TWO CASES OF RESOURCE PARTITIONING IN AN INTERTIDAL COMMUNITY: MAKING THE RIGHT PREDICTION FOR THE WRONG REASON

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An important ecological goal is understanding patterns of coexistence and exclusion of species in the same geographic area. Because most multi-species ecological systems are exteremely complex, it is probably impossible to describe all the component populations in terms of their physiological status or demographic characteristics such as age distributions and birth and death rates. One current method of studying such ecological systems is to design a generalized model, based on a few premises or simplifying assumptions, which will generate testable predictions. If, upon being tested, these predictions are falsified, the simplifying assumptions are changed accordingly; but if the predictions are verified, the assumptions are often considered to be substantiated.

This hypothetico-deductive approach has influenced ecologists to focus on more general questions rather than on specific factors which may have small effects and which, when applied to more general situations, lead to intractable mathematical equations. Here I emphasize, with Levins (1966) and Cohen (1968), that the use of generalized models can be misleading because of uncertainty as to whether a positive result depends on the reality of the model and the simplifying assumptions, or on entirely unrelated factors. I therefore urge that, whenever possible, simplifying assumptions themselves be tested as hypotheses and resultant models be based on a thorough understanding of the relevant natural history and, when possible, on experimental manipulation.

Here I will test predictions generated by two models which might be used in the construction of a general competition-based theory of the structure of an intertidal community. In both cases, the predictions generated by these two models are verified, suggesting that their simplifying assumptions are based on parameters sufficient to describe the community process in question. In both cases, however, acceptance of the superficially plausible models is due to inadequate appreciation of natural history. Simple experimental manipulation shows that each model makes the right prediction for the wrong reason.

SPECIES PACKING AND AN ANEMONE

Consider an intertidal community with three top carnivores. Since these species have no important predators, their coexistence cannot be attributed

to a reduction of competition resulting from predation on them (Paine 1966), and the competitive partitioning of their diet should be more evident than it would be with lower-level consumers. They tend to be long-lived organisms, and it is possible that their populations are limited by rare and unobserved physical disturbances, but it seems more likely that such carnivore populations are limited by requisite resources. MacArthur and Levins (1967) proposed a model of limiting similarity with competition as an important premise. This model appears applicable to such a system and assumes, in this case, that a linear array of the diets of the three carnivores would show that the two species on either side of the array would overlap relatively little with each other (β overlap) while the middle species would overlap either or both of the other two species (α overlap). Assuming with MacArthur and Levins (1967) the highly improbable premises that all three species share the same K values and that resources are renewable, this model predicts a critical α value of 0.544 beyond which the middle species cannot coexist "between" the others. In addition, their model predicts that, if the middle species overlaps either of the other species beyond a critical point, L, its diet will converge toward that with which it overlaps, and over evolutionary time, replace it. If it does not overlap beyond that critical point, the diet of the middle species will tend to centralize between that of the other two species. These predictions can be partially tested by sampling diets of the three predators; if verified, the competition-based model might be considered to have been substantiated.

The diets of three such upper-level carnivores are known from the rocky intertidal community at Portage Head and Shi Shi reef (Dayton 1971) on the Olympic Peninsula in the state of Washington (table 1). Diets of the asteroids *Pisaster ochraceus* and *Pycnopodia helianthoides* overlap very little (average $\beta = 0.006$) as *Pycnopodia* tends to specialize on the echinoid *Strongylocentrotus purpuratus*, while *Pisaster* has a broader diet, but tends to specialize on the barnacles *Balanus glandula* and *B. cariosus* and on the mussel *Mytilus californianus*. The diet of the middle carnivore, the anemone *Anthopleura xanthogrammica*, overlaps the diets of *Pisaster* and *Pycnopodia*, but none of the observed overlaps (table 1) is above 0.544, and therefore, they are not sufficient to jeopardize the persistence of the anemone.

