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THE BIOLOGY OF AN INTRODUCTION: RHITHROPANOPEUS HARRISII

by

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INTRODUCTION

When I first arrived in the Hawaiian Islands on a teaching assignment in 1970 I naively expected to be greeted by a landscape clothed in the native flora. Instead, what I saw as I left the airport was a collage of introduced species which I took to be natives. It was not long before I realized the error (interestingly, one of the first courses I was to teach was entitled "Plants and Animals of Hawaii", a little surprise for the man fresh off the boat.) Curiously, I had to travel 2,300 miles from my native California to be made aware of something that had so blatantly surrounded me all my life: that human habitations tend to assemble communities of exotic organisms. One look at any neighborhood garden with its many ornamentals should confirm this.

With such a variety of exotic organisms living somewhat unrestrained in each town it is perhaps surprising that so few of them are able to invade the surrounding natural areas. It may be generally suggested that these organisms are being maintained under artificial conditions so that some aspect of the physical environment is supplied or controlled (e.g. water) or that biological interactions are controlled (e.g. parasites, herbivores, etc.) thereby permitting the existence of the exotics. Occasionally a few of these species are able successfully to invade natural areas, in some cases with dramatic results. Interestingly this tends

to occur more often on islands or remote continents (e.g. Hawaii, Australia). The reasons for these successful invasions are often unclear, but seem most often to include freedom from predators and parasites, available niches, reduced competition, etc. Predicting such success appears even more difficult, yet it is becoming increasingly important that we be able to do so, particularly when evaluating the potential of agricultural pests and biological controls.

Let me take a moment at this time to define a few terms. I will take invasion to mean the appearance of a population of a species in an area where it hitherto had not occurred, and introduction to mean an invasion where humans have been the agent of dispersal. A successful invasion would mean that a relatively stable, reproducing population has become established.

As already mentioned, the factors that affect the success of an invasion are often unclear, as evaluations of wildlife introductions (Levi, 1952) and biological controls (Krebs, 1978) testify. This makes generalizations about invasions difficult, even with the advantage of hindsight (Wilson, 1965). For this reason most workers have chosen to study invasions by examining specific cases (Egler, 1942; Fisher, 1948; Elton, 1958; Morley & Katznelson, 1965; Hairston et. al., 1968). My approach in this paper will be essentially the same, however, I will begin by looking at some of the ecological factors that potentially affect invasions, and then attempt to apply these in an evaluation of a specific case: that of the intro-

duction of Rhithropanopeus harrisi(Gould) to some of the estuaries on the Pacific Coast of North America.

GENERAL PATTERNS IN INVASIONS

Generalizations about invasions are difficult to come by. Wilson(1965) notes that even with the advantage of hindsight we can make few useful generalizations. This may be because in each specific case the success of the invasion was affected by combinations of ecological interactions, many of which remain obscure. Simpson(1953) suggested that the success of an invasion was basically one of access: physical, evolutionary, and ecological. Obviously an organism cannot invade a new zone if it cannot get there first; it must have physical access. Evolutionary access means that the organism must have at least minimal adaptations (preadaptation, if you will) to the environmental conditions it will meet. Ecological access refers to the presence of an adaptive zone(niche) which is either vacant or occupied by competitively inferior organisms. As you can see, these criteria include most of the possible ecological interactions. In the following sections I will outline some of these interactions and attempt to evaluate briefly their role in determining the success of an invasion.

Physical Access

Since Tertiary times there has been a gradual homogenizing of the world's fauna brought about by the joining of previously disconnected continents, thereby allowing access

for various terrestrial organisms(Elton,1958). In recent times mankind has accelerated this process by transporting organisms both intentionally and accidentally wherever he has gone(Elton, 1958; Bates,1956). The speed of many forms of modern transportation makes even very fragile organisms potential passengers, and our efforts at reducing this hazard consist mainly of spot checking. In the case of marine organisms this is particularly so, although some guidelines have been established (Snow, personal communication; Smith, personal communication).

Of course organisms have been gaining physical access to new areas long before the appearance of Homo sapiens, and many have developed quite efficient dispersal mechanisms(Ridley, 1930; Darlington, 1965,1966; Carlquist, 1974). Unfortunately I have not the space to treat such a broad topic here, suffice it to say that there are many avenues that lead to physical access and that human activities represent one of the main thoroughfares.

Evolutionary Access

In order to understand evolutionary access it might be best to consider some of the physical factors that limit or control abundance, distribution, etc. of organisms as outlined by Odum(1959). The first of these was Liebig's "law" of the minimum which, simply stated, says that organisms need certain materials in order to exist, so the essential material that is closest to the organisms' minimum requirement would tend to be limiting. If a certain tree species

