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Predation and community organization on Eastern Pacific, temperate zone, rocky intertidal shores

Depredación y organización de comunidades en el intermareal rocoso de la zona templada del Pacífico Este

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ABSTRACT

Our review deals with questions of how intertidal communities are organized in Chile and Western North America. To answer these, the paper focuses on seven functional groups which embrace species belonging to high trophic levels: 1) Sea otters, 2) birds, 3) fishes, 4) crustaceans, 5) starfishes, 6) gastropods, and 7) mankind.

Our first goal is to illustrate ecological processes and the factors that modify, exaggerate or mute them, and in the process, to identify the structure and dynamics of such communities. In so doing we explicitly avoid direct comparisons of natural communities in both coastal regions; instead we emphasize process-oriented studies which employ controlled manipulation. We believe that experimental manipulation is the most powerful field tool for identifying factors responsible for community patterns. We propose that predation-related links provide the most effective experimental, empirical and theoretical path for understanding under what conditions mutualism (in its broader sense) evolves.

Our second goal is to identify gaps of enquiry in the two coastal areas and to highlight what appears to us as challenging ecological problems: the ecological role of mankind; aspects of body size, mass or shape; the existence of critically strong interacting species or guilds; and the extent to which recruitment to benthic populations is limited by events in the plankton.

Key words: Rocky shores, Eastern Pacific, North-South comparison, community ecology, predation, otters, birds, fishes, crabs, starfishes, gastropods, mankind.

RESUMEN

Esta revisión se refiere a la interrogante de cómo están organizadas las comunidades intermareales rocosas de las costas de Chile y del Oeste de los Estados Unidos. Para responderla el trabajo centra su foco en siete grupos funcionales de alto nivel trófico: 1) nutrias de mar, 2) aves, 3) peces, 4) crustáceos, 5) estrellas de mar, 6) gastrópodos y 7) hombre.

El primer objetivo es la ilustración de procesos ecológicos y discusión de los factores que los modifican, amplifican o cambian radicalmente, y que ayudan a comprender la estructura y dinámica de tales comunidades. En este sentido evitamos explícitamente comparaciones directas de comunidades naturales entre ambas regiones costeras, y en lugar de ello hacemos especial énfasis en estudios orientados hacia la comprensión de procesos en que se han utilizado manipulaciones controladas. Creemos que la manipulación experimental es la herramienta de terreno más poderosa para identificar los factores responsables de los patrones comunitarios. Proponemos que las conexiones de depredación proveen las avenidas más efectivas, desde el punto de vista experimental, empírico y teórico, para comprender las condiciones en que el mutualismo (en su más amplia acepción) se desenvuelve.

El segundo objetivo es la identificación de vacíos de conocimiento en ambas regiones costeras y, más aún, llamar la atención sobre lo que a nosotros nos parecen problemas ecológicos desafiantes. El papel ecológico del hombre; aspectos del tamaño corporal, masa o forma de los organismos; la existencia de especies críticas o gremios de especies, que son interactuantes fuertes y el tema de la dispersión planctónica de las larvas, son discutidos en la sección final de la revisión.

Palabras claves: Intermareal rocoso, Pacífico Oriental, comparación Norte-Sur, ecología de comunidades, depredación, nutrias, aves, peces, jaibas, estrellas de mar, gastrópodos, hombre.

INTRODUCTION

Probably the most frustrating, and in some fashion, least rewarding task in all of ecology is to compare natural communities in two or more regions differing in biogeography and thus in faunal (and floral) composition and evolutionary history. On the one hand, there are no null models which are taxon independent and thus there is no common baseline against which to judge similarities or differences. Equally, ecological knowledge of the component species is bound to be incomplete, often to an alarming extent, which in turn makes dynamical reconstructions difficult. We suggest here that in com-

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parative ecological studies the single most important consideration is that of research philosophy. The communities being compared are bound to differ in species composition, geological history, water mass properties, seasonal phenomena, primary productivity, etc.– in fact in probably all the key factors one can identify. Community descriptions will obviously reveal these differences but by themselves can only hint at the mechanisms or processes underlying the patterns.

We believe controlled manipulation to be the single most powerful means of identifying the sundry factors generating pattern. The experimental methodology need not be identical, and often cannot be. For instance, the species will obviously be different, and may respond differently to different techniques. The intertidal rock pavement will vary in hardness, geology, rugosity and exposure. Other major factors will be the spatial dimensions of the area available for manipulation, financial support for the project, level of human intervention, and so on. A commitment to experimentation, however, whenever possible, ensures that the investigators will be thinking about the ecological mechanisms causing the patterns, about the dynamics of interaction and change, and about factors modifying their endeavors and increasing sampling variance. Both of us have approached questions on how communities are organized with a similar philosophy and commitment to experimental manipulation. Thus, while our biases may differ, we have been considering "our" respective intertidal assemblages in entirely comparable and compatible ways.

Consideration of the marine predation processes must involve a set of interrelated processes. On the one hand there are a series of behaviors determining individual food preference and its variation and the degree of trophic capabilities and dietary specialization. These interact reciprocally with prey availability, itself influenced by "refuges" which may be strictly biological in their origin. We refer, especially, to the newer topic of induced defenses (Harvell 1984, Lively 1986) and the more traditional of size refuges (Paine 1965, 1976, Connell 1975, Woodin 1978). More synthetic constructions or representations of community structure involving two or more trophic levels cannot avoid utilization of food web terminology. Especially significant here are "interaction strength" (May 1974), trophic cascade (Paine 1984, Carpenter *et al.* 1985), and critical or keystone species (Paine 1969). Once one has admitted to intertrophic level effects, an ecological Pandora's box has been opened to a newer dimension intimately associated with predation, *i.e.*, indirect effects (Levine 1976, Vandermeer 1980). Just as consumers can diminish prey populations, they can also facilitate them, and predation-related links seem to provide the most effective experimental, empirical and theoretical routes to understanding if, when, or under what conditions mutualism, in the broadest sense, evolve (Boucher *et al.* 1982).

The following section provides a comparison of data gathered in North America and Chile on rocky intertidal shores. We have subdivided the consumers into seven different groups, all of which contain members of high trophic level status. Although these often share common prey species, their foraging modes are distinctive enough to justify their separation. We have identified within each of these groupings studies on Eastern Pacific, temperate zone, rocky intertidal shores which appear to be especially general, novel or suggestive. In a few selected cases we have extended our analysis to papers which focus on areas out of our geographical scope. Our goal is both to relate specific predation-related processes to community patterns and to identify gaps of inquiry.

However, it is unlikely that useful generalizations will be discovered unless they are actively sought. Certainly just cataloguing one study after another, species by species, will yield little progress towards understanding whether communities are organized and how. One way to identify, or discard, potentially useful generalizations is to compare communities apparently convergent in their major features, yet characterized by taxonomically different species. This we do next, focusing on higher taxa, within each of which are individuals or species that belong to high trophic levels. In addition we have tried to be sensitive to the fact that relatively few studies have been conducted along the 1000's of km of the two Eastern Pacific, temperate shores. Therefore the specific ecological findings on one species at one place may not be repeatable elsewhere, and thus all generalizations are suspect. To counter this problem, solvable only when all species have been studied everywhere, we have focused on the mechanisms of interaction between predator and prey, and on its consequences.

ECOLOGICAL STUDIES ON SELECTED TAXA: NORTH AMERICA

In this section we identify studies we believe to be especially characteristic or enlightening, and present the particular details by taxa. Our goal is not to compare directly Chilean and Western North American shores, but rather to assemble studies which illustrate particular ecological processes. The capability to compare communities effectively, and especially to identify sources of differences or variation, will become possible only when the underlying processes are understood. These are highly unlikely to be taxon-dependent, given the possibility of functional convergence (Paine & Suchanek 1983 or complementarity (Schall & Pianka 1978).

