Introduced Marine Mollusks
of
Washington and Oregon

by

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Introduction

With the Broadening of man's world-wide communications and economic endeavors, it has almost inevitably followed that the distributions of many organisms, both of economic value and those undomesticated but closely associated with man's activities, have been greatly effected by his movements, developement of culture, and attempts to increase his productivity and material well-being. Instances of the dispersal of species, such as crop-plants or diseases, by man are common and well-known. However, less well-known, documented, or studied is the occurence of "exotic", introduced species of marine mollusks in the bays and estuaries of the Pacific coast of the United States. This paper will deal primarily with the exotic mollusks found in the bays and estuaries of Washington and Oregon, a region with which the writer is somewhat familiar, and will be concerned with the species to be found, some notes concerning their biology and ecology, their possible significance in the "native" ecosystems, reasons for their appearence and survival, and their possible usefulness in examining some aspects of the process of colonization and evolution of organisms and ecosystems.

A Historical Review

With the developement of culture and commerce on the West Coast of the United States during the last century, came the developement of the shell-fishery indusrty. Quite early, businessmen hit upon the idea of transplanting well-known Atlantic

Coast shell-fish, notably the Virginia oyster, <u>Crassostrea virginica</u>, into seemingly suitable habitats on the West Coast. Such transplants were attempted from the 1870's until about the 1930's in many presumably suitable waters in the Pacific states, with little long-term establishment of the species. (Hanna 1966)

The attempt to establish and cultivate <u>C. virginica</u> was apparently largely abandoned in our waters when it was found that the cultivation of one of the native Japanese oysters, <u>C. gigas</u>, would prove to be more financially feasible. The first plantings were made in 1902 in Puget Sound, and the industry has since spread from Alaska to California, although it has had to be maintained largely by periodic shipments of young spat from Japan. (Galtsoff 1932, Hanna 1966) These attempts to establish these two commercially important species in our coastal waters has brought about the establishment of quite a number of exotic species of soft-bottom-dwelling or estuarine mollusks from the Atlantic coast of the United States and Japan.

The literature which deals specifically with the occurence of exotic mollusks in our waters is, as yet, only beginning to be developed. G. Dallas Hanna was probably the first worker to gather into a whole the known occurences of exotic mollusks in the terrestrial and freshwater as well as marine environments of the Western United States. His work appeared originally in 1939 as the article "Exotic Mollusca in California". In 1966, he revised and updated this work into the paper, "Introduced Mollusks of the Western United States", in which he documents all of the known or probable occurences of exotic mollusks in the Pacific Coast states and

Hawaii. This paper is probably still the best source of general information on the subject to date.

With regards to the waters of western Canada, D. B. Quayle published a report in 1964, "Distribution of Introduced Marine Mollusks in British Columbia Waters", in which he discussed the exotic marine mollusks then known from the waters of, principally, southern British Columbia and the Strait of Georgia region, the main oyster-culturing areas. Unlike Hanna, Quayle has been able to collect some interesting information on the reproduction and dispersal of at least a few of these species, and has attempted to give some explanation for why they are distributed the way they are, in the region. The occurence of exotic molluscs in Washington or Oregon has apparently undergone no detailed study, at least in recent years, and most of the information is available only as short notes or articles in various journals or brief mentions in works of more general interest.

For the economically important species, such as Crassostrea, a considerable research effort and literature has grown up concerning their biology and the various aspects of their fishery. Indeed, often there are laboratories wholly devoted to the study of these shell-fish. Occasionally, there are references made to various other exotic species as well in their reports, notably those which have some injurious effect. In general, a good deal of information concerning the biology and ecology of introduced Atlantic coast forms can be obtained by an examination of the research efforts of the various East-Coast based research centers. Information concerning the introduced Japanese forms, however, is virtually non-existent, or at least, quite inaccessible to the student.

Established Exotic Species

Following is a list of the introduced mollusks that can be found common, at least on a local basis, in the bays and estuaries of Washington and Oregon. Although I will confine my discussion of specific species to those found in this area, and the centers of introduction of many of them seem to be in this region, no discussion of the subject would be complete without at least a mention of the occurence of exotic mollusks in the marine waters of California.

The San Franscisco Bay area, for example, contains, or did once contain, a large contingent of exotic mollusks in its marine benthic fauna. This is not too surprising, considering that the Bay area has long been a center of commerce and shellfishery, and was probably the first area into which a number of alien species were first introduced. With subsequent transplantation attempts of the same commercial species to other localities on the Pacific Coast, and movements of stocks and equipment from one cultivation area to another, it has come to pass that most if not all of the common and widespread exotic species to be found in Oregon and Washington are also to be found in suitable habitats in California. However, some interesting Atlantic species, such as the ribbed marsh mussel, *Volsella demissus*, and the large whelk, *Busycon canaliculata*, have become common in the San Franscisco Bay area, but have apparently not yet become established in our area. (Hanna 1966, Ricketts et al 1968)

Crassostrea gigas (Thunberg)
(= C. laperousi)

The Japanese oyster is commonly cultivated on protected tideflats and some subtidal soft-bottomed areas on the West Coast from southern Alaska to San Diego. Over the great extent of this range, the waters are apparently too cold for regular natural spawning, and the industry is dependent on regular importation of new spat from Japan. (Hanna 1966) However, in the Georgia Strait region of southern British Columbia, conditions are, for some reason, apparently more favorable, and spawning has occurred on a regular basis for some years. Because of the fact that Crassostrea has a planktonic larval stage, the result has been the spread of the species from the areas of original introduction and culture over a fairly wide area, even to become one of the dominant sessile intertidal invertebrates on some of the protected and secluded rocky shores. (Quayle 1964)

As an epibenthic filter-feeding bivalve in quiet-water situations, C. gigas could concievably be a competitor for food and living space with the native oyster, Ostrea lurida, whose commercial industry it was largely meant to replace. How tight a competitive interaction there is between these two forms is not known, but the writer has found the two species co-occurring and yet both common in areas of southern Puget Sound.