needs a minimum of 30 inches of rain annually, it would normally be unable to grow in places where the precipitation was less. Shelford expanded this idea in his "law" of tolerances by including the upper limits as well as the lower. Thus any factor near the tolerance level of an organism would tend to be limiting. The obvious corollary, according to Odum, is that any factor that is relatively constant and for which the organism has a wide tolerance would not likely be limiting. In addition, he points out that the period of reproduction is usually a critical one during which environmental factors are likely to be limiting. It should be added that various environmental factors may interact in such a way that they are limiting (Cox et.al., 1973), for instance increased temperature often raises the minimum tolerance level for oxygen in many marine organisms (Kinne, 1964). This synergistic effect may often be as important as it is difficult to detect. Dansereau (1957) proposed vitality (the optimum fulfillment of life cycle) as a measure of the degree of environmental stress experienced by an organism. In this way at least a rough estimate of the degree of stress could be made. This seems to be in line with Odum's comments on the sensitivity of the reproductive period. With this in mind it is interesting that organisms often occur in nature where conditions are not optimum with regards to some physical factor (Odum, 1959). This is normally because some other factor exerts an even greater effect. To complicate matters even more, it seems that the tolerance limits or optimum levels of a factor may vary over the geo-

graphical range of a species (Odum, 1959). Yet all these conditions need be considered when gauging the success of an invasion.

The manner in which environmental factors fluctuate has an effect upon the success of an invasion. Darlington (1965) believed that dominant groups of organisms tended to evolve in favorable climates and spread to less favorable ones. The idea is that the greater the amplitude of the environmental fluctuations the greater the chance that it will exceed the tolerance levels for a particular organism. The amplitude and regularity of these fluctuations is known as the predictability of the system (Ricklefs, 1976; Connell & Slatyer, 1977). Hence highly predictable systems have very regular fluctuations of low amplitude and tend to support more species (Sanders, 1968). Slobodkin and Sanders (1969) believe that organisms from areas of low predictability are more likely to invade areas of high predictability than vice versa. In most cases they feel such invasions are prevented by competition, but when they do occur they tend not to result in the elimination of the resident. This view appears to conflict with the general evolutionary trend outlined by Darlington (1965), but perhaps not. Logically one should expect it to be quite difficult for organisms to invade an area of low predictability particularly when adapted to the opposite conditions, and so such invasions should be infrequent. On a much larger time scale however, such infrequent invasions could account for the trend Darlington describes.

Thus areas of low predictability should experience few invasions while areas of high predictability should expect many more invasions, but usually do not due to competitive interactions. This is essentially the model developed by Terborgh (1973) to explain plant invasions, however, he proposes a somewhat greater flow of species into areas of low predictability (which he calls peripheral habitats).

Just as environmental predictability affects the potential for invasion so too should community stability. In order to avoid some of the difficulties with this term it should be defined, so I will take stability to mean the ability of a community to withstand or recover from externally caused change (Ricklefs, 1976). Now, how can it be measured? Dunbar (1960) used population oscillations as an indicator of stability when comparing tropical and temperate marine communities. Hairston et al. (1968) considered evenness of species abundance and distribution as a measure of stability. The classical view that greater species diversity indicated greater stability (the diversity-stability hypothesis) has come under criticism lately (Goodman, 1975) and is probably not a good measure of stability. Diversity of trophic levels may prove to be a measure of stability (Hairston et al., 1968; Ricklefs, 1976), however more data need to be gathered before such a measure can be used with confidence. The main question facing us here is whether unstable communities are more vulnerable to invasion than stable communities. According to the definition of stability this should be true; unfortunately considering the rel-

iability of the methods for measuring community stability I do not see this as a valuable tool for predicting successful invasions.

Perhaps some of the most common examples of successful invasions occur during the process of succession, so a short look at this phenomenon may reveal some of the basic adaptations of invading species. Succession can be generally described as an orderly process of community development that culminates in a stabilized ecosystem (Odum, 1969). Throughout the process species are successfully invading the system, often modifying it in such a way as to allow other organisms to invade, until a climax stage is reached. Species of the early seres tend to have high reproductive and growth rates while those of the late have lower growth potential but better competitive abilities (Odum, 1969). A compromise of species types occurs in "pulse stability" communities, in which more or less regular and dramatic physical changes occur and thus maintain the ecosystem at some intermediate point in the sequence (Odum, 1969). It would seem then, that certain competitive strategies adapt invading species to particular stages of succession, and hence the success of a particular invasion would be mediated by these two factors.

Since organisms seem to be adapted to particular successional stages it should not be surprising to find that many ubiquitous species are not adapted to a wide variety of conditions but rather to particular situations created by human activities such as agriculture, livestock rearing,

road building, etc.(Bates,1956; Harper,1965). For example the Klamath weed(Hypericum perforatum) invaded overgrazed pastures in Northern California during the early 1900's and became quite a pest until successful biological control was achieved (Krebs,1978). Additional examples of this phenomenon are plentiful(Allen,1936; Egler,1942; Morley & Katznelson,1965; Harris, 1971).

So evolutionary access will be governed to a large extent by the physical tolerances of the species, the predictability of the environment, the particular successional sere, and perhaps the community stability. Many times evolutionary access is accomplished through habitat modification as a result of human activities.

Ecological Access

Of the many types of species interactions perhaps competition has the most significant effect on the outcome of an invasion. Competition can be defined as the active demand by two or more organisms for a common resource(Miller,1969). If the resource is limiting then there are generally three possible outcomes: extinction, competitive exclusion, or character displacement(Emmel,1973). As I will try to show later, coexistence is another possibility. When competition is interspecific it favors the specialization of resource use by each species. On the other hand, when it is intraspecific it tends to favor a broadening of the range of resource utilization (Collier et.al.,1973).In the case of invasions competition should

be interspecific, as far as the success of the invasion is concerned, and hence should tend toward specialization of resource use.