1. *Sea Otters*

These marine mammals have been intensively studied in North America for three reasons: they are attractive animals and have caught the public's imagination; their tragic overexploitation in the last century drove them close to extinction and therefore for a lengthy interval they were considered endangered; they are readily observed, and when dense, appear to be an important ecological force in the community. A recent book (VanBlaricom & Estes 1987) reviews much of the rich literature on *Enhydra lutris.*

This species forages over both rocky and soft sediment intertidal and subtidal communities to a maximum depth of about 35-40 m, and can dive to 97 m. The diet consists almost exclusively of benthic invertebrates and fish, and changes with latitude, habitat and population density. Otters themselves were exploited by aboriginal inhabitants of the Aleutian Islands, who appeared capable of controlling otter densities, at least locally (Simenstad *et al.* 1978). However, it was the elimination of the otter over much of its geographical range, from the Aleutian Island to Central California (Estes *et al.* 1981), that produced the conditions necessary for understanding its major community role. The earliest comparative study (Estes & Palmisano 1974) demonstrated unequivocaly major differences between islands with and without otters. Later studies (Duggins 1980) on previously occupied habitat reinforce earlier conclusions: otters can control both the size distribution and density of sea urchins, themselves major consumers of algal tissue. The otter, especially in the northern part of its range, is a major factor in the organization of the associated community (Estes *et al.* 1982). It influences indirectly the dynamics of numerous species at several trophic levels, and thus is an excellent example of a keystone predator (*sensu* Paine 1969). Its community effect appears to be reduced in the southern portion of its range, and with the exception of the work of Kvitek & Oliver (1987), is virtually unknown for soft sediment assemblages. In summary, sea otters at high density influence the distribution and abundance of a host of species by preying on them. Because some of these prey species are economically significant resources (*e.g.*, clams, abalone, sea urchins), otters are in direct competition with mankind. Further, otters generate patches in both mussel beds and soft sediment communities, and therefore can exert a major influence on the assemblage's spatial structure. Finally, because the otters' influence extends indirectly both down the food web and laterally within trophic levels, communities with otters are ecologically distinct from those lacking these voracious predators, and major community shifts occur with otter invasion or removal.

2. *Birds*

The impact of avian predators on intertidal and shallow subtidal invertebrates has generally been ignored, with the conspicuous exception of oystercatchers (*Haematopus* spp.) (*e.g.*, Hockey & Branch 1984) and there is currently insufficient evidence available to assess their overall importance. The most recent review is that by Feare & Summers (1986), who note that many bird species routinely exploit shore-based resources, that the use is often targeted on particular prey species, and that birds are highly mobile and have high metabolic rates. Thus the role of birds in general should not be summarily discounted. On the other hand, their effects may be seasonal, bird species are usually uncommon relative to oher consumers, for non-diving birds the predation acts are restricted to surfaces exposed to air (and thus predation is time limited), and birds are difficult experimental subjects under natural conditions.

In Western North America the major consumers fall into five general groupings: small passerines (sparrows, wrens) eating intertidal insects, especially chironomids; large passerines (corvids), which effectively exploit snails, urchins and limpets; gulls, generally omnivorous; a variety of diving ducks, especially effective predators of mussels; and shrorebirds. The impact of each group will be a function of its density, foraging effectiveness, the exact nature of its prey, and the prey's role in the community. Such information only exists for black oystercatchers (*H. bachmani*) (Frank 1982, Marsh 1986), known to restrict limpet distributions which in turn bears implications for the distribution and abundance patterns of specific algae.

Studies of avian predation on mudflats also suggest that birds can be ecologically important consumers, reducing prey populations significantly and substantially (Quammen 1984, Feare & Summers 1986).

Because birds are readily observable and continue to be popular objects for study, vast quantities of data exist on their diets. For instance, for the glaucous-winged gull, reports suggest regional changes dictated by availability (Irons *et al.* 1986) or breeding behavior (Vermeer 1982). If sea otters are present and have modified the resource spectrum, the diet of these gulls changes accordingly (Trapp 1979). It is likley that all birds foraging along the shore will show similar levels of trophic variability. However, the extent to which birds regulate their prey populations remains generally unknown. Thus gulls consume urchins, sometimes in great quantity, but do they eat enough to control urchin abundances to the point that algal dynamics are secondarily enhanced? Marsh (1986) has examined the community effect of shorebirds feeding on small mussels. The effects, however are subtle, and are most easly interpreted in terms of the habitat's relative heterogeneity, rather than mussel population regulation.

The bird research illustrates most clearly many of the problems associated with studying highly mobile and experimentally difficult species. It is difficult to imagine a realistic bird enclosure study: all work to date known to us employs exclosures. However, on shores characterized by mixed foraging flocks, it would be useful to identify the effects of individual species. This is difficult to achieve, especially when the species are of equal body dimensions (for instance, gulls and oystercatchers). It may well be impossible when the species vary widly in size, as oystercatchers and smaller shorebirds do. Thus a balanced experimental design involving birds x crabs, or birds x carnivorous gastropods has yet to be achieved, although these species surely interact, and clearly mutually affect their common prey species (Quammen 1984, Marsh 1986).

3. *Fishes*

Two recent reviews (Choat 1982, Hixon 1986) acknowledge the relative paucity of data on temperate zone fishes. Although fish should be more important in the subtidal than in the intertidal because of increased feeding time and reduced or nonexistent physiological stress, it is clear that their intertidal role cannot be summarily dismissed. For instance, Dethier (1980) showed that small cottids capable of eating 1000 copepods per day were more significant predators in tide pools than were anemones. It seems likely that if copepods are at risk, the free-swimming larvae of most invertebrates would also be, and thus that the general absence of many sessile invertebrates from tide pools might be explained by fish predation.

An important ecological role for shore fishes is suggested by the following observations. (a) Substantial numbers of behaviorally and trophically different species can be found on most North American shores: 28 species on the West coast of Vancouver Island (Green 1971), 16 species in Washington State (Cross 1981), 23 species in Northern California (Moring 1976). (b) Most of these fish are carnivores (Hart 1973, Cross 1981), although Cross (1981) found that 31% of the Washington tidepool fishes were omnivores, and that the tendency to consume benthic algae increased with size (or age). (c) Finally, fishes can be quite abundant: Cross (1981) found mean densities of the 16 species he studied to range from 1.2-11.9 m^{-2} in tide pools on rocky headlands. The density range for cobble beaches was 0.9-11.4 m^{-2}. Although such estimates exaggerate local abundance because only inhabited pools were counted, they nonetheless suggest that fishes are common enough to influence the dynamics of numerous associated species, especially vulnerable and ecologically critical invertebrate larvae or early life history stages.

If intertidal fish are abundant, diverse and observable, why are their potential influences on rocky intertidal community structure so poorly understood? Two reasons seem paramount: neither explanation is restricted to fishes and both represent real challenges yet to be resolved. First, as noted by Choat (1982) and others, dynamics and interactions can be studied experimentally by using exclosures or enclosures, by modifying the habitat, or by direct density manipulation. Effective exclosures almost certainly generate caging "problems", and enclosures, if they are of an experimentally tractable size, may alter or severely modify the foraging behavior of highly mobile species. The last two approaches have difficulties with appropiate controls or in the maintenance of experimentally constant densities. In one sense, ecologists have not yet learned how to manipulate highly mobile, generally uncommon organisms whose effects are spatially variable.

