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CONVERGENCE OF ECOLOGICAL PROCESSES BETWEEN INDEPENDENTLY EVOLVED COMPETITIVE DOMINANTS: A TUNICATE-MUSSEL COMPARISON

R. T. Paine and T. H. Suchanek
Department of Zoology, University of Washington, Seattle, Washington 98195

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It has long been recognized that physically comparable environments often are inhabited by morphologically similar species. The phenomenon is termed convergence, especially where there is some but not extreme genetic distance between the species, and it has become a popular comparative tool. The basic hypothesis is well-stated by Orians and Solbrig (1977): ". . . that, given 2 regions with identical climate, geology and topography, ecosystems that are identical in structure and function will result . . . despite differences in the initial flora and fauna." Marine ecologists are familiar with at least two community level derivatives of this approach, long practiced by terrestrially-oriented biologists. Thorson (1957) expanded parallel level-bottom community comparisons to a worldwide description; Stephenson and Stephenson (1972) have fostered a universal or "widespread" scheme of intertidal zonation. When convergence is expressed on a strictly morphological basis marine invertebrate groups provide numerous examples, often discussed under "homeomorphy." Cloud (1948) assembled many striking examples which include the near morphological identity, when viewed externally, of a Devonian tetracoral, a Permian brachiopod and a Cretaceous bivalve.

Most ecological comparisons invariably involve species which share some degree of taxonomic closeness: lizards (Schall and Pianka, 1978), plants (Leigh, 1975; Cody and Mooney, 1978) or birds (Cody, 1974), for instance. The comparative questions asked are purposely constrained by the common taxonomic heritage. But suppose the focus is on the *role* played by some particular species or life form, where role is defined in terms of the organism's behavior, the type and range of its ecological interactions, and especially its influence on other community members. In phyletically rich marine communities comparable functional roles can be occupied by sea urchins or herbivorous fish, by carnivorous crabs or predatory snails, or by bryozoa or sponges. Many examples are provided by Woodin and Jackson (1979). Thus the phenomenon of complementarity in which taxonomically distant but functionally similar groups either compete with or replace each other geographically (Brown and Davidson, 1977; Wright, 1979) is apt to be commonplace. If one is interested in how similarly organized the communities are, then the appropriate comparisons between different communities are often not taxonomic. Our purpose is to examine a suite of ecological traits common to species potentially dominating a comparable limiting resource, space. The main comparison is purposely biased towards the extreme condition: surely, if similarities can be identified between such taxonomically distant examples as a chordate and a mollusc, then the same influences should also characterize less extreme comparisons since at some point the interphyletic examinations converge on those within orders, families or those with still closer genetic ties, and in the process gain that strong bias produced by immediate common ancestry.

We begin by describing those processes thought to determine the distribution and local abundance of the tunicate *Pyura praeputialis* (Heller). These new data are then compared with our standard, the much better known mussel *Mytilus californianus* Conrad. Such comparisons can serve to identify common rules, requirements or liabilities associated with particular ecological life styles. In this paper, then, the primary comparison is between a mollusc and a chordate, species occupying similar zones and roles in their respective communities yet having remote common ancestry.

The Distribution and Abundance of Pyura praeputialis

Geographic Distribution.—*Pyura praeputialis* has a conspicuously disjunct distribution. The most extensive intertidal beds are known from southeastern Australia, especially on rocky, wave-swept headlands. Anecdotal references to its ecology are to be found in Dakin (1953), Goddard (1972), and Anderson et al. (1976). A small population exists near the city of Antofagasta, Chile (23°42′S, 70°27′W). We have examined the shore immediately to the north of Antofagasta and found no *Pyura.* We attempted to establish the southern limit but were unable to, although the tunicate beds were becoming noticeably attenuated 40 km to the south. Extensive examination of other seemingly appropriate localities from 20°S to 53°S, while revealing populations of the closely related species *Pyura chilensis* Molina, failed to reveal more *P. praeputialis.* This impression of a strict geographic limitation is confirmed by our Chilean colleagues. Moreover, the species appears to be relict, rather than introduced, in that subfossil individuals are found in raised beds adjacent to living populations (C. A. Viviani, pers. comm.). The data discussed below were gathered in Sept. 1974, Oct. 1975, June 1976 and Jan. 1978.