One of the probable outcomes of competition is competitive exclusion. The principle was first outlined by Gause(1934) and consists basically of two aspects: that when two species occupy the same niche one will be superior and eliminate the other, and the converse, if two species coexist then they occupy different niches(Grant,1977). The principle seems fairly obvious and appears to hold for most situations as long as its limitations are considered, Its application should be restricted to resource limited species and to stable(predictable) environments(Collier et.al.,1973). Determination of the latter could be a source of difficulty since what might be a highly predictable environment for one species could be of much lower predictability for another. In addition some workers have demonstrated a lack of competitive exclusion even though the above limitations apply. Ayala(1969) used two species of Drosophila in which the larvae competed for food and the adults for space. While one species was the superior competitor in the adult stage it was inferior in the larval stage. Under these special circumstances Ayala found that competitive exclusion did not occur. Others have attacked the principle semantically, redefining niche, etc.(Kroes,1977). I believe that these arguments do not invalidate the principle , but rather provide a better definition of its limits. In this way it may help to explain why some invasions do not result

in competitive exclusion.

Character displacement can result in coexistence and will be discussed later, while extinction is perhaps best understood by examining the mechanisms of competition.

Competition can take two main pathways: exploitation or interference. Competitive exploitation involves a basic scramble for the resource(s) in that if two or more organisms have free access to a limiting resource the outcome of their competition will be determined by their relative abilities to use the resource (Miller, 1969). Unfortunately, gathering evidence for competitive exploitation requires sophisticated techniques (largely unavailable at present) for measuring the efficiency of utilization (Collier et. al., 1973). Competitive interference involves direct detrimental effects of one organism on the growth, survival, etc. of another. Mostly this is brought about by preventing access of a competitor to a resource. Bird territories are a prime example (Collier et. al., 1973; Miller, 1969).

As mentioned earlier the competitive strategy of invaders during the stages of succession shows a shift in pathways. During the early stages the most successful species are generally those that compete through exploitation. Winning competitors in the later stages tend to be more effective at interference (Connell & Slatyer, 1977). Again the success of an invader would depend upon its mode of competition and the successional stage of the community.

The competitive pathway is likewise affected by the

physical attributes of the ecosystem. In areas where the physiological stress is high (as in areas of low predictability) the community tends to be controlled by physical factors, and organisms that compete through exploitation are often most successful. In ecosystems where physiological stress is low (as in areas of high predictability) the community tends to be biologically controlled and organisms that compete through interference are most successful (Miller, 1969). Hence the potential success of an invasion would depend upon the level of environmental predictability and the particular competitive pathway of the invader.

An organism attempting to invade an area generally meets with a certain amount of ecological resistance, that is, competition from the established organisms of the ecosystem (Elton, 1958). As we have just seen, the success of a particular competitive pathway is related to the physical attributes of the ecosystem. In addition, if we assume that neither species has competitive superiority over the other then the resident species normally has the advantage and holds off the invader (Connell & Slatyer, 1977). This being the case then the invading species must have a significant edge in competitive ability if it is to be successful.

Competition then, can prevent invasions unless the newcomer has superior competitive abilities. The most successful competitive pathway depends upon the predictability and successional state of the ecosystem.

Since competition apparently plays such a major role in

determining the occurrence of competing organisms it would seem that coexistence of competing species is not possible. Yet there are circumstances under which competitors can coexist for varying periods of time. Organisms can reduce competition through temporal separation, for example. They may tap the same resource but do so at different times of the day (Cox, et. al., 1973). For example two species of intertidal crabs may utilize the same food resource but one may be active by day while the other is nocturnal. As long as one species did not depress the resource below the minimum level required by the second species the two could coexist. Competing organisms may also coexist if they are in an incomplete stage of replacement (Grant, 1977). Laboratory experiments have shown that this period of coexistence can be increased when: conditions more nearly meet the optimum requirements of both species and do not favor one over the other, the species have more or less equal abilities, or when the volume of the environment is increased (Miller, 1969). Coexistence may occur when the populations of the competing species are kept small enough so that the level of competition is low. This is often accomplished when other organisms crop these populations (Grant, 1977). The Mytilus-Pisaster-Pollicipes system illustrates this well. Mytilus and Pollicipes compete for space along the rocky intertidal zone of the Pacific Coast of North America; however Mytilus is a more efficient competitor and would eventually crowd Pollicipes out if not for predation by Pisaster. Experiments

in which Pisaster was removed from the study area showed a rapid increase in the Mytilus population coupled with a decrease in the Pollicipes population to the ultimate point of elimination. Reduction of other species occurred as well, but the point here is that predation by Pisaster enabled Mytilus and Pollicipes to coexist (Paine, 1974). Another system that enhances coexistence is one of cyclic equilibrium (Grant, 1977). In this case one or several environmental factors vary in a rather regular pattern so that species are alternately favored (Collier et.al., 1973). Hence each species would be able to maintain itself by building up larger populations under favorable conditions which would then serve as a buffer under conditions that favored the competitor. Finally, competing species may coexist by seeking the microhabitats that favor them. Since most environments contain a range of conditions for some critical factor each species could maintain a population by living in the preferred areas (Ross, 1957). One additional mechanism of coexistence has been described (Pimentel et.al., 1970) which involves a fluctuating rate of genetic change. In this system the evolution of the dominant species would tend to become static, or at least slower than the subdominant competitor which would then gain an advantage and become dominant. The roles are then reversed. To my knowledge such a system has not yet been demonstrated.