Data in table 1 show that the *Anthopleura* diet more strongly overlaps that of *Pisaster* (average $\alpha = 0.396$) than that of *Pycnopodia* (average $\alpha = 0.054$). Depending upon the calculated value of L (MacArthur and Levins 1967), the model predicts that the *Anthopleura* diet should converge toward that of *Pisaster* or tend to centralize between *Pisaster* and *Pycnopodia*. These overlap data probably would predict a centralization, but in this case the actual calculation is not important because, depending on precisely where in the intertidal the anemone diet is sampled, it would appear to be either converging or centralizing. As the sampled area increases, a larger number of localized patches with up to 80% of the *Anthopleura* consuming *S. purpuratus* would be included, and the anemone diet would overlap more with that of *Pycnopodia* and less with that of *Pisaster*, and

TABLE 1
PERCENTAGE OF PREY ITEMS IN DIET OF EACH PREDATOR

Prey	Pisaster (N = 17,520)	Anthopleura (N = 226)	Pycnopodia (N = 150)
Mytilus californianus	15.6	69.4	1.3
Balanus glandula	47.4	0.4	...
B. cariosus	9.5	17.7	...
Chthamalus dalli	11.6	...	...
Tegula funebralis	11.3	...	...
Acmaea spp.	1.3	0.4	...
Pollicipes polymerus	0.7	...	...
Katharina tunicata	0.7	...	...
Strongylocentrotus purpuratus ...	...	2.7	91.3
Cancer sp.	...	4.0	2.0
Pagurus sp.	...	2.2	...
Pugettia gracilis	...	0.8	...
Protothaca staminea	...	1.3	...
Pisaster ochraceus	...	...	1.3
Unidentified fish	...	0.8	0.7
Others	1.9	...	3.4

NOTE.—*Pisaster* simplified from Paine (personal communication), *Pycnopodia* from Mauzey, Birkeland, and Dayton (1968), and *Anthopleura* from Dayton (unpublished). "Others" in the diets of *Pisaster* and *Pycnopodia* are rare occurrences and are not the same species for both predators. The overlap calculations of MacArthur and Levins (1967) have the following values: *Pisaster* affected by *Anthopleura* = 0.446 and by *Pycnopodia* = 0.009; *Anthopleura* affected by *Pisaster* = 0.246 and *Pycnopodia* = 0.067; *Pycnopodia* affected by *Pisaster* = 0.003 and by *Anthopleura* = 0.041.

would appear to be centralizing between the diets of the two asteroids. Again, with the low overlaps observed, this centralization would be predicted by the model.

An important component of the natural history of *Pisaster* is that it forages at high tide by moving up in the intertidal from a protected tidepool or surge channel to capture barnacles and mussels which comprise most of its diet, and then retreats back into tidepools or surge channels to digest its prey. Frequently when a *Pisaster* wrenches loose a large *Mytilus* or *B. cariosus*, it dislodges or loosens several others. I have demonstrated that this predation, as well as damage from drift logs, can indirectly cause many mussels to become detached from the substratum by wave action (Dayton 1971). As a result of these factors, these usually sedentary components of the *Pisaster* diet are tumbled about by wave action, and are washed into surge channels or stable depressions such as tidepools, where they are captured by *Anthopleura* which occur in relatively dense concentrations in these areas. Anemones in such pools, therefore, have a high dietary overlap with *Pisaster*.

The typical foraging behavior of *Pycnopodia* probably involves a random search until it locates a dense patch of *S. purpuratus;* on the outer Washington coast such patches are usually found in tidepools or surge channels. A *Pycnopodia* usually remains in such a pool for only a few weeks and appears to need approximately 24–48 hours to digest an urchin (personal observation). The actual consumption of urchins does not have an overwhelming effect on the urchin patches, which have densities as high as 263/m². However, when a *Pycnopodia* moves into an urchin patch, the

urchins within 5–10 cm of it clearly respond to its presence by moving their spines and pedicellariae and retreating from the *Pycnopodia*. I found that a *Pycnopodia* in an aggregation of *S. purpuratus* stampedes an average of 7.4–12.8 urchins per day (Dayton, unpublished).

In tidepools and surge channels of Portage Head and Shi Shi Reef (areas described in Dayton [1971]), extremely high densities of sea urchins and, therefore, low availability of rock substrate, usually force the fleeing individual urchins to climb onto the backs of others. When *S. purpuratus* is on a rock substratum, particularly in a depression, it is extremely well attached and very difficult to dislodge; however, when it is on the back of another urchin, it has a tenuous grip, and, in addition, the individual below appears to attempt to dislodge the intruder with its spines and pedicellariae. Therefore, the fleeing urchin is very susceptible to being dislodged by wave agitation; most of the urchins that retreat from the presence of *Pycnopodia* are indeed removed by wave action, much like those prey inadvertently dislodged by *Pisaster*, and many are swept into the *Anthopleura* patches.