Population Size Structure.—Two aspects of *P. praeputialis* bear particular ecological significance. First, individuals (of unknown age) can become large, and we have measured numerous tunicates exceeding 30 cm in height. Second, although the species is technically solitary, as opposed to compound, contiguous individuals are cemented together and exceedingly difficult to pry apart. Thus aggregations of individuals attain a collective unity or pseudo-coloniality which may impart distinct competitive advantages (Jackson, 1977, 1979).

The relationship between height (measured from the substratum to the upper "rim" of contracted individuals) and diameter (the distance between opposing edges of the rim measured across the siphons) is non-linear in the intertidal zone (Fig. 1). *Pyura* attached directly to the primary substratum appear to grow to a near maximal diameter, attaining an asymptote of 9–11 cm, while continuing to increase in height. Initially, space acquisition is important as the organism grows in the lateral plane. This process is followed by a further increase in height due to self-crowding or nutrient competition. However, nutrient considerations are unlikely to apply to an aggregation of contiguous *Pyura* in which all the matrix-forming individuals are approximately the same height. Increases in both major dimensions appear to make *Pyura* less susceptible to predation (see below), and individuals which survive beyond some threshold size seem to attain a relatively secure refuge, as in other species (Paine, 1976*a*).

The size distribution of those individuals forming the living matrix of a typical mature, intertidal bed is given in Figure 2. Samples were taken at 1.0 m intervals down a gently sloping shore. *Pyura* height increases gradually in a seaward direction, probably reflecting increased feeding time. It tends to drop slightly before the abrupt lower intertidal limit is reached, perhaps due to continual removal of the largest individuals by wave action. In addition these large individuals are festooned with smaller *Pyura.* In 1975 we estimated, on the basis of ninety 100 cm^2 quadrats, a mean density of 154 small *Pyura* (<2.0 cm diameter) per m^2 of adult surface. Subtidal observations (using SCUBA) revealed scattered beds of very large attached individuals, and numerous clumps of *Pyura* rolling around. Many of these were severely eroded, and none appeared to have