It would seem then that coexistence can occur under a variety of circumstances. When coexistence does occur there

are several immediate effects upon the species involved. In most cases each species experiences a certain amount of ecological compression, that is each population is depressed by an amount related to their degree of ecological similarity (Ricklefs, 1976). In addition character displacement may be displayed in that competing species show greater differences (morphological, ecological, behavioral, or physiological) in areas where they coexist than in parts of their ranges that are distinct (Brown & Wilson, 1956; Emmel, 1973). Although not particularly numerous, examples of character displacement do exist. Littlejohn (1965) compared the mating calls of two species of Hyla in Australia. He found the calls of allopatric populations quite similar while those of sympatric populations were much more distinct. Blair (1955) uncovered a similar relationship between two species of Microhyla in North America.

Since ecological resistance tends to block invasions we find in the various modes of coexistence a set of mechanisms by which invading organisms can establish themselves, and do so in a way that does not mean the elimination of the native species.

Invasions of islands have provided some of the most dramatic examples of species interactions and replacements (Carlquist, 1974). Coexistence is uncommon, but when it does occur it is usually because replacement is in some intermediate stage. The vulnerability of island environments is legendary. The reasons for the widespread success of island

invasions are several. Darlington(1966) believes that many mainland species are just superior competitors. In addition many island organisms have adapted to habitats that lack predators and competitors and hence are unable to cope with invaders from similar mainland habitats(Ricklefs,1976). Due to their isolation, islands are often said to be impoverished or unsaturated with respect to the numbers of species they could support(Mayr,1965; Holdgate & Wace,1971). Also we find that competition often occurs between wider taxonomic groups on islands. Lack(1976) found that competitive exclusion among Jamaican birds occurred between different genera on islands while on the nearby mainland such competition was most often between congeneric species. He attributed this to the fact that island residents had broader niches, a result of the ecologically poorer conditions on islands. Such conditions stem in part from the difficulties of physical access as well as the limitations of area. In the latter case it has been found that the smaller islands have fewer species. The effect is rather gradual in that there is no critical size, so species diversity decreases as area decreases (Preston,1962; MacArthur & Wilson,1967). The explanation is that on smaller islands competition is more apt to result in extinction than on larger islands(MacArthur & Wilson, 1967). Two species of the genus Lacerta illustrate the effect of area on the outcome of competition. On larger islands in the Adriatic Sea these lizards are found to coexist, but on the smaller islands competitive exclusion results in

only one resident species. A slight difference in habitat preference is evident on the larger islands and the mainland, but not so on the small islands (Nevo et. al., 1972). The implication is that the limitations of area on islands as well as the broader niches occupied by each species result in more intense competition, and hence less coexistence. Of course competition is not the sole reason for the great success of island invasions, we must not forget that human activities (agriculture, grazing of livestock, etc.) represent a drastic form of habitat modification to which many invading forms are adapted and to which the natives are not (Harris, 1971). In summary, the success of island invasions can be generally attributed to habitat modification, introduction of superior competitors, and perhaps available niches (unsaturated ecosystems).

There are many areas that could be considered island-like in nature: caves, tidepools, estuaries, mountain tops, etc. (MacArthur & Wilson, 1967). The island effects in these environments should parallel those described for geologic islands. In addition, when organisms attempt to invade these areas they will naturally encounter somewhat different physical conditions along with different species combinations and abundance. Hence if they are to be successful they must assume a somewhat different niche (through ecological displacement), the degree of difference depending upon how drastically the new conditions digress from those of the source area (MacArthur & Wilson, 1967).

Finally I should mention that the success of an invasion will depend to a certain degree upon the size of the colonizing population. This must be large enough for a sufficient number of the members to find each other and reproduce. Field entomologists prefer to release an introduced species for biological control in one area for just this reason (Andrewartha & Birch, 1954).

It is difficult to separate ecological access from evolutionary and even from physical access since they are so intertwined. However, I have attempted to illustrate some of the general features of each category and think that they will be of some use during the analysis of the specific case that follows. As you have no doubt noticed I have considered mainly competitive interactions under ecological access, basically because they appear to be most important, particularly in the case that follows.

THE INTRODUCTION OF RHITHROPANOPEUS HARRISII TO THE PACIFIC
COAST OF NORTH AMERICA

Rhithropanopeus harrisii, a small Xanthid mud crab, is native to the Atlantic Coast of North America, where it is found in estuaries from Mexico to Miramichi, New Brunswick (Ryan, 1956).

