. The topological position of three consumers (C) and four resource states (R) are identical. The superscript identifies the proposed direction of change (—, decrease; ++, major increase; 0, no change) following removal (=) of a species. The heavy line indicates a strong interaction; the four species C_2 , R_2 , C_3 , R_3 comprise a module (see text); the dashed line signifies the dependency of the module on the C_1 – R_1 relationship.

consumers which, under conditions favouring maximal coevolution, will behave as a functional unit. May (1973) alludes to these as subsystems; Gilbert (1977) refers to them as coevolved food webs. In the engineering terminology of dynamical systems they may be components or subsets. Whichever term is applied, they are obviously important within food webs both because of the unit nature of their response and for the large number of species, and therefore potential number of links, involved. A module involving four species and linked to a strong interaction is shown in Fig. 1. Removal of C_1 produces an immediate increase in R_1 and initiates the disappearance of the modular components C_2 , R_2 , C_3 and R_3 .

VARIATIONS IN LINKAGE

Food webs are idealized pictures of complex trophic patterns that change seasonally and geographically. When emphasis is placed on the linkage arrangements per se, perspective is lost on the extent of their variability and responses to local environmental change. Because connectedness in natural webs can be observed directly, and forms the basis for most mathematical exploration of web properties (Cohen 1978; Gallopin 1972; Levins 1975; May 1973) I present here two webs constructed from observations at Cape Flattery, Washington state, and Torch Bay, Alaska (Fig. 2). I have ignored tradition and not attempted to cast the participants into trophic levels. The arrows point towards the predator. Further, the symbolism of Fig. 1 is used to identify strongly interacting pairs and dashed lines and brackets suggest modules or interaction dependent subgroups.

The Cape Flattery web encompasses earlier research at mainland sites (Paine 1966; Paine & Vadas 1969) and more recent material from Waadah and Tatoosh Islands (Paine 1976, 1977). Although forty-four taxa are given, this remains but a small portion of over 300 possible (Suchanek 1979). Nonetheless, I believe that all the major components

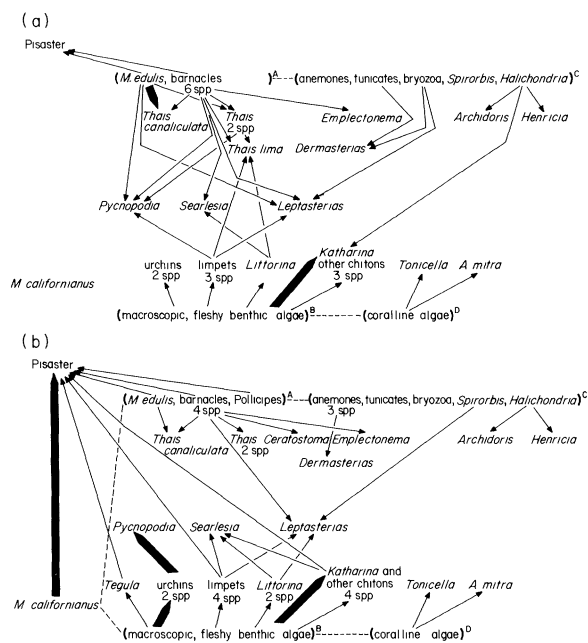


FIG. 2. Two eastern Pacific rocky intertidal food webs. (a) Torch Bay, Alaska (b) Cape Flattery area, Washington. The topological positions of species common to both is identical. Symbolism is the same as in Fig. 1.

have been identified with the exception of the anemone *Anthopleura xanthogrammica* (Brandt), two uncommon gastropod species (*Thais lamellosa* (Gmelin) and *Onchidoris bilamellata* (Linnaeus)) and five species of crab. This intertidal community is also subject to avian predation by oystercatchers (*Haematopus bachmani* Audubon), black turnstones (*Arenaria melanocephala* (Vigors)), surfbirds (*Apriza virgata* (Gmelin)), and glaucous-winged gulls (*Larus glaucescens* Naumann). None of these omissions is thought to be functionally significant, although the anemone is clearly partially coupled to the foraging activities of starfish (Dayton 1973) and both gastropods join a complex of others primarily if not solely exploiting barnacles. Other studies supplementing these trophic patterns are Mauzey (1966); Mauzey, Birkeland & Dayton (1968); Connell (1970); Dayton (1971); Menge (1972a, 1972b); Menge & Menge (1974); Nicotri (1977) and Louda (1979). Hewatt (1937) and Menge & Sutherland (1976) present more abbreviated summaries of the same food web.

The Torch Bay web is not as well known primarily because of the remoteness of the site. The community has most of the same taxa as that at Cape Flattery although *Mytilus californianus* Conrad is rare, occurring mainly in tide pools. Experiments and strong inference indicate the distribution of its smaller and thinner-shelled congener, *M. edulis* Linnaeus, is controlled by the predatory gastropod *Thais canaliculata*. (Duclos). The intertidal algal community appears controlled by the herbivore *Katharina tunicata* (Wood).