Second, are the pair of related problems effectively discussed in Menge *et al.* (1986). Most communities are complex assemblages with numerous species characterizing each guild or functional group. If the functional group (for instance, crabs, herbivorous gastropods, or large fish) is identified as the experimental unit, the implied aggregation of many taxa disguises each species' individuality or ecological importance (see also Castilla 1981a). Thus in the Menge *et al.* (1986) study, 15 species of large fish were lumped into one category. It is not at all clear that alternatives were available, or even what they might have been. Tropical fish are known to exert important influences on their prey (Bakus 1964) yet are rare and mobile. A similar problem exists on temperate shores. In addition, when species change functional group with size or age, or differ naturally among themselves in adult size, it may be impossible to balance the experimental design and isolate the separate effects. Thus, one might be able to exclude all fish, and all large fish, but be unable to design a treatment capable of revealing large fish effects in the absence of small fishes.

The above problems are general to all experimental ecology, let alone the study of temperate rocky intertidal shores, and there is little available evidence to either support or dismiss as insignificant the role of fishes.

4. *Large Crustacea*

Large bodied crustacea (i.e. > 10 cm major dimension) are not uncommon on western North American rocky shores. Most tend to be herbivores (Morris *et al.* 1980) and both of the two major carnivores are primarily subtidal species utilizing the intertidal as a fringe habitat. The potential community influence is known for only one.

We have included large crustaceans in our review because they are well known to be influential community members. For instance, Tegner & Levin (1983), in an analysis of spiny lobster (*Panulirus*) predation on Californian sea urchins, suggested that over-exploitation of lobsters has contributed significantly to the localized high densities and destructive grazing by urchins. Seeley (1986) has suggested that the intertidal crab *Carcinus* has exerted a potent selective influence on snail morphology as it has invaded rocky shores along the Northeastern USA. Likewise, Palmer (1985) has shown *Cancer productus* to be an effective predator of carnivorous gastropods on northeastern Pacific shores. Muntz *et al.* (1965) argued that large crabs could control sea urchin distribution in Ireland, albeit in the shallow subtidal. Calculations by Griffiths & Seiderer (1980) suggest that rock lobsters (*Jasus*), feeding primarily on mussels, are the dominant invertebrate predators off the west coast of South Africa. Finally, although continuing debate clouds the issue, both lobsters and large crabs may be causally implicated in the control of urchin populations in Nova Scota, Canada (Mann 1985, Pringle 1986). These and other large crustaceans are popular food items, and because they are often under extreme human exploitation pressures, their densities tend to be reduced and their apparent influence minimized. Nonetheless, the evidence is sufficiently general to implicate any common large crustacean as a potentially major contributor to local assemblage structure.

Only one field experimental study, an exclusion, is known to us. Robles (1983, 1987) excluded spiny lobsters (*Panulirus*) from low intertidal plots on a Californian rocky intertidal shore. In the enforced absence of these predators the community changed: two species of mussels increased significantly in abundance to the detriment of other species. Neither open nor cage control sites showed any change.

Large crustaceans are not apt to be characteristic of, or abundant on, exposed intertidal shorelines. However, there are sufficient indications to suggest that if they occur commonly subtidally, are naturally resident, or are invading the region because of a recent introduction, they must be considered as potentially important. However, because of their mobility they are not apt to be easy experimental subjects. Thus, exclosures should be the easiest way to determine their community effect, if the roles of other species consuming the same prey spectrum can be discounted. This is often not possible, and therefore the same hurdles to understanding that exist for birds and fish characterize this functional grouping as well.

5. *Starfish*

In Western North America asteroids can be diverse, dense and conspicuous on rocky intertidal shores. Their collective diets span the entire range of animal prey, including even such unlikely items as seapens, anemones, sponges, other starfish and fish (Mauzey *et al.* 1968, Birkeland 1974, Morris 1980, Robilliard 1971). They thus are prime suspects to be significantly involved in both specific prey-predator interactions and, more generally, in the organization of intertidal and shallow subtidal communities. Studies on starfish have been particularly revealing of processes relevant to community organization. Some of these are discussed individually below.

Dietary flexibility: A species position in a food web is usually based on direct observation of what it consumes. North American starfish can be divided into three broad categories: a) specialists eating a limited variety of prey, and characterized by dietary constancy throughout their range (i.e., *Hippasteria*); b) species consuming a restricted variety in any one habitat, but characterized by extreme between-habitat change (i.e., *Dermasterias, Pycnopodia*); and c) more truly generalized species which consume a wide range of prey wherever they forage, and whose diet seems to be determined by local availability (i.e., *Pisaster ochraceus, Leptasterias*). Details of seasonal, local, or geographic dietary variation (Mauzey *et al.* 1968, Paine 1980) underscore some of the difficulties with trophic generalizations. Not only can the diet change dramatically from place to place or time to time, but position in a food web or web linkage patterns can as well. The latter observation is relevant only to the extent that ecologically useful food web theory can be devoloped.

Indeterminate growth: For most marine invertebrates size is not an adequate indicator of age; mean individual body size can change by an order of magnitude between habitats (Paine 1976), and the onset of reproduction is size–, not age-dependent. Models of the phenomenon have been developed by Sebens (1979). Its significance is that body size is often a good predictor of prey size, and larger individuals may be less susceptible to predation than smaller ones, as well as more fecund. Starfish have figured prominently in examining the phenomenon, beginning with Mead (1900). The range of size variations found between average individuals in natural populations is impressive: for *Leptasterias,* 3.8-8.4 g wet weight (Menge 1972); for *Pisaster,* 150-2640 g (Paine 1976). Laboratory and field transplant experiments both indicate that these starfish are normally food limited, often to an extreme degree. In fact Menge (1972) grew a *Leptasterias* to a 44 g size in the laboratory. In summary, body size influences many aspects of community dynamics, and its variation implies a similar variation in those aspects of community structure influenced by starfish.

Interaction strength: Asteroids provided the initial suggestion that certain species might influence community dynamics disproportionately to their abundance (Paine 1966, 1969). This research, on *Pisaster ochraceus,* done at two sites (Paine 1974, 1984), shows a major community change in the experimental absence of *Pisaster,* and very slow reversion towards the original state once *Pisaster* is permitted to return (Paine *et al.* 1985). Similar patterns, evident when starfish are removed or naturally absent, can be seen in the work of Paine (1971), Menge (1976), Peterson (1979), and Chiristie (1983). The pattern repeats itself on pilings from which *Pisaster* was excluded (Wolfson *et al.* 1979). In all the assemblages, species of mussels are the competitive dominants and, on the west coast at least, their superiority is expressed despite the presence of numerous other smaller bodied predators, some of which may be abundant. The comparability of these starfish dominated assemblages is discussed by Menge (1982).

There is no reason to expect that all guilds, let alone communities, will have strongly interacting species. However, an alternative proposition that none do is demonstrably incorrect, as indicated by a substantial body of support, much of it from fresh water communities. There is at least one other reason to suspect that some species may be more "important" community members than others, independent of their density. Just as different predators consume different prey, so the latter differ in their intrinsic competitive abilities. The evolved, natural variations in predator-prey combinations tend to generate some strong interactions. It is unknown why some communities are characterized by such combinations and others are not.

6. *Gastropods*

A journal specializing in molluscan studies (The Veliger), a relatively stable and well known taxonomy, and their experimental tractability have all contributed to the extensive literature on gastropod biology. Two types of studies seem specially relevant to understanding predator-prey interactions on rocky shores. These are considered below as *examples* of what has been or can be learned.