Sometime in the latter part of the 19th century it spread to Holland where until recently (1949) it had been identified as Heteropanope tridentata. It is now considered a subspecies of R. harrisii, variety tridentata (Wolff, 1954). It wasn't until the 1940's that this mud crab was first noticed in San Francisco Bay, and some ten years later in Coos Bay (Ricketts & Calvin, 1968). Carlton (personal communication) believes it now occurs in Netarts Bay, Oregon. I have found it to occur in Yaquina Bay as well (see appendix).

Physical Access

Since Rhithropanopeus is native to the Atlantic Coast and has managed to invade both Europe and the Pacific Coast of North America it obviously has had physical access to these areas. General consensus (Elton, 1958; Ricketts & Calvin, 1968) places human activities as the agent of dispersal. Transportation of plankton in ballast tanks of ships is a likely occurrence (Chesher, 1968) and may have been responsible for the movements of Rhithropanopeus. Elton (1958) explains that the Chinese mitten crab, Eriocheir sinensis, probably found its way to the North Sea by this method. The crab is a native

to the coast of China, living in rivers and migrating to brackish water to breed thus allowing ample opportunity to book passage in ballast tanks. The probability that Rhithropanopeus was carried in the same way or by clinging to algae on ships was considered unlikely by Wolff(1954). He felt that this "... is a brackish-water crab that could scarcely withstand transportation for several weeks through seawater of high salinity."(Wolff,1954). Apparently this was before the salinity tolerances of Rhithropanopeus were examined in any detail because it is very capable both as larva and adult of withstanding full strength seawater(Kalber & Costlow,1966; Smith,1967). I have kept these crabs in seawater(30-32%) in the lab for six weeks at a time and found that they are able to survive (even better than those kept in lower salinities). Hence it is quite capable of withstanding the high salinities it may encounter as a passenger in ballast. The main problem I see with this mode of access is the low probability that the zoeae from a ballast tank would settle near enough to each other to be able to reproduce. Coupled with this is the notoriously high mortality of planktonic larvae. In short I do not see a passage in ballast tanks as a likely method of establishing that initial breeding population.

Another often proposed method of introduction is as a stowaway in oyster seed. Elton(1958) lists five organisms that could likely have utilized this method of transport: Crepidula fornicata, Ursosalpinx, Paphia, Tritonalia, and Rhithropanopeus harrisi. Each of these is normally found

associated with oyster beds. Ryan(1956) suggested that the movements of oysters could have affected the distribution of Xanthid crabs in Chesapeake Bay, and that Rhithropanopeus was the dominant species in seed beds in the upper part of Delaware Bay. This being the case it seems reasonable to expect some sort of correlation between the Pacific Coast estuaries planted with the American Atlantic oyster, Crassostrea virginica, and the occurrence of Rhithropanopeus. However it appears that the majority of the plantings along the Pacific Coast have been of the Japanese oyster, Crassostrea gigas (Matthiessen,1971). C.virginica was first planted in San Francisco Bay in the late 1800's and continued through 1910 when bay conditions made further plantings unfeasible. Apparently cool water temperatures prevented reproduction, so for at least ten years C.virginica seed was brought to the bay from the Atlantic Coast(Matthiessen,1971) providing ample opportunities for stowaways. The advantages of this form of transport are immediately obvious- the crabs would be seeded with the oysters and so end up in the same general area and in a habitat(oyster bed) to which they are adapted. In addition, ovigers of Rhithropanopeus have been found from June through September(Ryan,1956) which means they could be found among the stowaways. Unfortunately, literature on C.virginica in Oregon is scant. No mention is made of it being planted in any of the bays(Bruse & Wick, ____). In Tillamook Bay plantings of C.gigas began in 1931 and continued through the present(excluding the war years).

Presumably, it was the only species planted in Netarts Bay as well(Hayes,____). In talking to oyster growers in Yaquina and Coos bays I found that C.virginica spat had been brought in on a number of occasions, but never did well. The same seems to be true in Washington State(Cumbow, personal communication). It is probably this latter fact, the poor performance of C.virginica, that is responsible for their absence from most treatments of oyster culture on the Pacific Coast, but most surely there have been plantings in all of the oyster bays of the Pacific Coast. I think it likely that Rhithropanopeus occurs in more than the four bays where it has been observed(for instance Tillamook and Puget Sound) but has escaped notice(as in Yaquina Bay) either because it has been taken for Hemigrapsus oregonensis which it superficially resembles or that its general confinement to the upper parts of estuaries has allowed it to go undetected. Remember that if it was via oyster spat that the crab first entered San Francisco Bay, then its presence went unreported for a minimum of thirty years. I think it likely that a little field work in the rest of the oyster growing estuaries of the Pacific Coast will extend the range of Rhithropanopeus and further support oyster spat as the mode of physical access. The other half of the field work, demonstrating its absence in Pacific estuaries where oyster culture has not occurred, would be much more difficult.

Evolutionary Access

Whereas the exact method by which Rhithropanopeus gained physical access to the Pacific Coast is uncertain, its evolutionary access is less of a problem. Ryan(1956) found this crab living in nearly every arm of Chesapeake Bay, even into freshwater zones. It was not found in deeper waters nor was it common in lower parts of the bay. In nearly every case in which Rhithropanopeus was collected there was some sort of bottom shelter available: oyster bars, living and decaying vegetation, cans and debris, etc.