The topological placement of the taxa in both webs (Fig. 2) has been maintained to emphasize the regional changes in connectedness despite the great similarity of the species complements. At Torch Bay, *Pisaster ochraceus* (Brandt) is probably 'just another starfish,' in part because *M. californianus* is a minor community component. Rather than

TABLE 1. Between region shifts in diet of three major invertebrate predators.
C.F. refers to Cape Flattery region, Washington and T.B. to Torch Bay, Alaska.
Data are given as numbers of prey individuals consumed

Predator Location	Pisaster		Leptasterias		Pycnopodia	
	C.F.	T.B.	C.F.	T.B.	C.F.	T.B.
N. observations	20749	922	221	131	110	108
Prey taxa						
Barnacles						
<i>Balanus glandula</i>	8592		24			
<i>Balanus</i> spp.	2699	182	64	85		8
<i>Chthamalus dalli</i>	2141		23		4	
<i>Pollicipes polymerus</i>	691		1			
Mussels						
<i>Mytilus edulis</i>	1602	733		21		43
<i>M. californianus</i>	2084		7		7	
Chitons						
<i>Katharina tunicata</i>	132	1				1
<i>Tonicella lineata</i>	46					
<i>Mopalia</i> spp.	101		1			1
Herbivorous						
gastropods	10		4	1	3	5
<i>Tegula funebris</i>	2184					
limpets	220		14	18		21
<i>Littorina</i> spp.	27		9			
Carnivorous gastropods	75	6	4	1		9
Echinoderms						
<i>Strongylocentrotus</i> spp.	1				93	2
Cucumaria				1		11
starfish					2	1
Annelids (Spirorbis)			57			
Crabs	21		3			1
N. species	41	4	19	11	5	23
H'	1.90	0.24	0.96	0.65	0.26	0.94
Other	123	0	10	4	1	5

being linked to forty-one species, it only connects to four at Torch Bay (Table 1). Sea urchins, though abundant, are not functionally significant in the lower intertidal at Torch Bay. On the Washington coast they predominated in the diet of the starfish *Pycnopodia helianthoides* (Brandt) whereas in Alaska they are a minor component. The number of interactions directly involving *Pycnopodia* changes by a factor of 4.6 between regions (Table 1). Conversely, the diet of *Leptasterias hexactis* (Stimpson) seems moderately constant, an observation that might be related to its small body size. There are other major changes in the pattern of connectedness. *Dermasterias* switches its prey entirely between regions, and at Torch Bay *Katharina* is a major sponge consumer and another species of *Thais* has been added. These changes may be due, in part, to regional changes in the character of the exploited resource. For instance, on the Washington coastline, the sponge *Halichondria* occupies about 5% of the available substratum (Paine 1974). At Torch Bay, where I have estimated 20% coverage, this species is heavily consumed by *Katharina* and the starfish *Henricia*. On the other hand, *Katharina* is consistently abundant at both sites (Cape Flattery; $\bar{X} = 27.2 \text{ m}^{-2}$, S.D. = 17.7, $n = 76$; Torch Bay: 24.8, 15.9, 8), lives at comparable tide levels, yet is connected differently to both its prey and predators (Fig. 2).

Although factors underlying these switches cannot be interpreted presently, they surely are not minor. They represent major changes in the pattern of connectedness and therefore of material and energy transfer. Evidence for regional lability in structure is obvious

and includes two important web traits: the number and pattern of linkage connections of the higher order consumers and a measure of the diversity (H' ; Pielou 1975) of this linkage (Table 1).

Two further sources of variation in trophic pattern can be examined. Table 2 shows the geographic variability of *Pisaster*'s diet over 30 degrees of latitude. Although the intertidal community retains its essential composition (Ricketts, Calvin & Hedgpeth 1968), *Pisaster*'s diet changes substantially, especially in terms of the number of links. Table 3 gives an indication of variation by habitat. The data set encompasses 7633 *Pisaster* observed between June 1963 and August 1971 in four portions of a mosaic environment. Although the total number of prey links is roughly similar, the major connections are highly variable, especially if barnacles are excluded from the comparison. Further, these within-habitat differences seem constant through time. I have shown that in the boulder field, the herbivorous gastropod *Tegula* is consistently the major source of food energy for *Pisaster* (Paine 1969). On mid-intertidal rock platforms, trophic conditions vary little from year to year (Paine 1974) when *Pisaster* is present, and barnacles and mussels are the main dietary items. On low intertidal benches most of the nutrition is derived from chitons. I believe these variations, be they geographic or within habitat, provide little insight into community organization.