Predator exclusion devices. Cages, with their appropriate controls, are a traditional way in which to discover what happens when a predatory gastropod is excluded from a 100 cm^2 surface. Two major studies (Connell 1970, Dayton 1971) have used this approach to examine the predator's influence on competition for space. The predators have been *Nucella* (*Thais*), that prey on a number of barnacle species or mussels. The experiments are relatively easily replicated with these simple devices placed at different tidal heights or geographic locations. The major conclusions seem relatively straight-forward: the predators can alter the outcome of interspecific competition, predator food choice is an importat ingredient, and body size or dimension of both prey and predator must be considered.

Although caging as a technique is not without its flaws, readily performed extensions have encouraged other types of data to be generated. For instance, Connell (1970) has used cages as enclosures, to measure predator feeding rates in the presence of known prey quantities. Palmer (1984) has extended both the techniques and analyses in his examination of *Nucella* foraging. As another example, Dayton (1971) followed the fate of barnacles once the cage and the protection it afforded had been removed. Smaller barnacles were consumed and larger ones survived in the presence of their potential predator. Size limits to effective predation bears major implications for the structure of communities, and has been studied in a variety of contexts (Paine 1965, 1976).

Foraging behavior: What a predator consumes, and the relative competitive abilities of the prey population are fundamental considerations in community ecology. They should not be divorced from one another. Here we mention two approaches to foraging behavior to indicate the complexity of the interactions and the experimental tractability of gastropods.

West (1986) has shown conclusively that individually numbered *Nucella,* of similar body sizes and foraging in the same area, were characterized by strikingly different diets. That is, some ate barnacles while others specialized on limpets or mussels. Such consistent, between-individual variations has important consequences for optimal foraging theory (Pyke 1984) and community ecology. Its basis, whether it be genetic, reflecting a dietary polymorphism, or simply an acquired taste (Wood 1968, Castilla 1972), is unknown. Palmer (1984) has also examined the foraging behavior of *Nucella,* employing a variety of cages, barriers, and laboratory techniques to test whether foraging behavior under field conditions was generally consistent with a hypothesis of optimal foraging. In general, his snails were characterized by a prey selection decision motivated by energy maximization. When they deviated from the predicted behaviors, the causes appeared related to prior learning and consideration of mortality or risk.

In summary, intertidal gastropods provide exceptionally fine experimental (and observational) material. Because of this, the studies have been more mechanisms-than simply phenomenon-oriented. In particular, the work has highlighted the range of behaviors, and the relative importance of food choice and prey body size. However, most North American rocky shore carnivorous gastropods are on the small side (< 10 cm body length) and although dense (> 250 m^2) seem incapable of altering the major features of their respective communities.

7. *Mankind*

Seashores, as a ready source of animal protein, have always proven attractive to humans, and if anything, the pressures have increased in recent times due to larger population numbers, greater mobility and better access. The potential impact is seldom acknowledged, and may be especially difficult to recognize where human populations have been exploiting marine resources for 1,000's of years, but at unknown levels of intensity. The evidence of prehistoric activity comes primarily from excavation of middens or shell mounds, and indicates that mankind exploited a wide range of invertebrates, fish and even sea otters (Dall 1877, Hubbs 1967, Simenstad *et al.* 1978). Some of the prey, sea urchins and otters especially, are strongly interacting species (Paine 1980), and therefore the ecological effects of human predation are apt to have had broader ecological impacts.

The general effects of human activities on the shore today are certain to be substantially more severe. Exploitation pressures have been maintained or even extended to the point that concerns are voiced about the welfare of certain stocks. There is also a wide range of newer anthropogenic influences whose effects are potencially devastating on regional bases. Pollution, either organic or thermal, increased sedimentation or land-filling activities, and hydrocarbon spills provide examples. Finally, there are more localized impacts which may be equally capable of altering community structure in more subtle and geographically restricted ways. Specimens of particular species are routinely disturbed or collected for teaching or research purposes. The very process of examining or visiting a shore produces a trampling effect (Beauchamp & Gowing 1982), and the presence of humans can influence negatively the breeding success of gulls (Roberts & Ralph 1975) or increase the rate of predation by crows (Verbeck 1982).

It should be assumed that mankind has been an integral component of near-shore communities for the past 10,000-30,000 years, at the least. Some of the modern influences can be reduced by conducting research at remote ("pristine") sites. Others, such as capricious oil spills or the effects of observer presence cannot be avoided. Probably the most revealing approach, not yet attempted in North America to our knowledge, will be to exclude totally humans from heavily exploited shorelines not exposed to industrial pollutants, and record the ecological changes. Such studies, properly conducted and controlled, can reveal the immediate influence of mankind, but also provide invaluable information on the potential for, and rate of, recovery of such shores.

ECOLOGICAL STUDIES ON SELECTED TAXA: SOUTH AMERICA

1. *Otters*

Two species of otters are present on Southeastern Pacific rocky shores: the sea otter *Lutra felina,* known in Chile as "chungungo", ranging from central Perú to Cape Horn and the State Islands (Torres *et al.* 1979, Sielfeld 1984)[1] ; and the river

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[1] SIELFELD W (1984) Hábitos alimentarios del huillín (*Lutra provocax*) (Mammalia, Carnivora, Mustelidae) en el medio marino de Chile Austral. Seminario de investigación para optar al Grado de Licenciado en Ciencias Universidad Austral de Chile, Escuela de Ciencias, Valdivia 19 pp.

otter, *Lutra provocax,* known as "huillín" which is found in Chile and Argentina (García-Mata 1978). In Chile *L. provocax* ranges from Cape Horn to Cauquenes river (Reed 1877). This otter was formerly considered a truly fresh water species; nevertheless, Sielfeld (1984)[1] has recently shown that in Southern Chile the species is well adapted to sheltered marine environments.

Both otters are listed in the IUCN Red Data Book as endangered species. It has been claimed that their populations have been depleted along Southeastern Pacific shores (see Brownell 1978) but there is no solid scientific evidence supporting this statement. In 1835, Darwin (1945) reported dense otter populations (*L. felina*?) in the Beagle Channel zone and Castilla (1981b) found densities of approximately 2-2.5 individuals per kilometer of coast there. Greater densities of "chungungos" have been spotted around Chiloé Island by Osgood (1943), and Cabello (1978) reported densities of about 10 per kilometer of open coast for that island.

Castilla & Bahamondes (1979) studied a small population of *L. felina* at Los Molles and described the main behavioral characteristics of the species. The "chungungos" spent part of the day fishing in rough nearshore waters (see also Castilla 1981b) and used exposed and broken shores as well as small islands as their permanent land residences. They selected rocky caves as burrows, although in southern Chile they are known to occupy bushy areas (Sielfeld 1983). Cabello (1983) discussed their behavioral ecological features based on observations in Chiloé Island.

Castilla & Bahamondes (1979) and Castilla (1981a) in central Chile, and Cabello (1983) and Sielfed (1983, 1984)[1] in southern Chile, studied *L. felina* food items based on direct observations of individual feeding in water or on land, and by analyzing feces and food remains. It appears that *L. felina's* diet changes geographically. Thus, in central Chile, Castilla & Bahamondes (1979) reported fishes, crustaceans and molluscs as being the main items. It is especially important to highlight prey such as the carnivorous muricid gastropod *Concholepas concholepas,* considered a keystone species in Chilean intertidal rocky shores (Castilla & Durán 1985, Moreno *et al.* 1986a), and several species of *Fissurella,* also ecologically critical molluscs (Moreno *et al.* 1984, Oliva & Castilla 1986). South of 48°50`, Sielfeld (1983, 1984)[1] reported basically the same prey items in the diet of *L. felina,* and the sea urchin *Loxechinus albus.* Sielfeld (1984)[1] indicated that in southern Chile the predation of "chungungos" on *L. albus* could be qualitatively important given that their feces and food remains showed a frequency of about 20% of this echinoderm. It is unknown to date whether *L. felina* eats *L. albus* in southern Chile but not in central Chile as a response to the increased density of this echinoderm in southern latitudes.