Temperatures in estuaries tend to be highly variable (Caspers, 1964) so it is not surprising to find that Rhithropanopeus is eurythermic, able to tolerate a range from at least 7°C up to 30-34°C(Vernberg & Vernberg,1972). Temperature data I had gathered in various arms of Coos Bay from October through December ranged from 9°C to 16°C, well within the limits of the crab.

Salinity within estuaries is also highly variable. Rhithropanopeus has been found in parts of estuaries that at times are entirely fresh(Jones,1940;Ryan,1956). In some preliminary investigations, I have kept specimens up to four weeks in freshwater. That Rhithropanopeus is euryhaline is well established(Smith,1967; Capen,1972; Vernberg & Vernberg, 1972), and its distribution in Coos Bay seems to reflect this tolerance(see appendix). I have found the crab in areas of highest salinity variation. For example, during October 1977 (at the end of a very dry year) salinity for a 24 hour period

ranged from 12‰ at highest tide to 3‰ at lowest tide, while in November (immediately after a storm) the range was 5‰ to 0‰. That Rhithropanopeus can live in seawater but "chooses" reduced salinities poses some interesting questions; however it has been this crab's ability to osmoregulate at these reduced salinities that has been the focus of most research. Apparently as salinity drops the crab's inward permeability to water also decreases (Smith, 1967). It has been suggested (Capen, 1972) that this change is due to a change in the activity of the gill epithelial cells and/or cuticle, and that it is not linked to ion transport systems. Interestingly, this osmoregulatory capacity is greater at lower temperatures (e.g. 7°C) than at higher (e.g. 20°C) (Vernberg & Vernberg, 1972).

The salinity tolerances of the larval stages have also been an area of much research. Generally speaking, larval stages of estuarine organisms require certain ranges of physical factors for maximum survival, and often these are different from those of the adults- usually narrower and less harsh (Kinne, 1964). Costlow et. al. (1966) examined larval development of Rhithropanopeus under a variety of temperatures and salinities, and found a wide range under which development could occur. Generally the survival was highest at 20-25°C with salinities between 15-25‰. Later investigations (Christiansen & Costlow, 1975) revealed that a cycling temperature ($\pm 5^\circ\text{C}$) produced highest survival at a range of salinities (5, 20, 30‰). So it appears that even the larvae are well adapted to the fluctuating conditions that are normally

found in estuaries. I might point out that unfortunately they are not so well adapted to a variety of insecticides and pollutants that seem to work their way into estuaries (Christiansen & Costlow, 1975; Rosenberg & Costlow, 1976; Christiansen et. al., 1977 ; Payen & Costlow, 1977).

The ability of Rhithropanopeus to adapt to environmental variations can be illustrated by differences in temperature-related metabolic patterns of various populations along the Atlantic Coast. Careful study of these variations revealed that they were environmentally induced (Vernberg & Vernberg, 1972), indicating an ability to acclimate to local conditions. Even larval development was shown to be adaptable to local conditions (Christiansen & Costlow, 1975).

Before leaving the topic of evolutionary access mention should be made of community stability and environmental predictability. The wide fluctuations of temperature and salinity that occur in estuaries would seem to qualify them as environments of low predictability. As discussed earlier, invasion of such areas from zones of higher predictability (the sea or rivers) is less likely than the reverse. Estuaries then, would be relatively difficult to invade by organisms from more predictable environments, although rare invasions should occur. This idea is reinforced by the paucity of species that inhabit brackish waters, particularly those with salinities between 5-15‰ (Remane & Schlieper, 1971). Rhithropanopeus however, comes not from an area of higher predictability but rather from a quite similar environment, and hence should

be very capable of tolerating the physical conditions it encounters.

The stability of the estuarine community is difficult to determine. Studies of trophic levels and energy flow (deSylva, 1975; Vernberg, 1975) reveal fairly complex food webs, and if these indicate a fair degree of stability (Ricklefs, 1976) then invasions should be more difficult. However, in light of the difficulty in measuring stability and the lack of conclusive evidence relating it to ease of invasion, any conclusions remain speculative.

So how might have all these factors affected the introduction of Rhithropanopeus? We have seen that the crab is well adapted to the fluctuating salinity and temperature levels, as well as other physical aspects of estuaries. Therefore it comes to the Pacific Coast well prepared both as larva and as adult to deal with the physical conditions it will encounter. Hence the low predictability of the environment should not adversely affect the success of the introduction. The stability of the community could prove something of a barrier, but this is difficult to evaluate. Ecological resistance could play a substantial role as well, and this I will discuss next.