STRONG INTERACTIONS: REALITY AND IMPLICATIONS

One of the continuing triumphs of experimental ecology has been in identifying species native to marine benthic and small freshwater ecosystems that play major roles in community organization. The results nicely complement comparisons of natural communities either with or without some major native species, or before or after its reintroduction or exclusion. I believe this body of literature is overwhelmingly convincing, and because its primary message is that nature is complex, subtle and interactive, I will discuss the evidence for strong interactions and some of their consequences as a unit. I exclude from

TABLE 2. Latitudinal variation in the primary diet of *Pisaster ochraceus*

Source	Paine Punta Baja, Mexico	Feder 1959 Monterey Bay, California	Paine Outer Coast, Washington	Mauzey 1966 Friday Harbor, Washington	Quinn 1979 Torch Bay, Alaska	Paine Torch Bay, Alaska
Latitude ($^{\circ}$ N)	29°54'	36°36'	48°19'	48°37'	58°27'	58°27'
N. Observation	97	633	20749	1554	592	336
Major prey taxa; proportion of total						
<i>Mytilus</i> spp.	0.30	0.17	0.18	0.12	0.80	0.77
<i>Balanus</i> spp.		0.30	0.54	0.51	0.18	0.23
<i>Tetraclita</i>	0.45	0.26				
<i>Chthamalus</i>			0.10			
<i>Pollicipes</i>	0.10	0.04	0.03			
Carnivorous gastropods		0.02	< 0.01	0.04	0.02	
Herbivorous gastropods	0.10	0.11	0.12	0.25		
Chitons	0.03	0.04	0.01	0.07		
Number of links	7	33	41	25	4	2
Diversity (H') of links	1.40	2.08	1.90	1.99	0.54	0.53

TABLE 3. Major dietary components of *Pisaster ochraceus*, by habitat. Data taken at Mukkaw Bay, Washington, June 1963–August 1971

	Habitat			
	Mid-intertidal rock platforms	Dissected rock platforms	low intertidal rock platforms	Boulder field
Total <i>Pisaster</i> examined	1866	1588	1253	2926
Number of censuses	66	45	36	99
Prey taxa				
Barnacles				
<i>Balanus glandula</i>	3025	2512	904	1871
<i>B. cariosus</i>	863	603	87	113
<i>Chthamalus dalli</i>	316	1004	68	639
<i>Pollicipes polymerus</i>	39	47	28	
Mussels				
<i>Mytilus</i> spp.	1453	608	629	40
Chitons				
<i>Katharina tunicata</i>	3	3	108	1
<i>Tonicella lineata</i>		1	43	
<i>Mopalia</i> spp.	1	6	8	81
Herbivorous gastropods				
<i>Tegula funebris</i>	5	208		1761
<i>Acmaea scutum</i>	14	21	76	39
<i>Acmaea digitalis</i>	26	26	4	3
Other limpets	8		15	5
<i>Littorina scutulata</i>	9	17		1
Carnivorous gastropods				
<i>Thais emarginata</i>	17	14	1	24
Other {total individuals	11	10	53	49
{species	9	6	13	12

consideration below the many dramatic examples of major change subsequent to the introduction or exclusion of exotic species (Darwin 1859; Elton 1958; Zaret & Paine 1974), primarily because these impose an influence beyond the evolutionary experience of the assemblage.

The eastern Pacific near-shore community previously mentioned is both biotically rich and roughly comparable from Baja California to the western Aleutian Islands. The experimental exclusion of *Pisaster* in Washington leads to the competitive elimination of all the bracketed categories (Fig. 2) by *M. californianus* (Paine 1966, 1974, and unpublished) despite the presence of numerous other predators. The results obtain because the competitively-dominant mussels become large too rapidly to be controlled effectively by other potential consumers. *Pisaster* consumes most mussel size categories and therefore escapes are relatively scarce in its presence. The experimental exclusion of the sea urchin *Strongylocentrotus purpuratus* (Stimpson) in the same community yields a comparable impact for identical reasons: this urchin controls the growth and distribution of competitively superior benthic algae and it is capable of destroying them at all body sizes. Thus sea urchin removal produces a lush plant community where none had existed previously; urchin addition causes a reversion to a seemingly barren, herbivore resistant flora (Paine & Vadas 1969; Paine 1977). An associated species-rich complex of other herbivores seems to have little influence on the outcome of such manipulations. These modular species are described later. Comparable results obtain when urchin populations elsewhere are manipulated or exploited, as a rich literature attests (Kitching & Ebling 1961; Ogden, Brown & Selesky 1973; for instance).

Human activities have provided useful though ecologically discouraging insights on the significance of linkage patterns within this same community. At one time sea otters were

patchily abundant. Their removal has generated a well documented cascade of effects (Estes & Palmisano 1975). Sea otters, although consuming a wide variety of prey, effectively control the abundance of urchins which, in turn, control the algal community. Islands with and without otters are conspicuously different because destabilizations at the highest trophic level induce structural changes which cascade through the community, transmitted by a chain of strongly interacting links. Despite limited opportunity for experimentation, two lines of evidence extend the latter conclusion: the impact of otter reintroduction can be predicted with accuracy (Duggins 1980), and examination of stratified Aleut middens shows that otter remains are inversely correlated with those of urchins (Simenstad, Estes & Kenyon 1978). Although there is as yet no evidence for modules, the cascading influences generate major interisland differences in gull foraging activity (Trapp 1979), and one can argue that the now extinct, enormous, Stellar's sea cow was dependent on the lush algal community maintained by effective suppression of urchins (Haley 1978). A highly comparable cascade is known from the Canadian maritime provinces in which lobsters play an ecologically equivalent role to otters (Mann & Breen 1972; Mann 1977).