Sielfeld (1984)[1] studied populations of *L. provocax* along 45 stations between *ca* 48°50° S., and reported that in that area the "huillín" should be characterized as a marine otter rather than as a freshwater species. Indeed, the author reported as main food items marine fishes, gastropods, bivalves and crustaceans. Sea urchins were also present among food remains but not in important amounts. Little attention has been paid to the "huillin's" food items north of 48°50'S., but see Housse (1953).

In summary, the ecological role played by *L. felina* or *L. provocax* either on subtidal or intertidal hard bottom communities in Chile is unknown. Trophic webs have been described for central and southern Chile but no experimental work has yet been conducted on these highly mobile animals. No evidence exists whether marine communities showing high otter densities along the Chilean coast line are distinct from those lacking otters. However, as indicated by Castilla & Bahamondes (1979), *L. felina* (and possibly *L. provocax*) cannot be considered ecological equivalents of *Enhydra lutris,* the North American sea otter.

The most important recent finding regarding Chilean otters is that their diets change along latitudinal gradients and that both species are marine to some extent. Further, the fact that *L. felina* eats sea urchins in southern Chile and that *L. provocax* includes in its diet large key-hole limpets should also be explored.

It should be kept in mind that Southeastern Pacific otters, marine birds and other high trophic-level vertebrates and invertebrates, usually characterized as "generalists", are part of complex assemblages and guilds. As earlier suggested by Castilla (1981a) these functional groups may be extremely important for our understanding of community ecology (see also Menge *et al.* 1986). However, a critical challenge, that of identifying and quantifying the roles of individual guild members still remains.

2. *Birds*

Little is known about the ecological role of birds on the Chilean rocky shore. Castilla (1981a) suggested that the kelp gull *Larus dominicanus* and the black oystercatcher *Haematopus ater* were two important predators on undisturbed rocky shore habitats of central Chile and that in such isolated environments these birds may play critical ecological roles. Later, Bahamondes & Castilla (1986) documented in detail that the kelp-gull at Los Molles, central Chile, preyed upon 30 different species of rocky shore marine invertebrates. Gastropods were among the most important items. Indeed, predation on intertidal gastropods such as *Concholepas concholepas* and key-hole limpets (see Castilla & Durán 1985, Oliva & Castilla 1986) should be highlighted. Further, the frequent consumption of intertidal crabs, such as *Acanthocyclus* spp. (see Castilla 1981a, Sotomayor & Zamorano 1985) may be extremely important because these crustaceans prey on competitively dominant intertidal species such as the mussel *Perumytilus purpuratus* and barnacles in the genera *Jehlius* and *Chthamalus*. Predation by *L. dominicanus* on the limpet *Scurria scurra,* (Bahamondes & Castilla 1986) which lives almost exclusively on the fronds of the common intertidal kelp *Lessonia nigrescens,* deserves a comment. Santelices *et al.* (1980) discussed the *L. nigrescens* - *S. scurra* interaction in central Chile, showing that *S. scurra* had a pruning effect on the largest and heaviest stipes of the kelp and suggesting that this could prevent *L. nigrescens* from becoming so heavy as to be susceptible to detachment by wave action. If *L. dominicanus* can significantly reduce the number of *S. scurra* on *L. nigrescens,* it could produce a negative ecological effect on the population structure and abundance of *L. nigrescens.*

Additional observations on *L. dominicanus* predation on intertidal subantarctic communities have been recently published by Branch (1985) and Castilla & Rozbaczylo (1986). Branch (1985) demonstrated that predation by the kelp gull on the limpet *Nacella delesserti* at Marion Island (South Africa) accounted for about 50% of the known annual mortality of limpets between 3.5 and 6.5 cm shell length. At South Shetland, Castilla & Rozbaczylo (1986) found that the density of kelp gulls in rocky intertidal zones was similar to that reported by Branch (1985) and that predation on the common limpet *Nacella (Patinigera) concinna* encompassed all sizes from 1 to 6.5 cm. No manipulative experiments were performed either by Branch (1985) or by Castilla & Rozbaczylo (1986).

Other species such as surfbirds *Aphriza virgata,* ruddy turnstones *Arenaria interpres,* and an endemic South America bird *Cinclodes nigrofumosus,* have been reported as intertidal predators in the Southeast Pacific coast (*i.e.,* Atkins 1980). At Las Cruces, central Chile, two species of *Cinclodes, C. nigrofumosus* and *C. patagonicus,* as well as the above mentioned surfbird and ruddy turnstone are particularly common and may play important ecological roles (R. Bustamante, personal communication). Indeed, *A. virgata* has been shown to influence community structure in a rocky intertidal community in the Northern hemisphere (Marsh 1986). *Aphriza interpres* has been reported as a predator reducing the patchiness of the sea urchin *Echinometra lucunter* in a tropical reef flat in Panamà (Schneider 1985).

The role of birds as predators is not well understood, particularly on rocky substrate communities of South America. Their impacts probably have been underestimated. Highly localized effects in time and space and the ability of these mobile predators to produce some of the patchiness of rocky intertidal communities ought to be investigated through manipulative experiments.

3. *Fishes*

Little work has been done in Chile regarding the importance of fishes on rocky intertidal or shallow subtidal communities. The main papers on fish dietary breadth which also touch upon their potential community influences are: Moreno & Osorio (1977), Moreno & Zamorano (1979), Duarte & Moreno (1980), Moreno (1980), Moreno (1981) and Moreno *et al.* (1986b) for Antarctic Nototheniid fishes; Moreno & Zamorano (1980) for benthic fishes at Corral, southern Chile; Moreno & Jara (1984) for the subantarctic fish fauna associated with *Macrocystis pyrifera* kelp beds in the Beagle Channel; Moreno (1972) for the Labridae *Graus nigra;* Viviani (1975)[2] and Fuentes (1981, 1985) regarding the Chilean sheephead (pejeperro) *Semicossyphus maculatus;* and Paine & Palmer (1978), Castilla (1981a), and Cancino & Castilla (in press) with reference to the unique amphibious marine clingfish *Sicyases sanguineus,* known in Chile as "pejesapo".

Three examples can be mentioned. First, Moreno & Jara (1984) found remarkable differences when comparing the ichthyofauna and organizational features of *M. pyrifera* kelp beds between the Beagle Channel (Chile) and California. In the Chilean kelp beds they reported 18 species of fishes and no fish was found to be herbivorous or to prey on the abundant sea urchins; their diets were mostly dominated by detritivore species such as amphipods and isopods. This is in contrast to what has been found in Californian *M. pyrifera* beds (*e.g.,* see Quast 1968 and North 1979).

Second, Viviani (1975)[2] called attention to the fact that the Chilean sheephead *S. maculatus* may be an important, high trophic level predator around the lower intertidal fringe and shallow subtidal of northern Chile. Later, Fuentes (1981) studied the diet of this species based on an analysis of 17 individuals caught at Iquique. He found that this trophic generalist consumed over 30 species of invertebrates. No experimental manipulations have been attempted with this highly mobile species and its ecological role in the intertidal or shallow subtidal marine communities of northern and central Chile remains unknown. However, the species is subject to intensive spearfishing along the Chilean littoral (Fuentes 1985) and comparisons of sites with natural versus reduced populations could generate useful insights.