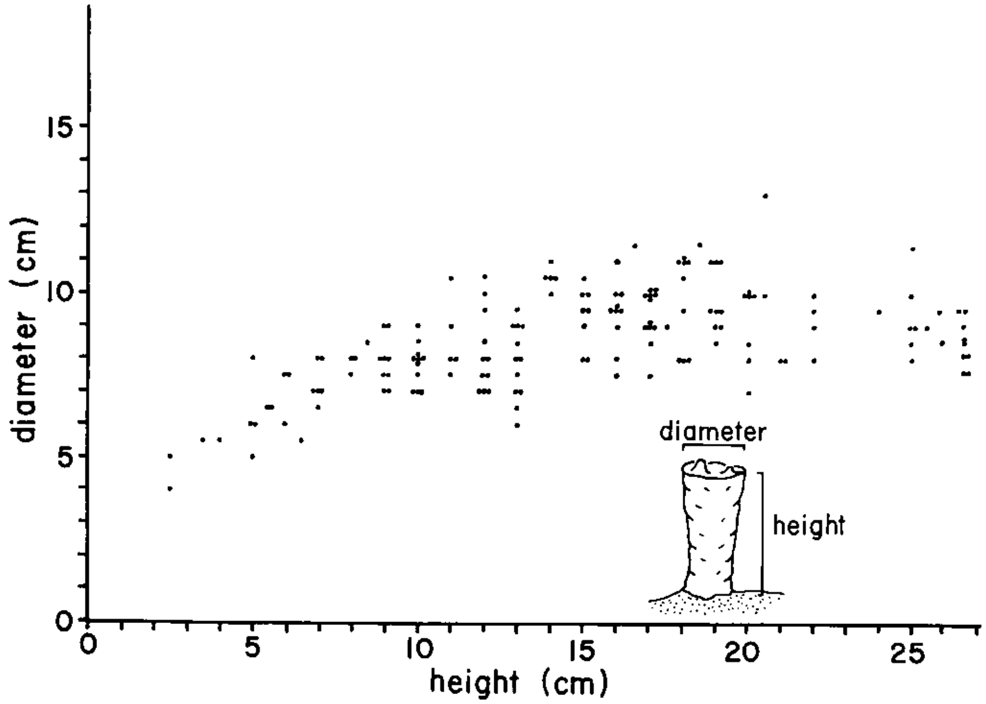

FIG. 1. Diameter-height relationships in the tunicate *Pyura praeputialis*, as measured in the field from "contracted" individuals exposed to air.

the capacity to reattach. Nonetheless these mobile aggregations had retained their continuity even after death, attesting to the effectiveness of the attachment of individual to individual.

Effects of Disturbance.—Figure 2 suggests that the main bed at Antofagasta can occupy a 15 m wide band along the shore. Measurements of tidal height, using a transit level, indicate that the band extends vertically from +0.49 m to +1.01 m. On a shore with a relatively constant slope and a range of 1.52 m, this amounts to about 34% of the intertidal zone. Such spatial domination is common; further, within the *Pyura* zone the tunicates tend to monopolize the space. Quadrat sampling in 1974 and line transects normal to the shore in 1975 (Table 1) indicated that 80–84% of the space within the broad *Pyura* zone was occupied by this single species. However, in Feb. 1976 the bed was disrupted by a major storm (J. Tomicic, pers. comm.). When we examined the same site in June 1976, percent cover had been reduced to 21–25%, even after some repopulation. By 1978 the recovery process was well underway as measured by spatial domination although the size structure of the tunicate bed had not attained pre-disruption levels.

This pattern of disturbance and recovery is characteristic of many dominant life forms (Paine and Levin, 1981). In *Pyura* large size also increases its susceptibility to storm waves. A suggestion of the size-selectivity of such storms is indicated in Figure 3 which shows that even after 4–5 months of growth, the average diameter of larger tunicates was still 4 cm smaller than before the disruption. Larger tunicate individuals, like larger trees, are thus more susceptible than smaller ones. We do not know what the average interval between such disruptions might be. Our 1976 observations indicated that it was a gen-

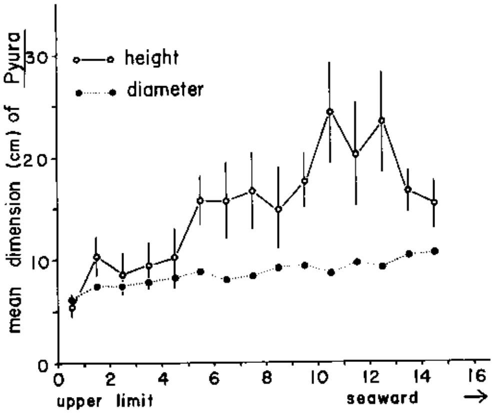

FIG. 2. Size structure of *Pyura praeputialis* measured along a gradient normal to the shore. Error bars are 1 standard deviation on either side of the mean, calculated from the height of the 10 largest individuals at each meter interval. In this data set, no individuals were found beyond the 15 m interval, suggesting an abrupt termination of the *Pyura* band.