Ecological Access

On the Pacific Coast the upper reaches of most estuaries are inhabited by a small, aggressive crab, Hemigrapsus oregonensis. Occasionally one may also find juveniles of Cancer magister, but neither of these seem to enter the zone that occa-

sionally becomes fresh. Of the two, H.oregonensis is much more common and a year round resident, and therefore deserving of attention. H.oregonensis can usually be found along the shores of estuaries hiding under rocks and in holes and crevices. At low tides it tends to occur at the lower levels where water may be found in sumps under rocks and debris, or in any situation where the body may be bathed more or less continually in water(Knudson,1964). Rhithropanopeus occupies essentially the same type of habitat, but more often constructs burrows under rocks and debris in which water collects (personal observations).Both crabs are active at night and quiescent during the day, perhaps an adaptation to avoid visually cued predators. Symons(1964) found that H.oregonensis was most active between midnight and 0400 hours, with males reaching another peak of activity at 0530 hours. Specimens of Rhithropanopeus that I kept in the lab were active(out of their burrows and moving about) only at night, so it appears that their periods of activity correspond. Hence it would be unlikely that the two would avoid competition through a circadian separation.

Feeding activity at night seems to have encouraged the use of tactile and chemical senses by H.oregonensis while visual stimuli are least important(Symons,1964). To my knowledge, no such data is available on Rhithropanopeus but with such similar nocturnal habits, similar sensory importance in feeding is not unlikely. The diet of H.oregonensis consists of dead fish and animals, living animals, algal film on rocks,

and Zostera(MacGinitie,1935; MacGinitie & MacGinitie,1968). Knudson(1964) believes the crab to be primarily herbivorous, gleaning algae and diatoms off rocks and surfaces, but also taking animal material. Rhithropanopeus appears to be omnivorous. Specimens I have kept in lab readily took chopped clams and blades of Zostera. Examination of stomach contents from specimens I had collected in the field showed a variety of algae along with various pieces of arthropod skeleton, including about half the carapace of a very small crab(perhaps they are cannibalistic as well). In all respects then the diets of both species appear to be very similar.

Reproductively the crabs are not quite so similar. Knudson(1964) found H.oregonensis ovigers from mid February through early September. Females generally produce two broods per year, the first hatching in May and the second in early September. With an average of 4,500 eggs per brood and approximately 70% of all females producing two broods the annual egg production per female is approximately 7,650. Ovigers of Rhithropanopeus were found by Ryan(1956) from June through September, with juveniles being most common July through October. Sexual maturity is reached at about 5mm(carapace width), which usually occurs in the second summer. It appears that H.oregonensis has the edge in egg production since Rhithropanopeus seems to produce only one brood per year; however there are no real data other than relative occurrence of ovigers to support this assumption. Further, there are no data on larval mortality save the wide salinity and temperature

tolerances of Rhithropanopeus (Christiansen & Costlow, 1975). It is conceivable that a higher survival of Rhithropanopeus larvae could compensate for a presumed lower egg production, but this remains pure speculation.

The osmoregulatory abilities of both crabs were compared by Jones (1941). As the salinity drops both crabs conform at higher salinities and osmoregulate at the lower salinities, however, as salinity approaches zero Rhithropanopeus maintains its ability to regulate while H. oregonensis cannot. This means that the osmoregulatory capacity of Rhithropanopeus is superior to that of H. oregonensis at much reduced salinities.

It appears then that the two crabs have nearly identical habitat preferences, activity patterns, and food preferences. Reproductively, H. oregonensis may be superior but the data are insufficient for anything but speculation here. Rhithropanopeus appears to have superior osmoregulatory ability at lowest salinities. From this comparison it looks as if these crabs have very similar demands and interactions in the ecosystem, and as Jones (1940) said "... the two occupy practically the same ecological niche...".

If these crabs occupy nearly the same niche, as the comparison indicates, then an invasion attempt by Rhithropanopeus could only result in a competitive interaction. Such an interaction should depend to a certain extent upon the characteristics of the environment. Estuarine environments generally have low predictability, and as such should harbor organisms who compete via exploitation. If the estuarine ecosystem also

corresponds to earlier stages in succession, as in a pulse stability system, then exploitation should again predominate. With this in mind, and in the absence of any reported behavioral activities that might indicate some interference mechanism, it seems likely that competitive exploitation, probably for food and shelter, is the mode of competitive interaction between these two crabs.

The probable result of this competitive interaction can likewise be reasonably deduced. If estuaries can be considered islands then the factors that affect island invasions should enable us to predict the results of the interaction between Rhithropanopeus and H. oregonensis. The analogy is one of an island creature invading another island. Since island organisms have broader niches we would expect the interaction between two similar species to result in competitive exclusion. Both crabs are omnivorous, which may be taken as an indication of a fairly broad feeding niche (compared to a specialist herbivore for example) and hence one should exclude the other. Also, the smaller the island the greater the tendency toward competitive exclusion, yet this is difficult to apply in practice. Probably any estuary large enough to support an oyster industry would be large enough to support both crabs as well. Overall though, the tendency toward competitive exclusion is probably moderately high.

While examining the range of Rhithropanopeus in Coos Bay I found it to be confined to only two areas at the very upper end of the bay (see appendix). Its range did not over-

lap with that of H.oregonensis, in fact there was nearly a mile of unoccupied territory separating them. In San Francisco Bay however, there do appear to be periods of coexistence between these crabs. During dry years the water in the Carquinez Strait remains relatively high in salinity. As a result H.oregonensis becomes increasingly abundant in this area, normally occupied only by Rhithropanopeus. The two coexist for a short time in what appears to be a stage of replacement. However in wetter years the water in the strait becomes fresh, and this apparently kills off the H.oregonensis population (Jones, 1940). So the coexistence is only temporary, a result of a fluctuation in normal salinity which allows H.oregonensis to become established and begin to replace Rhithropanopeus.