I have removed a starfish, *Stichaster australis* Verrill, from an intertidal shoreline in New Zealand, producing rapid domination by a mussel (*Perna*) at the expense of other resident-space-requiring species (Paine 1971). Although no modules were identified specifically, the competitive dominant had monopolized virtually all the space within 15 months, with the elimination of nineteen other species. Not only was a strong interaction demonstrated, but the influence of *Stichaster* was independent of the variety of prey consumed. I have now collected 365 feeding observations on this starfish: 76% of them are on mussels and, further, there is little tendency towards dietary breadth despite the local abundance of phylogenetically diverse, potentially suitable, alternative prey. The contrast with the trophic generalist *Pisaster* is sharp, and yet the experiments yielded similar results for similar reasons. The top predator's influence is due to the strong, competitively asymmetric, cross-linkages which translate changes in either *Pisaster* or *Stichaster* abundance into changes in allocation of the limiting requisite, space.

Birkeland (1974) has detailed a food web with only nine major constituents characterizing a subtidal sandy bottom community in Puget Sound, Washington. The web is unusual in that a single prey, the sea pen *Ptilosarcus guernei* (Gray), provides the primary trophic base for a complex of at least eight consumers. In one sense, then, sea pens are key industry (Elton 1927) organisms. Birkeland established connectedness patterns and rates of prey consumption through hundreds of hours of scuba diving. Figure 3 is slightly modified from Birkeland, and gives the essence of the relationships. All species consume *Ptilosarcus*, and three of them (*Hippasteria*, *Tritonia* and *Armina*) exclusively so. There is a single top predator, the starfish *Solaster dawsoni* Verrill, and Birkeland was able to calculate that if it was removed, *Mediaster* would increase and eventually out-compete the module of specialists. All other species would persist, albeit at greatly reduced densities. In sum, not only were a strong interaction and a dependent module comprising 3/8th of the species identified, but the study also indicates the potential fragility of the ensemble to perturbation of a single resident species.

The studies just discussed reveal the significance of certain key predators, the importance of cross-links and the reasons underlying cascading alterations in structure. They suggest patterns that can be extended with some caution to many other benthic and aquatic communities.

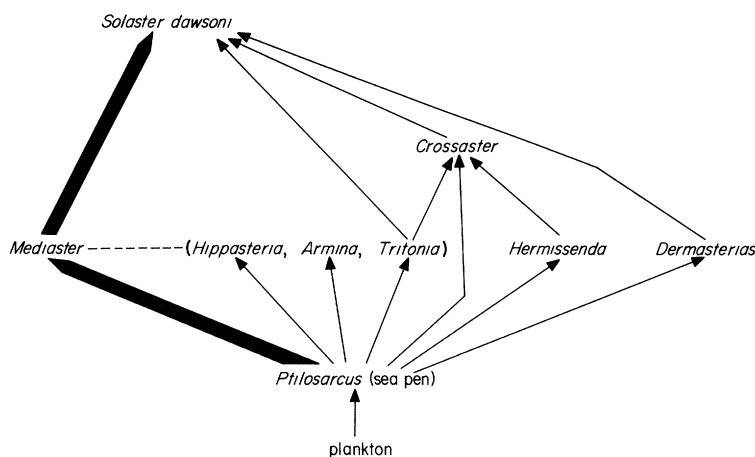


FIG. 3. A shallow subtidal food web of Puget Sound, Washington. Redrawn from Birkeland (1974), employing the symbolism of Fig. 1.

Lubchenco & Menge (1978) and Menge (1979) have studied a low, rocky intertidal community along the western Atlantic shore. Starfish (*Asterias*) are strong interactors: their removal produces monocultures of mussels at the competitive expense of barnacles and algae. However, starfish influence occurs sporadically, not chronically, and is ecologically unpredictable. No associated modules appear to have evolved. In addition, other experiments suggest that *Thais lapillus* (Linnaeus) is almost as strong an interactor: its removal (Menge 1976) leads to a mussel dominance not attained in its presence. Apparently, in communities subject to extensive physical disturbances, competitive dominants can evolve which in turn generates strong interactions. However, because the dominant is essentially a fugitive, superior defensive attributes have not evolved. Thus, such a species remains susceptible to many consumers which may regulate its distribution and abundance. The Torch Bay intertidal community (Fig. 2) could be similar, and the pattern of multiple key consumers reappears in the work of Kitching, Sloane & Ebling (1959) and Peterson (1979), in which *M. edulis*, though clearly competitively superior under most conditions, never achieves the body stature to escape from all predators.

The influence of event predictability, in the sense that organisms can adapt and evolve responses to it, is further revealed by studies on the destruction wrought by *Acanthaster planci* (Linnaeus) on Indo-Pacific coral reefs (Endean 1976). Starfish plagues occur sporadically in space and time. When they do occur there is a substantial impact on community composition exerted by a single native species of high trophic status. *Acanthaster* is obviously a strong interactor. However, it is also unpredictable, and it is probably not coincidental that no modules seem associated with its activities. Its destructive influence is clearly related to the competitive status of its prey (corals) again emphasizing the significance of cross-linkages in community organizational schemes. There are no signs that the awesome trophic complexity of such communities, glimpses of which can be seen in Hiatt & Strasberg (1960) or Kohn & Nybakken (1975), exerts any ameliorating influence during outbreaks.