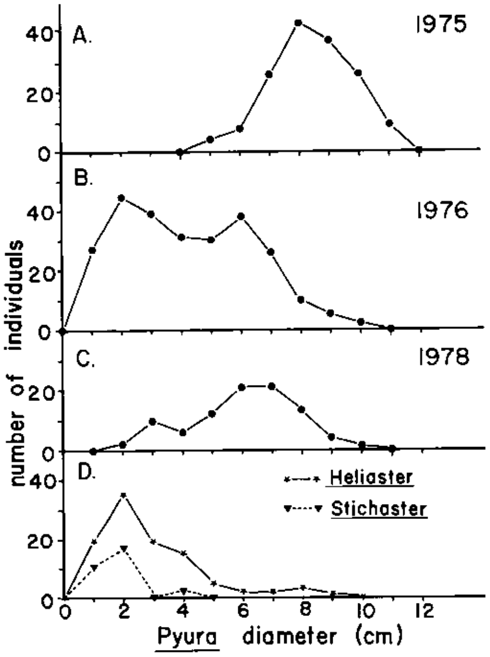

FIG. 3. Size-frequency distributions of *Pyura praeputialis* in the zone of overlap with the predatory sea stars *Heliaster* and *Stichaster* (A–C). D illustrates the size frequency distribution of *Pyura* in the diet of the sea stars, summed over all years.

eral phenomenon within the central portions of the Bay of Antofagasta. However, beds 20 km away on the bay's northern rim were spared. This disturbance to a spatial dominant is caused solely by the shearing power of large waves: the Chilean coastal system is a notorious desert and wave-carried debris such as logs simply do not exist (cf. Dayton, 1971). Recovery is initiated by larval settlement both on and adjacent to surviving individuals. The process is completed by downward and/or upward growth of a stolon-like projection, which eventually becomes the stalk, and by radial growth of the disc filling in open patches in the bed.

The Influence of Predation.—We do not know what factors set the upper limit to *Pyura*'s distribution. The beds end rather abruptly, and it seems unlikely that biological factors, for instance competition with *Jehlius* (formerly *Chthamalus*) *cirratus* or a common mussel *Perumytilus purpuratus* could be important. Rather, it is probably increased physiological stress

TABLE 1. *Temporal patterns of primary space coverage by* Pyura praeputialis *at Quebrada El Way, approximately 15 km to the south of Antofagasta. A major disturbance (storm) occurred about Feb. 1976. Statistical calculations on percent cover were made from arcsine transformed data.*

Date	Sampling method	Number of samples	Mean % cover by *Pyura*	SD
17 Sept. 1974	quadrat	12	80	13
		5	84	11
5 Oct. 1975	25 m line transect	6	82	10
21 June 1976	1 m line transect	14	21	25
		8	25	25
8 Jan. 1978	quadrat	15	65	29

and/or reduced feeding, both of which are functions of immersion or emersion time.

The primary factor determining the lower intertidal limit is more easily identified. *Pyura* seems capable of surviving fully immersed, as indicated by tide pool and subtidal observations. However, its lower limit is usually well demarcated in the intertidal zone. The reason appears to be predation, much as it is for *Mytilus californianus* (Paine, 1966) although the evidence for *Pyura* is entirely circumstantial.

Pyura praeputialis is eaten by at least five species, including man. The gastropods *Priene rude* and *Thais chocolata* feed primarily on the detached and battered subtidal clumps. Another gastropod, *Concholepas concholepas,* consumes larger individuals by either boring through the tunic or inserting its proboscis through one of the siphons. Although our feeding observations are limited ($N = 35$) the work of Castilla et al. (1979) and DuBois et al. (1980) implicate this species as a major subtidal predator on *Pyura*. The sea stars *Heliaster helianthus* and *Stichaster striatus* predominantly consume *Pyura* <5 cm in diameter and are probably the most significant predators in the intertidal zone. In their attacks on *Pyura,* their initial penetration appears to be through the siphonal openings. Figure 3 shows the size distribution of the available mid and low intertidal *Pyura* in three sampling years and the number of various sized *Pyura* being consumed by these sea stars. The mean sizes of the available and consumed *Pyura* are obviously significantly different: sea stars are selectively removing the smaller tunicates at their lower distributional limit.

Although we lack data on feeding rates, the sea stars are abundant enough at Antofagasta to be a major factor in controlling the distribution and abundance of *Pyura*. Quadrat sampling and 1.0 m wide belt transects along the shore were used to generate density estimates: *Heliaster* (0.1–0.5 m^{-2}), *Stichaster* (0.5 m^{-2}). The tendency to consume small *Pyura,* at least in the intertidal zone, probably causes two phenomena: the tunicate size structure and local distribution show both a bias towards larger individuals in mature beds (Fig. 3), and a sharp curtailment of *Pyura* at its lower limit (Fig. 2). Selective predation focused on the smaller size classes could explain these trends. Further, Figure 1 suggests that while diameter is asymptotic, body height is not. A growth pattern emphasizing increased height, which will make predation by benthic predators more difficult, should be expected.