Yet this coexistence tells us quite a bit about these two crabs. First the fact that allopatric ranges is the normal state indicates fairly severe competition. Second, since they both can tolerate a wide range of salinities they should be found throughout most of the bay, however since they are competitors each crab will be found in those areas that impart it with an advantage. That is, each crab will be found in those areas where it is the superior competitor. H.oregonensis, by this reasoning is superior in most of the bay and Rhithropanopeus only in those areas of the bay where the salinities occasionally reach very low levels. It is probably the latter's ability to survive at these lower salinities that allows it to take advantage of an area unavailable to H.oregonensis. In effect, Rhithropanopeus has found a vacant niche in the

Pacific Coast estuaries.

The presence of unfilled niches in Pacific Coast estuaries was suggested by Jones(1940), and is reminiscent of the impoverishment hypothesis used to partially explain the vulnerability of islands to invasions(Mayr,1965). Jones (1940) considered the Pacific Coast to be mostly open and rocky or sandy beaches, and generally deficient in bay areas as compared to the Atlantic Coast. Therefore, an abundant and diversified fauna adapted to estuaries would not have developed to the same extent as on the Atlantic Coast. This would leave a variety of niches unfilled on the Pacific Coast, niches which could be filled by Atlantic Coast species.

In this respect Rhithropanopeus has been able to capitalize on its superior osmoregulatory ability to exploit an area of the estuary inaccessible to H.oregonensis. By doing so it was able to avoid the ecological resistance of the native. H.oregonensis, the superior competitor throughout most of the estuary has forced a form of character displacement on Rhithropanopeus, confining it to the physiological limits of its salinity tolerance. On the Atlantic Coast the distribution of Rhithropanopeus in Chesapeake Bay (Ryan,1956) appears to be much more extensive relative to its distribution in Coos Bay.

It is interesting that another Xanthid crab commonly found in oyster beds of Chesapeake Bay has been unable to invade the Pacific Coast along with Rhithropanopeus. Eurypanopeus depressus is found somewhat lower in the bay than

its cousin (Ryan, 1956), and is apparently less adept at osmoregulation. Could the ecological resistance from H. oregonensis be responsible?

Several aspects of this examination lend themselves to further study. The competitive success of each species (Rhithropanopeus and H. oregonensis) under different salinities (both static and cycling) might prove an interesting comparison, and in addition demonstrate the competitive interactions proposed in this paper. The method of physical access might also be worthy of some additional attention. I think that a strong correlation between Pacific Coast estuaries that have seeded Crassostrea virginica and the occurrence of Rhithropanopeus could be demonstrated. In addition there seems to be something peculiar about the pattern of this crab's distribution in Coos Bay. For example along a hundred meter stretch of river bank with seemingly identical physical conditions I would find crabs for the first thirty meters. Then they would be completely absent in the next fifty meters, and then they would appear again. This type of patchy occurrence may have been due to oxidation levels of the substrate, or a difference in substrate composition, but the latter seems unlikely since preliminary investigations on particle size showed no obvious differences. Mud under rocks where crabs were found was usually light colored while in crab free sections the mud was usually quite dark. This may mean that Rhithropanopeus is sensitive to oxidation levels, or that their burrowing activity simply allows more oxygen to reach mud under rocks. In

either case it does not appear to be too difficult to test, and could prove quite interesting.

SUMMARY

I have tried to examine most of the factors that may affect the success of invasions, and applied them to the introduction of Rhithropanopeus harrisii to the Pacific Coast of North America. Successful invasions require physical, evolutionary, and ecological access. In this case physical access was probably provided by transportation with oyster spat, although passage in ship ballast cannot yet be ruled out. Coming from an estuary Rhithropanopeus was already well adapted both as larva and adult to the physical aspects of the environment, particularly the temperature and salinity extremes. Ecological access was something of a problem. Natural history comparisons between Rhithropanopeus and Hemigrapsus oregonensis revealed nearly identical food preferences, activity patterns, and habitat preferences, so that the two are most surely competitors. Because of the physical attributes of estuaries, competition probably takes the form of exploitation, with competitive exclusion the likely result. The two crabs do not coexist (except for short periods) and maintain exclusive ranges. Rhithropanopeus appears to have been able successfully to invade Pacific Coast estuaries because: human activities have introduced it, it is well adapted to estuarine conditions, and its superior osmoregulatory ability allows it to utilize a section of the environment unavailable to Hemigrapsus oregonensis.

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Appendix I

Field notes on Rhithropanopeus in Yaquina Bay

Three specimens collected on 27 April 1978: males- 20mm, 14mm, and 9mm(carapace width). Collected next to culvert of small creek under Yaquina Bay Drive between the Burchett and Brace residences. Specimens were hidden under loose rocks on bank near culvert.

Appendix II

The Distribution of Rhithropanopeus harrisii
in Coos Bay