Finally there is convincing evidence that aquatic webs show many of the same organizational features as benthic ones. Hrbáček (1958) and Brooks & Dodson (1965) demonstrated that the presence of certain fish species results in substantially different plankton

communities. Dodson (1970) suggested, and Giguère (1979) has experimentally proven, that the presence or absence of salamander larvae lead to one, or another, set of zooplankton. Recently, Dodson (1979) has extended this body of literature. I conclude that in these plankton webs vertebrate predators, be they fish, amphibia or birds (under appropriate circumstances), have the potential to interact strongly with certain prey and to mould community structure in a generally predictable fashion. Further, modules may be present: what Dodson (1970) terms 'complementary feeding niches' represent, from the community viewpoint, a predictable supplementation of the species list associated with a strongly interacting predator. However, little evidence on within module co-evolution is available, unless one interprets the predictable development of rotifer swarms in the presence of major vertebrate predators and the well-documented chemical signalling between them (Gilbert 1966) in this fashion.

Three final examples can be given to document events in aquatic food webs. Power & Gregoire (1978) have examined a land-locked seal → fish relationship in which lakes with seals have significantly altered fish communities as compared with those without these effective predators. Fraser (1970) and Swanberg (1974) have re-examined the complex ctenophore → ctenophore → herring and cod web. Although the relationships are primarily inferential, all are realistic, and support the notion of a trophic cascade associated with a series of nested strong interactions. Similar conclusions can be drawn from the fascinating analysis of May *et al.* (1979) of the baleen whale → Antarctic krill situation: alteration of a dominant consumer set has instituted major changes within the community nexus. Augmentation of populations of supplementary species (penguins, crabeater seals) is associated with the demise of whale stocks. Modules were not observed in the sense that whale dependent species went locally extinct, but perhaps this is seeking too much in a system this remote and difficult to study except on an immense spatial scale.

WEAK INTERACTIONS

The ideal weakly interacting species in some respects is experimentally unsatisfactory: its addition or deletion causes no detectable change. Furthermore, such results are highly likely in natural communities in which the experimenter must contend with high levels of 'noise'. I record here the basic data on three experiments that reveal some of the nuances and difficulty of examining weak interactions.

The chiton *Katharina* is a large, abundant herbivore on mid and low intertidal rock platforms. Preliminary observations had suggested that it cannot suppress the brown alga *Hedophyllum sessile* Setchell. To test this view *Hedophyllum* was removed from large (17–27 m²) rock platforms but with all other organisms retained. Unaltered controls were adjacent. Experiment 1 was initiated 8 May 1978. By December the area was 50% covered, as determined by replicated quadrat samples, by *Hedophyllum*; by late April 1979 the value was 95%. Experiment 2 was identical in design. A second area was cleared 15 May 1979. By August *Hedophyllum* accounted for 35% of the canopy, by September 80%, and by December 1979 had decreased to 36%. Chiton density remained relatively constant throughout the study (Table 4); *Hedophyllum* exhibited normal seasonal changes in % cover in all areas (Table 5). Clearly, judged by an ability to control development of a dominant alga, *Katharina* is a weak interactor. On the other hand it exerts a major influence on associated benthic algae and is a functionally dominant grazer in Alaska. I have thus identified it as a strong interactor in Fig. 2, although this could be questioned.

TABLE 4. Effects of removing the chiton *Katharina tunicata* on the associated herbivores. C = control; E = experimental site. Data are given as number per m². An asterisk indicates a significant ($P < 0.05$) difference in specific grazer density between control and experimental sites

Grazer	Treatment	Date						
		8 May '78	18 Aug '78	28 Dec. '78	28 April '79	15 May '79	24 July '79	20 Sept. '79
<i>Katharina</i>	C	20	24	25	22	34	21	42
<i>Tonicella lineata</i>	C	9	7	4	11	14*	6	7
	E	7	4	—	—	7	3	2
<i>Acmaea mitra</i>	C	7	4	3	1	4	3	4
	E	4	4	—	—	0	0	0
<i>Acmaea pelta</i>	C	13	11	6	9*	19*	13*	4*
	E	13	7	3	17	26	16	27

Table 4 shows that *Katharina* exerts an influence on at least one of the associated grazers and perhaps others, based on results in the second year of experiment 1. The control for this manipulation was a site from which both *Hedophyllum* and *Katharina* had been removed and, since *Hedophyllum* recovers equally with or without *Katharina*, potential variations in algal primary cover are not a factor. The limpet *Acmaea pelta* (Rathke) increased significantly in abundance in the experimental area (Mann-Whitney U, Siegel 1956), due to competitive release. Conversely, both other grazers (Table 4) tended to decrease, probably because of changes in the quality of their resource. Although these species are dynamically coupled, none seem capable of controlling the dominant alga even when grazer density is increased by factors of 2–3. They, therefore, are weak interactors.