Since all sea anemones employ a "sit and wait" feeding strategy, it is not surprising to find *A. xanthogrammica* a generalist (Emlen 1966, 1968; MacArthur and Pianka 1966). In addition, observations on asteroid foraging behavior suggest that a major part of the diet of *Anthopleura* is an indirect result of the foraging behaviors of *Pisaster* and *Pycnopodia*.

To test this hypothesis, contents of anemone coelenterons were sampled in areas at Shi Shi and Portage Head characterized by normal *Pisaster* densities and no foraging *Pycnopodia*. At the same time, anemone feeding observations were made in *Pisaster* removal areas (Dayton 1971), in areas where the *Pisaster* population density had been artificially doubled, and in areas where *Pycnopodia* was observed feeding. Sampling was done by selecting a small area inhabited by approximately 100 anemones and checking the contents of each coelenteron. This eliminated bias of possibly checking only larger anemones. An anemone was considered to be feeding only if the potential prey item in the coelenteron was observed to include edible tissue. This precaution was necessary because frequently old mussel valves and barnacle plates, probably empty before they were ingested, are found inside anemone coelenterons. A systematic bias is here introduced because prey items which the anemone has finished digesting but not voided are omitted from the count, as are some totally soft-bodied prey. The presumably small effect of this bias probably only gives a low estimate of the percentage feeding. The relative abundance of various items in anemone diets in all four situations (table 2) were compared using a χ^2 test and differed from each other significantly $(P < .001)$. If competition had been involved, doubling the *Pisaster* density would have been expected to reduce the number of *Anthopleura* eating species shared with *Pisaster*. But the fact that the *Anthopleura* diet significantly shifted toward that of *Pisaster* in these areas is convincing evidence of facilitation. In addition, similar χ^2 analyses of the control observations in table 2 showed significant seasonal differences which correlate with the seasonal foraging behavior of *Pisaster* discussed by

TABLE 2

EFFECTS OF *Pisaster* AND *Pycnopodia* FORAGING ON FEEDING OF *Anthopleura*
xanthogrammica AT PORTAGE HEAD AND SHI SHI SITES

	Control (N = 1,507)	Area with Pisaster Removed (N = 680)	Area with Double Normal Pisaster Density (N = 428)	Area with Foraging Pycnopodia (N = 1,055)
Percentage *Anthopleura* eating:				
Mytilus and/or *Balanus*	12.2 ± 4.5	3.4 ± 2.4	32.7 ± 8.3	2.0 ± 1.1
Strongylocentrotus purpuratus ..	0.3 ± 0.5	0.3 ± 0.6	0.2 ± 0.4	63.9 ± 9.3
Others (fishes, crabs, etc.)	1.3 ± 0.5	0.8 ± 0.8	0.8 ± 0.8	2.3 ± 1.2
Percentage not feeding	85.5 ± 4.7	96.4 ± 2.9	66.3 ± 8.2	31.6 ± 7.9
No. surveys	18	10	5	12

SOURCE.—Dayton (1971).
NOTE.—Variance is given as the 95% confidence interval.

Paine (1969). Since it is impossible for anemones to procure these prey
items directly, the hypothesis that they acquire their prey as an indirect
result of the asteroid foraging appears to be verified.

In summary, a competition-based model generated the testable and correct
predictions that (1) the carnivores utilizing the two extremes of the
resource array would overlap each other very little, while the central
carnivore would overlap both the others but that the overlap would be
below a predicted level and (2) given the relatively low overlap values and
a sufficiently large sample area, the middle species tends to centralize. The
correctness of these predictions appears to support the basic assumption of
the model, that limiting resources are apportioned by competitive processes.
However, natural history observations and simple experimental manipula-
tions demonstrate that the anemones, far from competing with the starfish,
depend on these animals to release the greater portion of their food. Thus,
correct predictions of the model are based on false premises.