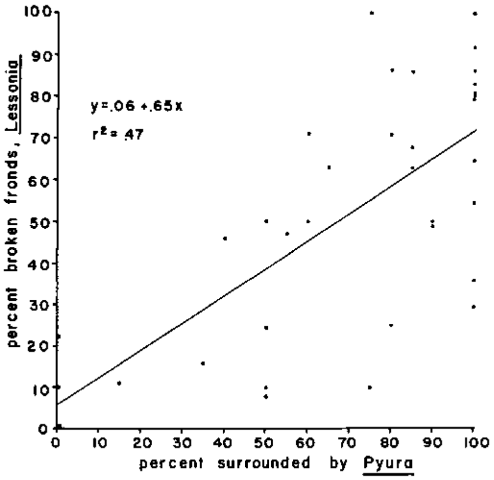

FIG. 4. The relationship between the condition of the laminarian alga *Lessonia* and the extent to which it was surrounded by *Pyura*.

Interspecific Competitive Ability.—*Pyura,* as suggested by its dominance of intertidal landscapes at undisturbed sites, is probably competitively superior to all other local species. Although no experimental data are available to support this view, a strong circumstantial case can be made. *Pyura* is the largest sessile animal life form in the intertidal zone at Antofagasta. In a might-is-right, space-limited system, larger body size seems to confer competitive superiority, as is known for other marine communities (Paine, 1977). We never identified another space-limited species which seemed capable of maintaining or improving its position in the presence of *Pyura,* despite hundreds of hours of observation. Although a large (basal diameter >5 cm) barnacle (*Megabalanus psittaceus*) is often abundant in the lower intertidal, it is overgrown by *Pyura*. Lastly, the assemblage returns to *Pyura* domination after disturbances, suggesting that alternative ecological solutions to dominance are not expressed even when opportunity presents itself.

The mechanism usually assumed to confer competitive superiority in the intertidal zone is "brute force": overgrowth, undercutting, crushing or smothering of the competitor. These mechanisms do not appear to be the primary ones for *Pyura*. For instance, most *Pyura* are attached directly to the substratum: we rarely found hard parts or skeletal remains of overgrown species associated with their basal areas. Instead, *Pyura* seems to increase its spatial coverage at the expense of other species in a novel way. The largest potential competitor is the perennial brown alga *Lessonia nigrescens* which, in southern Chile, can attain a basal diameter in excess of 80 cm. Although it is smaller in the vicinity of Antofagasta, it is still a large-bodied species and it is not unusual for rocky headlands to be dominated by it. Both it and *Pyura* can occupy such habitats. Where they do, such sites inexorably tend toward *Pyura* domination. The cause appears to be the complex of invertebrate grazers associated with, and possibly even dependent upon, the spatial refuges provided by the interstices within a *Pyura* bed.

Tunicate beds are known to harbor diverse communities. Zamorano and Moreno (1975) found a minimum of 61 species associated with *P. chilensis* from the intertidal zone in Chile. An equal richness can be inferred for this same species from the data of Gutierrez and Lay (1965), although in their study the tunicate species was misidentified. Approximately 70 species of invertebrates have also been found associated with beds of another closely related large tunicate, *P. stolonifera* (Heller) from the rocky shores of South Africa (Van Driel, 1979). Typically, some fraction of these associates (between 10 and 20% of the taxa) are mobile grazers: crabs, chitons, limpets, urchins and amphipods. Where contact is made between *Pyura praeputialis* and *Lessonia,* the latter species appears ragged. Figure 4 illustrates the correlation between the extent of this raggedness, as measured by the proportion of injured and non-regenerating *Lessonia* stipes and fronds, and the degree to which *Lessonia* is surrounded by *Pyura*. The correlation coefficient is significant ($P < .01$, $r = .69$, Spearman rank-correlation test) although substantial scatter exists. We have observed chitons attacking the holdfast proper and small gastropods feeding on the injured stipes. Santelices et al. (1980) report that stipe regeneration is possible in *Lessonia,* and that plants fail to survive if more than 50% of the stipes are lost or damaged. Where damage is in excess of this level, the holdfast degenerates and disappears within 3 months. Thus, although *Pyura* might prevent spore establishment or germination, or even might outcompete small (<20 cm frond length) *Lessonia, Pyura* clearly lacks the structures or abilities *by itself* to dislodge an established plant with a massive holdfast from which fronds can extend two meters or more. Competitive elimination is effectively accomplished by the associated animal community.