I further tested the hypothesis of weak interaction in a removal experiment on *A. mitra* Rathke, a species feeding exclusively on coralline algae (but certainly also ingesting any attached microscopic flora or spores of macrophytes). The species is moderately abundant at low tide levels on the Washington outer coast: cave mouths ($N = 18$, $\bar{X} = 1.23 \text{ m}^{-2}$ s.d. = 1.23), rock platforms (20, 2.22 m^{-2} , 4.6), or underneath sea urchins (44, 6.05 m^{-2} , 7.37). It becomes more abundant in the shallow subtidal.

Acmaea mitra was initially removed from a 15 m^2 *Hedophyllum* covered platform at the 1.0' level on Tatoosh Is. in June 1979. Since the species is not overly vagile, and many individuals remain within limited areas for long intervals (months), reinvasion does not pose a problem. An unmanipulated control area was adjacent. The coralline algal community initially showed no differences between control and experimental sites in the percent cover of five major types (Mann-Whitney U-test), so the data were pooled. Re-examination of the site 6 months later revealed no re-entry of *A. mitra*, no apparent compensatory changes in the abundances of other grazers, no differences in the cover of *Hedophyllum* other than normal seasonal changes, and two shifts in the relative abundance of the coralline algae (Table 5). These changes are probably causally related with one crust category (*Lithophyllum* spp.) tending to overgrow another in the absence of grazing pressure. Although the evaluation is made difficult by problems with coralline alga taxonomy and their patchy distribution (suggested by the generally great range in value of percent cover) I believe the conclusion of no or slight change to be sound. *Acmaea mitra* clearly is a weakly interacting species, at least at the level of population density manipulated and within the time frame of observation.

TABLE 5. Response of the coralline algal complex following removal of *Acmaea mitra*. Data are given as mean percentage cover and (range).
 An asterisk indicates a significant ($P < 0.05$) deviation from the control condition. N = number of quadrat samples

Date	N	Hedophyllum canopy	N	Coralline algal understorey				<i>Food webs</i>	
				Corallina spp.	Bossiella spp.	Lithothamnium type 'A'	Lithothamnium type 'B'	Lithothamnium spp.	Lithophyllum spp.
10 June 1979	20	100	8	32.9 (10-65)	4.5 (0-10)	30.0 (10-55)	19.2 (5-35)	13.5 (0-35)	
2 Dec. 1979	5	38*	12	31.7 (0-80)	4.6 (0-20)	29.2 (10-90)	28.5 (0-80)	6.3 (0-20)	
				31.3 (0-70)	2.5 (0-5)	30.8 (0-70)	14.6* (0-100)	20.8* (0-60)	

RELATIONSHIPS WITHIN THE MODULE

Competitive relationships within this coralline algal-specific grazer module appear to be as weak as the consumer-resource ones, although the conclusion is entirely inferential. The grazers *A. mitra* and *Tonicella* coexist peacefully, often within a few cm of one another for extended intervals (months). It is not clear how they react to the presence of *Katharina*. However, they may respond to the urchin, *S. purpuratus*; densities are often higher under urchins than on the rock platform itself (*Tonicella*, 14 m^{-2} , *A. mitra* 6.1 m^{-2}) implying that this relationship is a facilitating one. That is, urchin feeding biases the composition of the algal community in favour of species requiring coralline algae, and their spines might afford protection as well.

There seems little doubt that coralline algae, probably the most geographically ubiquitous group of macroalgae, require grazing for their establishment and persistence (Paine & Vadas 1969; Vine 1974). This proposition was examined experimentally in two ways. A strip $4 \text{ m} \times 0.5 \text{ m}$ was scraped down to the algal basal system or bedrock within a dense forest of *Corallina vancouveriensis* Yendo. Squares roughly $0.3 \text{ m} \times 0.3 \text{ m}$ in dimension were painted around their perimeter with a 10 cm band of anti-fouling paint which effectively reduces entry by benthic grazers. Four squares served as experimental, herbivore-free arenas. Five immediately adjacent scraped areas but with unimpeded herbivore access were the controls. The null hypothesis tested is that coralline recovery is independent of an herbivore presence. Figure 4 indicates this clearly to be not so: in the

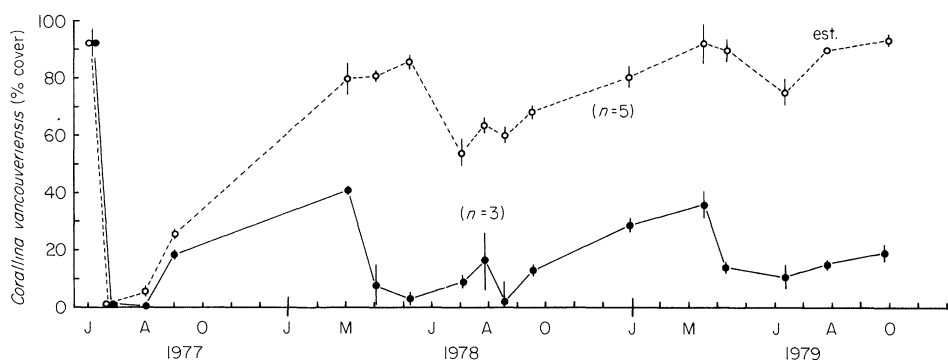


FIG. 4. Change in percentage cover of *Corallina* in experimental, grazer-free, plots (●---●) and control areas (○—○) with the normal grazer compliment. Vertical lines are ± 1 standard deviation, based on arcsine transformed data.