Third, one of the most interesting and unique fishes in the world is the clingfish *S. sanguineus.* This Gobiesocid ranges from southern Perù to southern Chile (De Buen 1960), and is characteristic of the upper, middle and lower rocky intertidal and shallow subtidal of exposed rocky littoral communities. According to Cancino & Castilla (in press), individuals of *S. sanguineus* attached to rocks in the intertidal zone range from less than 5 cm to about 28 cm in total length. These authors found that as the clingfish increase in size they tend to remain in the lower fringe of the intertidal and become sedentary. Paine & Palmer 1978) studied "pejesapo" diets from intertidal samples collected at Iquique in northern Chile and Montemar, central Chile; they concluded that the fish was a generalist. Indeed, their results indicated a broad diet with major prey categories, including three plant and three animal phyla. They indentified more than 40 species of algae and invertebrates in 48 stomachs analyzed. Cancino & Castilla (in press) expanded the known diet to include about 60 species and have pointed out that fish size and capture site can influence dietary composition. Moreover, Cancino & Castilla (in press) found that individuals under 15 cm were characteristically observed in the rocky intertidal and consumed prey occurring from the middle to the lower intertidal fringe; a large number of those prey were primary space users (*e.g., Ulva* sp., *Enteromorpha* sp., *Ectocarpus* sp., *Jehlius cirratus*).

Until experiments are done and quantitative estimates of "pejesapo" density are obtained the potentially significant role these interesting fish could play in Chilean rocky shore assemblages will remain unresolved.

4. *Crustacea*

A peculiar characteristic of the Chilean and Southeastern Pacific rocky shores is the presence of several large rocky intertidal and shallow subtidal carnivorous crustaceans (Antezana *et al.* 1965). The stone crab *Homalaspis plana,* a xanthid that can reach up to 15 cm or more in carapace width, is common along the rocky shores from Guayaquil (Ecuador) to the Magellan Strait (Chile). This species, with a vertical distribution ranging from 0 to 18 m, is particularly abundant on isolated rocky shores (Antezana *et al.* 1965). Its diet includes Malacostraca crustaceans such as *Allopetrolisthes* and *Petrolisthes,* porcelanids, barnacles, molluscans such as the gastropod *Tegula atra* and *T. tridentata,* mussels such as *Perumytilus purpuratus* and *Semimytilus*

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[2] VIVIANI (1975) Comunidades Marinas Litorales del Norte, Iquique, Chile, 196 pp. (Mimeograph).

algosus, echinoderms and other invertebrates (Morales & Antezana 1983).

Homalaspis plana is known to be heavily exploited by local fishermen (Castilla & Becerra 1975, Duràn *et al.* 1987) along the Chilean rocky shore, but it is unknown to what extent such exploitation affects stone crab populations (*e.g.*, densities, size structure). Preliminary evidence indicates that at nonharvested shores of central Chile (Estaciòn Costera de Investigaciones Marinas at Las Cruces, see Duràn *et al.* 1987) the intertidal density of *H. plana,* after four years of protecting the shore from human predation, has increased as much as 4-6 times when compared to the adjacent harvested shores (Castilla, personal observations). The ecological impact of such density changes has not yet been evaluated.

Three other species of Atelecyclid Decapoda are particularly important on the Southeastern Pacific rocky shore: (a) *Acanthocyclus gayi,* from Salaverry in Perù to Isla Chiloè, Chile; (b) *Acanthocyclus hassleri,* from Panamà to Bahìa San Vicente, Chile; and (c) *Acanthocyclus albatrossis,* from Talcahuano to the Magellan Strait and Falkland Islands. Two species are found in northern and central Chile: *A. gayi* and *A. hassleri;* Viviani (1975 [see footnote[2]]) and Castilla (1981a) pointed out that, given that they preyed upon competitively dominant species such as mussels and barnacles, they could play a critical role in the structure and dynamics of intertidal communities. Sotomayor & Zamorano (1985) reported that at Mehuìn, Valdivia, where these crabs fed on four main items: the reef-builder polychaete *Phragmatopoma möerchi,* the mussel *P. purpuratus,* barnacles, and amphipods. The first three food items are competitively dominant species at different levels of the rocky intertidal. Further, unpublished observations (JCC) in central Chile indicate that both species of crabs are commonly found in *P. purpuratus* beds, where they construct tunnels in the mussel matrix. Preliminary observations suggest that crabs may undermine the mussel beds, exposing them to mechanical disruptions by wave action.

5. *Starfish*

There is a high diversity of starfish species throughout the Chilean littoral. Viviani (1979) listed 24 species of which 9 are exclusively sublittoral (see also Brattstrom & Johanssen 1983). Nevertheless, there are striking regional differences in species composition along the extensive Chilean shores. Viviani (1978)[3] pointed out that while only five starfish species are commonly present in northern (and central) Chile, at least 20 are to be found in southern Chile (Chiloé Island and southern Chilean archipelagos and fjords). Indeed, Brattstrom & Johanssen (1983) described a marked change in invertebrate taxonomic composition at the northern end of Chiloè and in Seno Reloncavì, about 42°S.

Viviani (1978)[3] gave a comprehensive report of the feeding habits and behavioral aspects of northern Chilean starfishes: (a) *Heliaster helianthus,* a conspicuous sunstar present mostly in intertidal rocky habitats but also extending its vertical distribution to subtidal areas; (b) *Stichaster striatus,* commonly found around the *L. nigrescens* belt and subtidally; (c) *Meyenaster gelatinosus,* a subtidal species that occasionally reaches the intertidal; (d) *Patiria chilensis* found under boulders from the lower intertidal zone down to 10 m or more; and (e) *Luidia magellanica* occurring in sheltered subtidal zones deeper than 2 m.

Castilla (1981a) and Paine *et al.* (1985) studied the diet and ecological role of the sunstar *H. helianthus,* a common species in central Chile. They demonstrated experimentally that it is an important predator in rocky intertidal environments: the biotic community at the removal site rapidly (in months) became different from that characterizing the adjacent control.

In Chile, because of the comparatively small size of middle rocky intertidal prey, especially the mussel *P. purpuratus, H. helianthus* is capable of consuming all sizes of *Perumytilus* including the larger individuals of the mussel matrix, and thus no size refuges are effective. In addition, unpublished results (JCC) indicate that spatial refuges seem to be particularly important to *P. purpuratus* populations, as they are known to be for *Mytilus californianus.* In *P. purpuratus* beds, however, convincing experiments indicate that a mollusc, *Con-*

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[3] VIVIANI (1978) Predación interespecífica, canibalismo y autotomía como mecanismo de escape en las especies de asteroidea (Echinodermata) en el litoral del desierto del Norte Grande de Chile. Laboratorio de Ecología Marina, U. del Norte, Chile, 116 pp. (Mimeograph).

cholepas concholepas, is the most effective species in setting its lower limits (Castilla & Duràn 1985). Indeed, *H. helianthus* is much more effective when attacking mussel beds from rocky intertidal pools (in or around the center or upper border of the bed). Further, *H. helianthus* preys very actively on barnacle species (*e.g.*, *Jehlius cirratus* and *Chthamalus scabrosus*) at the upper intertidal fringe.

The absence of *H. helianthus* in southern Chile (*i.e.*, Valdivia and other southern localities) is bound to have critical consequences on the structure and dynamics of intertidal rocky shore communities. This point was raised by Viviani (1975)[2] who suggested that, at Valdivia, the ecological role of *H. helianthus* was apparently overtaken by an abundant carnivorous gastropod, *Nucella calcar.* This hypothesis has not been tested to date.