Although this demonstration is entirely inferential, it is supported by observations on the distribution patterns of *P. stolonifera* and the laminarian *Ecklonia radiata* in South Africa. These species overlap locally, and where they do, *Pyura* dominates (Morgans, 1959; Day, 1974) although the mechanism is unknown.

Comparative Features of Mytilus californianus

Relatively few marine intertidal invertebrates have the potential, whether realized or not, to form an extensive, even inclusive, matrix around which a complex of other species can develop. The best known of these, and the only one whose biology has been rigorously examined, is the mussel *Mytilus californianus* (Suchanek, 1979). It can attain a large shell length (25–30 cm), appears to be long-lived although actuarial data are missing, and dominates primary space in the absence of its predators (Paine, 1966, 1974, 1976*a*; Harger, 1972). It is susceptible to physical disruption which can remove as much as 60% of the mussels present (Levin and Paine, 1974; Paine and Levin, 1981). A variety of mechanisms facilitate recovery, suggesting that disturbance has been a predictable feature of this mussel's evolutionary history. The most significant attribute in the recovery from large scale disruptions is larval recruitment. Suchanek (1978, 1981) has shown that *M. californianus* settles selectively onto the byssal fibers of its own species, or onto those of a much smaller associated congener, *M. edulis* L.

The local distribution of *M. californianus* is strongly influenced by predation. Paine (1966, 1974) has shown, in experimental removals of a sea star, that the lower distributional limit in the intertidal is set by predation. Conversely, intertidal mussels can become too large for sea stars to consume (Paine, 1976*a*), and therefore mussels can persist in the presence of their primary predators.

The fauna associated with mussels is rich, yet little studied. Suchanek (1979, 1980) has found that at least 300 species utilize the physically complex structure afforded by multilayered *M. californianus* beds. A few of these species may be obligate inhabitants; most are more casual though abundant and simply treat the mussels as additional surface on which to settle or browse. The resultant association is complex and can influence areas beyond the physical boundaries of the mussel bed. Dayton (1973) and Suchanek (1978) have illustrated these "browse lines." They seem to be characteristic features of mussel beds everywhere; they are caused by grazers which inhabit the matrix of the bed and forage out a set distance (usually 10–20 cm), consuming resident algae and affecting barnacle distribution. Dayton (1971) and Suchanek (1978, 1979) have demonstrated experimentally the efficiency of this response.

The activities of such grazers and the presence of browse lines appear to enhance the movement and persistence of mussels by reducing the quantity and species richness of sessile organisms capable of overgrowing mussels or competing with them for space (Suchanek, unpubl.). Such detrimental overgrowth occurs on some subtidal mussels (Paine, 1976*b*). Suchanek (1979) demonstrated that intertidal mussels from which resident grazers were removed experimentally tended to be overgrown by potentially deleterious algae and/or barnacles. Consistently, only 20% of the surface area of control mussels was fouled. However, in those mussel beds where associated grazers were removed for 1.5 years, 60–90% of the area on their valves was fouled. Overgrowth of this type has been shown to be highly detrimental to adult mussel populations. Therefore, it is likely that mussels, like macroalgae (Black, 1976; Lubchenco, 1978), derive positive benefits from the associated fauna.