controls recovery to 80% cover occurred within 11 months, and to > 90% coralline cover within 21 months. Three of the herbivore-free sites failed to converge on the controls and have remained significantly different since the fourth month. The remaining experimental site behaved as though it was grazed, and was excluded. Re-establishment of *C. vancouveriensis*, at least from a basal system comparable to what would remain if the area had been severely grazed, is significantly facilitated by and requires grazers.

The second experiment examined the proposition that persistence of established coralline algae is enhanced by grazers. The manipulation takes advantage of the fact that *A. mitra* is often encrusted with corallines in the genera *Corallina*, *Bossiella*, *Lithothamnium*, *Lithophyllum* and *Mesophyllum*. Living *A. mitra* were collected, cleaned of their

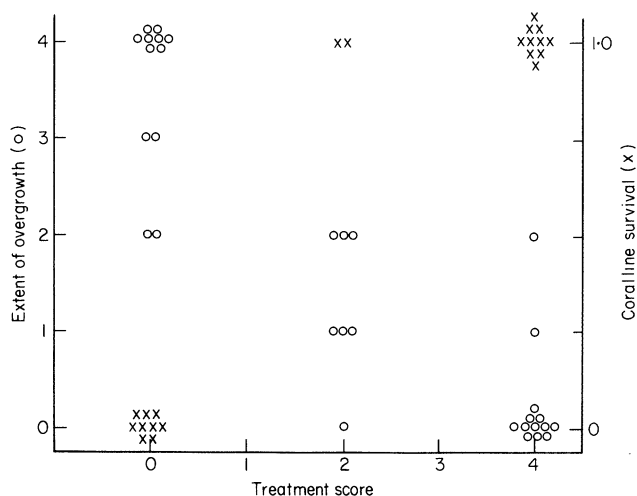


FIG. 5. The inverse relation between extent of overgrowth and coralline algal survival along a compound gradient of increasing herbivore pressure and increasing *Hedophyllum* cover.

flesh, and then bonded to the intertidal with Sea Goin' poxy putty, a non-toxic epoxy cement. The shells were placed in areas with and without *Katharina* and/or *Hedophyllum*, since this large alga both shades and whiplashes smaller, fleshy algae and diatoms, and the chiton consumes them. The results (Fig. 5) are clear. There is an inverse relation between extent of algal overgrowth on the limpet shells, and the combined influence of grazing pressure and *Hedophyllum*. This influence is positively related to crustose coralline algal survival after 3 months, scored on an all or nothing basis. In the absence of grazing pressure the crustose corallines become overgrown, predominantly by chain-forming diatoms, *Ulva* and *Halosaccion* (a red alga), and die. Erect, articulated coralline algal genera appear more immune to this mortality source.

Perhaps the most convincing, independently derived evidence of the tightness of modular bonding comes from work on settlement cues released by the algae, specifically attracting grazers. Barnes & Gonor (1973) showed that competent larvae of *Tonicella* settled almost exclusively on coralline algae and that the response was elicited by a water soluble algal extract. Morse *et al.* (1979) have chemically identified a well-known vertebrate neurotransmitter, γ -aminobutyric acid, from crustose coralline algae and demonstrated that it induces settlement by a grazer. Steneck (1977) has described morphological adjustments by corallines to obligate grazers that reduce the consumer's impact. The overall implication assembled from diverse sources is one of a mutualism characterized by loose but nonetheless positive interdependence and benefit to all participants. It can only exist in the presence of strongly dominating grazers which are minimally involved in the module's interactions and which protect the corallines from overgrowth by fleshy algae. The adaptive pathways seem to represent varying levels of transition from grazer-resistant to grazer-dependent status.

CONCLUSIONS

I began with the observation that the quest for a satisfactory solution to the diversity-stability relationship has been profitably frustrating. The answers remain remote but not

for lack of attention, since the issue bears both enormous theoretical and practical implications. The focus has swung, rightly I believe, toward attempts to understand the design of natural webs. Two previous viewpoints are especially prominent here, and I have attempted to oppose them with mine in Fig. 6. I have used as a setting the interactions between some of the invertebrate grazers and their algal prey. Although my preoccupation with aquatic webs may introduce some bias, it can be justified as follows. Rate processes seem generally faster than in terrestrially-based systems and therefore induced changes are more observable. Strong links tend to characterize some of the plant-herbivore relationships, and thus the cascade of change is more pervasive.