Other papers referring to the foraging biology of predaceous starfish along the Chilean littoral are those of Dayton *et al.* (1977) on *M. gelatinosus,* and of Vásquez & Castilla (1984) and Castilla (1985) on *Cosmasterias lurida. Meyenaster* consumes at least 30 prey species including almost all echinoderms and molluscs in its habitat. Most of the prey showed effective escape behaviors. The diet of *C. lurida* consists of 25 prey species, mainly molluscs, crustaceans, ascidians, fishes and brachiopods. The results suggested a lack of selectivity for any of the prey and the authors concluded that in the Beagle Channel this generalist species fed according to local prey abundance.

6. *Gastropods*

The marine gastropod fauna of the Chilean rocky shore is not only remarkable for its diversity (see Marinocovich 1973, McLean 1984) but also due to the presence of a unique monotypic species, *Concholepas concholepas* or "loco". This muricid is present along the Chilean shoreline, extending to central Perù (for a review, see Castilla 1982, 1983). It is of enormous economic importance to the country (Castilla & Jerez 1986, Geaghan & Castilla 1986) and probably played a key role in the subsistence of pre-hispanic native populations (Castilla *et al.* 1985, Moreno 1986). The coastal middens of rocky shores of northern, central and southern Chile are usually dominated by *C. concholepas* shells. Human predation on intertidal Chilean communities can be as old as 8,000 years (Dillehay 1976). Nonetheless, a recent study (Durán *et al.* 1987) has demonstrated that the intensity of human predation by "mariscadores" in rocky intertidal ecosystems of central Chile is currently extremely high and that one of their major prey is *Concholepas concholepas*. This species ranges from intertidal habitats down to 30-40 m and is heavily exploited intertidally by "mariscadores", and subtidally by hooka and skin divers. Only recently has it been realized that populations of this carnivorous muricid, that feed on mussels and barnacles, can be extremely dense in rocky intertidal and sub-tidal non-harvested zones. In fact, Castilla & Duràn (1985) and Moreno *et al.* (1986a) have demonstrated dramatic increases in "loco" density at sites in central and southern Chile from which humans have been excluded. At Punta El Lacho (Las Cruces) the dense beds of *Perumytilus purpuratus* were drastically reduced as "locos" increased, suggesting that *Concholepas concholepas* is playing the role of a keystone species. Moreover, experiments demonstrated that "locos" influence species diversity by controlling the distribution of competitively superior mussels. In the experimental absence of "locos" the barnacles *Jehlius cirratus* and *Chthamalus scabrosus* took over the primary space (bare rock) and species diversity was reduced (Duràn & Castilla unpublished results).

Castilla (1981a) and Farìas & Castilla (unpublished results) studied a drilling gastropod, *Crassilabrum crassilabrum,* on central Chilean rocky shores and found that the species can be ecologically important at sheltered microhabitats, namely crevices. However, its overall impact seems unlikely to match that of *Concholepas,* both because of its small body size (<3 cm) and relatively restricted diet.

In summary, there is no equivalent to *C. concholepas* in North America within gastropod taxa, and in this sense it remains ecologically unique. Studies on the "loco" at intertidal sites from which humans have been excluded indicate that it is a major force in organizing the associated intertidal assemblage. It is the only gastropod known to us capable of filling such an ecological role, and provides an important and necessary reminder of the dangers and difficulties of interpreting ecological interactions when human influences are not understood or explicity documented.

7. *Mankind*

In Chile, a recent and active research area has been the evaluation of the impact of mankind as a major predator on rocky intertidal shores. From a historical viewpoint, it is important to consider the rocky intertidal observations of Guiler (1959) in central Chile. This author observed that the kelp *Durvillaea antarctica,* known in Chile as "cochayuyo" and with considerable human demand as food, replaced *Lessonia nigrescens* on isolated and inaccessible coastlines with considerable wave action. This author reported that at a site of difficult access (south of Curaumilla, near Valparaíso) *Durvillaea* was the dominant alga at the lower intertidal. However, this species was practically absent in other wave-exposed localities nearby where *L. nigrescens* predominated. Guiler (1959) attributed the distribution pattern of *Durvillaea* to the effect of human interference. He argued that the continual harvesting of *Durvillaea* cleared the shore for populations of *Lessonia,* which in the absence of "cochayuyo" formed a monoculture. Such hypothesis has never been experimentally tested, but it is worth mentioning that Curaumilla has remained isolated over this period and that Guiler's observations are still valid to some extent (Castilla & Bustamante, unpublished results). Further, Castilla & Bustamante (1986)[4] have shown that, at Las Cruces Coastal Station, whose rocky shore was fenced in December 1982 to stop harvesting by "mariscadores" (see also Castilla & Duràn (1985), the population of *D. antarctica* has undergone a significative increase as compared to adjacent non-fenced harvested stretches of similar rocky shores.

Castilla (1981a) called attention to the fact that the intertidal populations of *Concholepas* at relatively pristine sites were denser and characterized by larger individuals than those commonly found along the harvested coast of central Chile. Later, Castilla & Durán (1985) and Moreno *et al.* (1986a) showed that in small marine reserves with anthropic exclusion dramatic ecological changes in landscape and community structure could be observed. These observations support the view of Paine (1980) in that functional food webs are useful tools for describing dynamic multispecies relationships.

Moreno *et al.* (1984) and Olivia & Castilla (1986) studied the human impact on herbivore species such as key-hole limpets of the genus *Fissurella* in southern and central Chile. In non-harvested areas the populations of key hole limpets greatly increased, due to the human exclusion for 2-4 years. On the other hand, a dramatic decline in macroalgal cover due to *Fissurella* overgrazing was reported (Moreno *et al.* 1984). Recently, Moreno (1986) described the "cascade effect" (Paine 1984, Carpenter *et al.* 1985) occurring throughout the intertidal community in man-influenced shores of southern Chile. Similarly, Castilla (1986) has underscored the ecological significance and improved understanding of the structure and dynamics of Chilean rocky shore communities, as a consequence of the establishment of a few marine reserves during the last decade.

In different areas of the world, mankind has been identified as a strongly interacting species in intertidal communities: In South Africa, by Branch (1975) and Hockey & Bosman (1986); in Alaska, by Estes & Palmisano (1974); in California, by Zedler (1978); in Chile, by Moreno *et al.* (1984, 1986a), Castilla & Duràn (1985), Oliva & Castilla (1986), and Durán *et al.* (1987). It has been found that as a result of the presence or absence of mankind the different communities may undergo dramatic changes. We believe that presently mankind not only has better access to these ecosystems but that the use of artisanal and sophisticated tools to obtain the desired resources is translated into an even stronger effect. From this point of view, mankind cannot be regarded as just one more species in marine trophic webs. Mankind's peculiarities-if well understood and properly studied under experimental situations-can provide invaluable information on how marine ecosystems are organized and consequently help in designing management policies.

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[4] CASTILLA & BUSTAMANTE (1986) Evaluación del efecto humano en una población de *Durvillaea antarctica:* densidad, biomasa y estructura de tallas. Biota, Osorno, Chile: 107.

CHALLENGING PROBLEMS

The following set of "problems" are those which appeal to us: they are not the only ones of significance by any means but simply reflect our combined interests and biases. Some are approachable by experimental methods, others are not. We pose them both to stimulate future endeavors on an increasingly well known Chilean shore, and because we feel that the answers will illuminate important questions in comparative community ecology.