DISCUSSION AND CONCLUSION

Dense populations of macroscopic organisms may provide a matrix or habitat for other species. The most familiar examples might be boreal forests or the upper portions of coral reefs in which *Acropora cervicornis* or *A. palmata* dominate. Squires (1964), for instance, lists between 200–300 species associated with cold water coral structures; tropical ones can only be richer. We have focused on two competitively-superior sessile marine species of large body size around which a complex assemblage of other species develops. The evidence for our discussion is gleaned both from patterns we have observed in natural populations of mussels and tunicates (including their abilities to dominate their respective environments), and from experimental results obtained from the well-known *Mytilus* mussel bed system. The generality of our thesis can be extended to Cretaceous bivalves, the rudistids (Kauffman and Sohl, 1974), and the upper Permian reef-forming productoid brachiopods (Cooper and Grant, 1975).

All these species have little immediate

common phylogenetic background and tend to be dissimilar in morphology and overall external appearance. On the other hand, because they are matrix-forming they show many ecological properties apparently developed as a consequence of their matrix role. Table 2 lists some of their qualitative properties, touching on many important life history features. We suggest that these constitute a set of convergent attributes common to competitively superior, matrix-forming species. In essence, once the role has been established evolutionarily, there appears to be surprisingly little latitude in the way the adaptive problems common to the role have been solved. None of these species are solitary although all are individualistic as opposed to protoplasmically colonial. Nonetheless they achieve, via four different morphological mechanisms, a measure of coloniality by binding, cementing, interlocking or gluing themselves together. They all seem to grow relatively rapidly, and probably owe their high competitive status to this capacity. For instance, Suchanek (1981) found that *M. californianus* increases much more rapidly in length than its associated congener *M. edulis* after the second year. The rudistids are exceptional among bivalves in that their massive shells are characterized by an open cellular wall structure. The resultant "carbonate economy" provides a mechanism for rapid growth, large size and its implied protection from predation, and enhancement of competition for space (Kauffman and Sohl, 1974). In contrast productoid brachiopod valves are solid structures with the exception of punctae, microscopic extensions of the mantle which penetrate the shell material (Williams, 1968). The growth rate of these Permian reef-forming brachiopods is unknown.

The major ecological differences between these species (Table 2) seem to relate to the mode of reproduction and length of the planktonic interval. In *Mytilus* spp. the sexes are separate and the planktonic period lasts 10–14 days at a minimum (Seed, 1976), permitting the larvae to be transported substantial distances. *Pyura praeputialis* and the closely-related *P. stolonifera* from South Africa are hermaphroditic (Day, 1974; Anderson et al., 1976). Further, both species are characterized by very limited dispersal abilities, with settlement and metamorphosis occurring within 14 h in *P. praeputialis* (only 1–2 of which are free swimming, Anderson et al., 1976), and less than one day in *P. stolonifera* (Griffiths, 1976). These large-bodied *Pyura* thus seem to be committed to maintenance of their immediately local populations through suppression of the dispersal stage, in contrast to the mytilids. Nothing is known about similar aspects of rudistid or richthofeneid brachiopod reproduction.

On the other hand, one aspect of reproductive biology seems to be convergent. The position of recently settled postlarvae can be determined for all five of the taxa being discussed. Juvenile *M. edulis* normally settle in storm-generated patches of bare space or on filamentous substrates in the mid or lower intertidal zone (Suchanek, 1978). *Mytilus californianus* postlarvae are usually found among the byssal fibers of conspecific or congeneric adults (Suchanek, 1978). *Pyura praeputialis* settles on bare rock adjacent to adults and on the adults' tunic. In the latter circumstance the stalk can be observed growing down towards the solid substratum. Kauffman and Sohl (1974) picture numerous rudistids encrusted with smaller conspecifics which suggests an identical growth tactic. The behavior of Permian brachiopods at settlement must remain obscure, but Cooper and Grant (1975) illustrate close associations between large and small conspecifics in the superbly preserved Glass Mountain material.