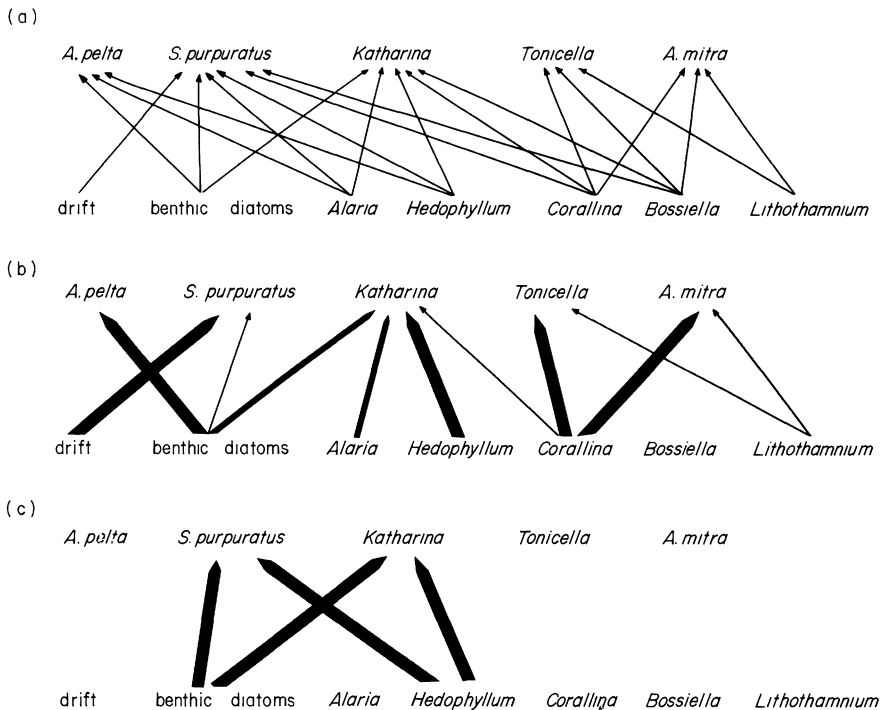


FIG. 6. Three conceptually and historically different approaches to depicting trophic relationships, illustrated for the same set of species. The connectedness web (a) is based on observation, the energy flow one (b) on some measurement and literature values, and the functional web (c) on controlled manipulation.

Connectedness webs have the most tradition behind them. They have served as the intellectual cornerstone for most if not all modern theoretical treatment because web membership and trophic interrelations can be generated by observation alone. Although some models (May 1973; DeAngelis 1975) consider interaction strength, others do not (Cohen 1978; MacDonald 1979; Rejmanek & Stry 1979), and the notion that randomly connected model ecosystems are a useful caricature of the real world has increasingly come into question (Lawlor 1978; Roberts 1974). The merit of the connectedness models is that they have maintained a lively and constructive debate which has identified certain significant food web attributes.

Less can be said about the relation between flow webs and community organization. They require substantially more information, much of it physiological, to construct. They

are statically descriptive at best and, further, assume importance is measured by the rate of material or energy flux through nodes in the web. This is hardly true. The approach is often remote from intimate biological detail, pays little heed to competitive cross-links, and has generated few or no insights into ecological processes.

I have spent most of my hour discussing a web in which what I call functional significance is emphasized. Unfortunately, it requires experimental manipulation for verification of the linkage strengths. However, as Fig. 6 notes, it can be adequately described by fewer interspecific relationships than the others, much in the fashion that Gilbert (1977) suggests for a tropical, terrestrial community. My approach places no weight on major energy flow pathways that have no bearing on community organization, for instance, a *S. purpuratus*—drift algal connection. It is immune to the observational artifact that often functionally significant prey are rare because of a strong, controlling interaction. Thus, *M. californianus* is hardly the most frequent item in *Pisaster*'s diet (Tables 1, 2). The approach finds both strength and reality in the following.

(1) Enumerating links through direct observation provides little information on a particular species' importance and the connectedness component of food webs is susceptible to enormous geographic and within-habitat variations. What counts is the competitive stature of the preferred prey, implying that cross-links will be as important as trophic ones.

(2) Trophic links are unequal in strength, and most benthic and aquatic communities seem to be characterized by high variance in this measure. Strong links are easily demonstrated experimentally, and their presence readily explains the cascading changes that characterize certain altered ecosystems, changes that may involve as many as four distinct 'trophic levels.' Further, predictable strong linkage can generate trophically different but persistent, alternative resource bases. These latter appear not to develop when the strong interaction is unpredictable in space or time.

(3) Finally, predictable strong interactions can encourage the development of modules or subsystems embedded within the community nexus. The individuals comprising these may be co-adapted to one another and exhibit sophisticated mutualisms. Many members are probably extremely specialized, and the module itself may be dependent on events biologically external to itself for continuity. Modules add much richness to ecological systems and many develop their own infrastructure but most members are probably not functionally significant and therefore are weakly-interacting species.

I wish to close with a final observation: pattern is generated by process. One embodies static description, the other more subtle and dynamical events. Food webs along with their associated cross-links provide a realistic framework for understanding complex, highly interactive, multispecies relationships. I believe the next generation of models must be more sensitive to interaction strength, less so to trophic complexity, for the answers to questions on the stability properties of complex, natural communities increasingly violated by mankind are vital, and our time is short.

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