NUMBER OF SPECIES SHARING A SIMPLE RESOURCE

Another competition-based model from which consequences of resource
partitioning are predicted can be applied to other aspects of my research
in the same geographical area. Consider a rocky intertidal community in
which all sessile species share the same potentially limiting resource of two
dimensional space. A hypothetical model based on the assumption that
succession within this community results only from competition suggests
the hypothesis that following a disturbance which makes free space avail-
able, the number of sessile species in the area will increase, but as space
becomes limiting, the number of species will decrease because of competition
for space. Partially as a test of this idea, I cleared all the organisms from
many small areas in the intertidal and counted the number of species re-
colonizing over time in the presence of natural disturbance factors.

These manipulations were done as a control for more elaborate experi-
ments in which I excluded three levels of biological disturbance (grazing

limpets, carnivorous gastropods, and a carnivorous asteroid) which are natural components of the community. These replicated experiments were done at each of three tidal levels for 3–5 years at three sites on the outer coast of the state of Washington and two sites on San Juan Island, Washington (Dayton 1971). Because the species' lists are somewhat different in these two general areas but are internally rather consistent from site to site, the two general areas are considered separately in figure 1. This figure summarizes the number of species present each month in the majority of the naturally disturbed control and the predator-free total-exclusion plots. In the control situation I cleared plots by scraping the substratum; in the total-exclusion plots I cleared the substratum as above and excluded all biological disturbance agents by means of cages.

As predicted by the hypothetical model based on the assumption that only competition for space causes the observed succession, the number of species
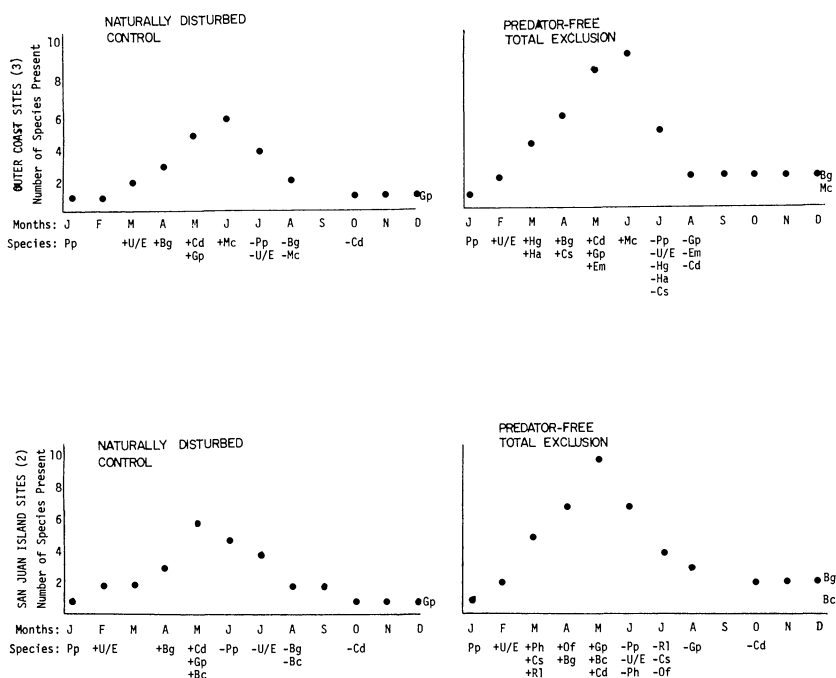

FIG. 1.—Species which were present in over half of the given plots in each month for 3–5 years in outer coast and San Juan Island, Washington sites (Dayton 1971). The substratum in the control plots was scraped clean; in the total-exclusion plots, the substratum was cleaned as above, and all biological disturbance agents were excluded by means of cages. *Pp: Porphyra perforata; U/E: Ulva* or *Entermorpha* (not differentiated in the field); *Bg: Balanus glandula; Cd: Chthamalus dalli; Gp: Gigartina papillata; Mc: Mytilus californianus; Hg: Hallosaccion glandiforme; Ha: Heterochortaria abietina; Cs: Colpomenia sinuosa; Em: Endocladia muricata; Bc: Balanus cariosus; Ph: Polysiphonia hendryi; Rl: Rhodomela larix; Of: Odonthalia floccosa. Mytilus californianus* initially occupies secondary space (Dayton 1971).