These comparisons suggest that a limited set of ecological rules characterize the role of a competitive dominant in shallow water marine ecosystems. We would not expect further comparisons to be exact; some latitude in expression is to be anticipated due to constraints imposed by morphological limitations in phyletically divergent taxa. On the other hand, we deem it especially significant that *M. californianus*, when used as a model, more accurately characterizes the salient ecological

TABLE 2. *Ecological traits shared in common by four matrix-forming species. In addition, comparable features are listed for* M. edulis *to facilitate comparison with its congener.*

Trait	Phylum, species or taxon				
	Mollusca *Mytilus edulis*	Mollusca *Mytilus californianus*	Chordata *Pyura praeputialis*	Mollusca, rudistid bivalves, especially *Barrettia*	Brachiopoda, productoids, especially *Scacchinella*
Relative body size	small	large	large	large	large
Predation size escape	no	yes	yes	?	?
Group connectedness	yes—byssus	yes—byssus	yes—"glue"	yes—interlocking flanges	yes—spines
Structurally complex matrix	no	yes	yes	yes	yes
Rich associated community	?	yes (>300 spp.)	yes (>60 spp.)	apparently yes	apparently yes
Competitive ability	intermediate	superior	superior	?	?
Susceptibility to disturbance	great	great	great	apparently great	?
Perennial	yes	yes	yes	apparently yes	apparently yes
Larval recruitment	on adult and adjacent space	on adult	on adult	on adult	on adult

features of a large tunicate than it does of its congener *M. edulis* (Table 2). Further, the intrageneric variability within *Mytilus* implies that similar morphological features do not, by themselves, restrict a group to a single role.

The current ecological and evolutionary literature lacks a terminology appropriate to discussing convergence in ecological properties between organisms which are at best only distantly related. Elton (1927) seems to have come the closest to identifying roles for species which are independent of their taxonomy. Such terms as decomposer, herbivore and predator, of course, refer to functional roles, but they are too general to be of much predictive value. There seems to be an enormous number of ways to fill the predator role. The same is not true for "top" predator, or, in the case just developed, the alpha competitor. In this latter instance the description of both ecological properties and their consequences can be stated with some precision. Recognition of functional convergence should provide a way of organizing communities in a fashion which is independent of taxonomy but which relies heavily on the essential functional, biological and ecological detail.

These preliminary results bear directly on a current major issue, that of how to determine the appropriate null state in ecological comparisons (Caswell, 1976; Simberloff, 1978; Ricklefs and Travis, 1980). When random communities are assembled for comparative purposes, the entities are always chosen on morphological grounds from closely allied taxa. Although such techniques may suffice for terrestrial comparisons, they clearly will not for benthic marine ones. In the latter situation the wide variety of phyla often precludes the existence of comparable lists of closely related species. Further, necessary ecological functions are often achieved by morphologically different structures. Thus, it is conceivable that two assemblages could exist which show little morphological or phyletic overlap, but which are organized according to some common set of rules.

Guild membership might even be comparable in terms of numbers of species and their interrelationships. If so, this would constitute strong evidence for order in nature, an order which would be missed by the comparative techniques currently employed. We are not arguing that such communities exist. However, comparisons like the mussel-tunicate one just developed indicate the reality of functional convergence. If it is commonplace, then another dimension must be added by ecologists in their search for repeatable patterns in community evolution.

SUMMARY

Species capable of competitively dominating space in marine intertidal communities seem to share a suite of traits and liabilities. A comparison between the tunicate *Pyura praeputialis* and a mussel, *Mytilus californianus,* suggests that large body size, relatively rapid growth, some mechanism insuring group morphological continuity, susceptibility to disturbance, and larval recruitment onto the adult proper are ecological features held in common. The data indicate that a diverse associated community may benefit these matrix-forming species by reducing overgrowths or even eliminating large-bodied potential competitors. Further, such features can be identified in a Cretaceous bivalve and a Permian brachiopod, species which were likely to have been matrix-forming community dominants themselves. The reappearance of this suite of traits in morphologically, temporally and phyletically distant forms suggests constraints or rules in the filling of this ecological role. Community comparisons based on taxonomically related groups would miss these important patterns in community organization.

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Corresponding Editor: R. E. Ricklefs