1. Mankind has been exploiting readily accessible marine invertebrates, usually those living in intertidal regions, for thousands of years (Volman 1978), and the Chilean shore is no exception. We pose two questions. The first: what are the immediate effects of this exploitation by humans? is being clearly answered in Chile, by Chilean researchers. Moreno *et al.* (1984, 1986a), Moreno (1986), Castilla & Duràn (1985), Oliva & Castilla (1986) and Castilla (1986) have shown in a series of human exclusion experiments that the rocky shore community structure changes dramatically under the experimental conditions. Obviously such research needs to be repeated at different geographic sites, and specially on soft, unconsolidated sediments because these seem to be markedly different from their solid surface couterparts (Peterson 1982). Similar research, specifically addressing the question of the role of human exploitation on rocky shores at the community level, has yet to be initiated in North America.

An equally challenging problem is the following. Because humans have been exploiting intertidal invertebrates (and algae) in Chile for many 1000's of years (see Castilla & Durán 1985 and Moreno 1986), could the exploited populations have evolved in response to this predation? Although the likelihood depends on the intensity of the exploitation, a positive answer is possible. Organisms are known to respond adaptively to intense predation (Endler 1986), and the changes can occur within ecological time frames in marine invertebrate populations (Seeley 1986).

Two closely related problems should also be considered. First if it can be shown that most shoreline assemblages have been or are being exploited, shouldn't extraordinary efforts be made to discover pristine environments in which population dynamics and ecological interactions can be observed in their "natural state"? Finding such sites should greatly improve the interpretation and understanding of the conditions under which specific morphologies, life history phenomena and ecological interactions evolved. Further, they may provide baselines to measure the extent of modification in altered shores. Second, in national parks or similarly protected situations, scientifically conducted, small scale and ecologically reversible experiments should be encouraged to permit measurement of the suspected differences.

2. Body size (or mass or shape) is an ecologically significant aspect of any species, and can influence reproductive output, susceptibility to disturbance, or relative freedom from predation. In sessile species excellent competitors tend to be large bodied or fast growers (Paine & Suchanek 1983); the answer is not as clear for mobile species. Why, then, do Chilean rocky intertidal, sessile invertebrates tend to be relatively small? We (Paine *et al.* 1985) have explored one of the consequences involving the mussel *Perumytilus,* nonetheless, the general problem remains. Taxa which attain large size in North America are on average smaller in Chile: for instance, *Mytilus californianus* can attain shell length of 30 cm at middle intertidal levels; individuals of the starfish *Pycnopodia,* even in the intertidal, can be occasionally found to exceed 1 m in diameter; barnacles, especially *Semibalanus cariosus* and *Pollicipes polymerus* commonly attain basal diameters in excess of 2 cm of body lengths greater than 20 cm; large bodied kelp (laminarian) species abound; and gigantism characterizes an octopus (*Octopus dofleini*) and one of the world's larger chitons (*Cryptochiton stelleri*). North American anemones are notoriously large: both *Anthopleura xanthogrammica* and various species of *Tealia* routinely attain column diameters in excess of 20 cm.

If these size differences reflect a general pattern, why should this be so? Primary productivity is high in Chilean coastal waters and ice scour does not occur. Is it because the shores are not geologically stable, being subject to unpredictable horizontal and vertical displacements? (Castilla, manuscript). Perhaps the relative frequency of El Niño (ENSO) events have been generally more frequent during evolutionary significant time scales in Chile than in

North America, thus selecting for smaller size or more rapid reproduction. Thus, just as the magnitude of ecological impact of El Niño can be shown to vary latitudinally in North America (Paine 1986), so it might vary in both intensity and, specifically, frequency at increasing southern latitudes.

3. Although no community is independent of its biogeographic roots, it still remains possible to identify universal schemes of zonation (Stephenson & Stephenson 1949), which suggests a general overriding pattern. Thus, in one sense, most temperate zone, rocky intertidal assemblages are dominated by barnacles or mussels with sea urchins, starfish, littorines and limpets comprising a major proportion of the mobile consumers. However, in coastal Chile secondary consumer groups such as flatworms, nemertean worms and nudibranchs seem relatively uncommon (Viviani 1979 and field experience of authors). If the observation is correct, it suggests a major reduction in species richness at certain high taxonomic levels. Is the cause historical? Can it be attributed to an absence of the resources required by these relatively specialized consumers? What are the consequences, if any, to the associated community?

The problem has another dimension worthy of consideration. The phenomenon of complementarity (Schall & Pianka 1978), in which ecologically similar higher taxa replace one another geographically, is well documented for terrestrial communities. If it occurs in marine systems as well, it might be appropriate to equate the small pejesapo (*Sicyases sanguineus*) with other grazers, and to discover whether the composition of the grazer guild changes where such fish disappears from the fauna. Does the extraordinarily rich Chilean *Petrolisthes* crab assemblage have ecological counterparts elsewhere, and if not, they replace or possibly even exclude other ecologically similar taxa?

In another vein, Castilla (1981a) has documented the presence of a number of ecologically critical or keystone species on exposed Chilean shores. *Healiaster, Concholepas, Sicyases,* perhaps even intertidal crabs. The finding is reminiscent of that of Menge *et al.* (1986) in Panamá in that a number of trophically important taxa existed rather than a solitary one. A comparison with North America would be dependent on latitude, exposure and how one wishes to treat sea otters. On exposed shores, in the absence of otters, *Pisaster* appears to be the most critical species. The same claim could not be made at lower latitudes (<35^{o}N) or in more protected environments. The problem of geographic differences remains intrinsically interesting because, by definition, such "critical" species control or influence the abundance and distribution of many other community members.

4. One of the currently debated issues in marine benthic ecology is whether local population or community structure is determined by events during a planktonic dispersal stage and at settlement, or by events impinging on the recruited stock. The issues were initially identified by Thorson (1946) and Lewis & Bowman (1975). Current views suggest that some assemblages may, while others may not, be strongly influenced by presettlement events: Roughgarden *et al.* (1985) provide a mathematical model while Connell (1985) comes to a similar view in an analysis of barnacle recruitment. We mention the debate here because the issues are nontrivial. If benthic community structure is usually determined by presettlement events, it focuses attention on the almost unknown areas of larval dynamics and pelagic-benthic coupling. Thus, variations in larval settlement rate can be expected to translate directly into spatial and temporal variations in the character of the adult stocks. At the other extreme, if larval settlement is sufficient to saturate consistently the limiting resources (usually space), community structure is much more likely to be determined by interactions between adults, with body size, adult longevity, and site holding tactics being especially significant. We agree with Connell (1985) that measurement of settlement rates should be one of the "prime future aims of marine benthic ecology". The careful work of Wethey (1984) provides an outstanding example.

5. All natural communities contain score if not hundreds of species which can be assumed to interact both directly and indirectly with each other. The problem is a general one in all community analyses: how to identify and quantify the nature, intensity or strength, and sign of these interspecific interactions? Clearly, populations do not exist in an ecological vacuum. However, when other species are added, the interaction network can become complex rapidly. (Paine (1980) provides one qualitati-

ve overview, Dethier & Duggins (1984) another. One of the most clear studies is that of Dungan (1986) of a three-way interaction between barnacles, limpets and algae. Addition of carnivorous gastropods would render the interpretation still more complex, especially if they were characterized by individual specific feeding behaviors such as those identified by West (1986). The challenge to all ecologists is how to incorporate interaction strength and relationships of different sign (*i.e.*, negative or positive), into the useful but entirely descriptive food web models. Little progress can be expected in the realistic understanding of the dynamics of multispecies interactions without solving these general problems.

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