in the control areas initially increased as different species settled in the cleared patches, and then declined with time. The major premise of this model is that these species disappear as a result of competitive exclusion, and the fact that the number of species does diminish in the controls could be considered as support of the model. However, careful observation reveals that there is always an abundance of unused substratum, the resource for which the sessile species potentially compete, and that there is never an indication of competition for space in these cleared, control areas. In fact, controlled experimentation demonstrates that the disappearance of the individuals in these areas is a result of various levels of disturbance: some of the *Porphyra* and ulvoid species eventually die of desiccation; the rest of the algae are killed by the effects of a grazing guild, mostly limpets, which acts as a generalized filter by grazing on settled algal spores and sporelings and by dislodging cyprids and young barnacles; most of the barnacles and mussels that survive this filter are killed by members of a carnivorous gastropod guild; and the remaining barnacles and mussels are killed by *Pisaster ochraceus*. The predator exclusion areas also had a strong bloom of algal species, followed by a dense settlement of two or three species of barnacles. These areas rarely have available primary substratum, and essentially all the sessile species which disappear are eliminated by severe interspecific competition for space, as the algae were undercut by the barnacles and the barnacles were smashed or overgrown by other barnacles or mussels (Dayton 1971). This demonstrates that the competition theory itself is valid and that the space can be dominated by one or two species. With the addition of natural disturbance agents in the unprotected control areas, space is no longer limiting and there is a tendency for more and different species to persist; and those species which do disappear, do so as a result of disturbance natural to the community rather than competition. In summary, the effect predicted by the competition-based model is indeed observed, but the model is correct only in the most artificial experimental situation in which all of the natural disturbance agents are excluded.

    The important point here is that, if we were testing the prediction generated by the competition-based model and did not know much of the natural history of the community, a condition true in many communities, such as the deep-sea community, in which such tests are or might be made, we would simply sample the situation which is here represented by the control and conclude that the data do support the model. Again, the model is misleading because the assumptions were not tested.

<div align="center">DISCUSSION</div>

    Here I have tested two models which, though hypothetical, do incorporate salient features of known natural situations. The models were based on the assumption that competition sets a limit (1) to the similarity of co-existing species and (2) to the number of species which share a simple

resource. Predictions of both models were verified, and the assumptions based on the primacy of competitive interactions seemed strengthened, but in each case insights into the natural history and simple experimental manipulations demonstrated that a quite different mechanistic interpretation is correct. Simple models like these are usually tested in much more complex communities or on an evolutionary time scale in which the investigator must remain essentially blind to the actual mechanisms underlying the observed phenomena. While ecological investigations of some situations may best be approached through the use of hypothetical models, my purpose here is (1) to demonstrate that blind application of such models may lead to serious interpretive errors even in a relatively simple community such as the intertidal, and (2) to emphasize the innate deviousness of ecological interactions. I suggest that, as the complexity of the system increases, overly simplistic models such as those based entirely on competition or on variants of the Lotka-Volterra equations are likely to be wrong with a frequency increasing as the number of complex interactions increases. For example, most such models are tested in terrestrial communities despite the known ubiquity of coevolved pollinator systems, plant-herbivore interactions, including complex chemical interactions such as summarized by Whittaker and Feeny (1971), the multitudinous effects of seed predation discussed by Janzen (1971), the various mutualistic relationships such as symbiosis, scavenging, and so forth. The chance of interpretive error is likely to be much greater when highly simplified models are tested in complex communities and taxocenes than when they are tested in the intertidal community.

I do not mean to deny the validity of the powerful hypothetico-deductive technique. In these examples I have demonstrated primarily that the premises of the models applied were not justified. The MacArthur and Levins (1967) model does not apply because the food niche is obviously too complex to fit their simplifying assumptions, as the anemone profits by a positive secondary interaction with the other two carnivores (see Dodson [1970] and Heatwole [1965] for other well-documented examples of this type of positive interaction in alpine lakes and with cattle egrets in tropical grasslands, respectively). In the second example, natural disturbances invalidate a simple competition-based model which is seen to portray the situation accurately only in those atypical situations in which there are no natural disturbances. The use of such models in complex situations seems appealing because they are thought to offer important shortcuts to correct generalizations; but it is clear that the models must be based on a thorough understanding of the relevant natural history, and, when possible, on some form of controlled manipulation. Once sufficient information is available to protect against the possibility of making the right prediction for the wrong reason, there often may be enough knowledge of the "organization" of the community so that it is an open question whether the use of some models really does offer any shortcuts to correct generalizations.

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