Venerupis japonica (Deshayes)
(= Tapes semidecussata = Paphia philippinarum (Adams and Reeve))

According to Quayle (1964), this small venerid clam was found first on our coast in 1936, in British Columbia, and was initially described as a new species. It had apparently been introduced with Japanese oysters. It has spread very rapidly through the marine waters of Washington, and southward at least as far as Willipa Bay. It is of local importance as an edible clam dug for sport or commercial use in some areas of Washington.

This clam generally inhabits middle intertidal mud and gravel areas in protected waters, and quite often lives intermingled with the rather similar native species, Protothaca staminea. However, it is said to have a wider range of possible habitation in the intertidal than Protothaca, and may slao live somewhat closer to the surface of the substratum. It is also said to be a major food item for some species of diving ducks in the Puget Sound region. (Glide 1964)

As a shallow-infaunal filter-feeder, this species could concievably be a competitor with P. staminea and other lamellibranchs as well for food and living space. This pair of species would be very interesting to study in terms of microhabitat differentiation, character displacement, niche dimension, etc., comparing mixed assemblages with pure assemblages of both species, although it may be that no pure P. staminea any longer occur, at least in Puget Sound. It would, of course, be interesting to determine whether or not the exotic species is indeed taking over, which may possibly be what is happening.

Although these two species are quite often intimately associated in the field, and appear to be quite similar, they seem to remain distinct species, with specimens in the field being able to be claarly assigned to one species or the other. This would seem to be in contrast to Kincaid's observation that the two forms freely interbreed. (Hanna 1966)

Mya arenaria Linnaeus

This clam is generally common in protected waters in mud, gravel, or sandy bottoms, and is perhaps the dominant, and often only, burrowing lamellibranch in brackish situations. It is of local economic importance in our area as a shell-fish dug for personal use. Attempts have been made to dredge the species commercially in northern Puget Sound.

There seems to be a lingering doubt amongst authorities as to whether this species is indeed exotic to our area. Most seem to feel that it was indeed introduced with oysters from the Atlantic Coast into San Franscisco Bay sometime in the 1870's. It was first described as a new species. (Hanna 1966) On the other hand, Canadian workers have described the species from Quaternary deposits in the area of southern British Columbia, a situation that could possibly be due to a mistaken identification. There has apparently been some confusion among workers in eastern Canada as to the distinguishing of fossil M. arenaria from certain fossil forms of the circumboreal M. truncata. (Laursen 1966) The interesting paleobiogeography of M. arenaria will be discussed later on in the paper. It is interesting to note that a very similar, and apparently native form, designated M. arenaria ? oonogai occurs in the waters of Central Japan and Korea. (Habe 1962)

If indeed M. arenaria is an exotic species, it is probably the most successful one that has yet been introduced, in terms of range extension and numbers. It is now reported to range between 37° and 55° N. Lat. on our coast. (Bernard 1970) It could concievably be a competitor for food and space with some of the native clams, yet it alone seems to be able to withstand the more brackish situations, such as at the heads of estuaries. Matthiessen (1960) has also suggested that in Atlantic Coast habitats, M. may be ecologically seperated from Venus mercenaria not only by being more eurytopic but by a difference in diet as well, with M. being more capable of using flagellates than diatoms from the phytoplankton.

Petricola pholadiformis Lamarck

This interesting little clam was first noted on the Pacific Coast in San Francisco Bay in the 1930's, having apparently been introduced from the East Coast with other shell-fish. In our immediate area, it seems to be found only in Willipa Bay, Washington, where it is localized but quite common, burrowing in hard clays in the upper middle intertidal. As the species has a planktonic larval stage, one might expect it to perhaps become more common and widespread. The species has also been introduced to be shores of Britian, where it is now reported to be slowly but steadily increasing its range. (Duval 1962) It can also apparently burrow into a variety of substrates.

This species is interesting in that, although it seems to be rather similar to clams like Protothaca in internal anatomy, morphologically it has assumed a form very similar to that of the pholads. Indeed, in Willipa Bay, the pholads Zirphaea pilsbryi and Penitella penita occur with Petricola, but somewhat lower in the intertidal. It would seem that there could be some sort of competition amoungst these various for food and living space.

Our only native species of the genus seems to be Petricola carditoides, a dweller of the lithome in the intertidal of the semi-exposed open coast.

Batillaria zonalis (Bruguere)

(B. cumingi (Crosse)= B. multiformis (Lischke))

This gastropod has become quite common on many tideflats in the Puget Sound area. It was apparently introduced into the region with Japanese oysters. (Hanna 1966)

The animal is epibenthic, roving slowly over the mud or sand. On mud flats, a certain percentage of the population will be found buried in the substratum. Populations occurring in Elkhorn Slough, California, are said to be feeding primarily on the alga, Enteromorpha. (McLean 1960) Puget Sound populations, on the other hand, seem to be feeding on detritus or microflora to be found on solid objects resting on the substratum.

Little seems to be known concerning the life-cycle of this species. It has been suggested by Quayle (1964) that the rather slow rate of spread of the form would seem to indicate that there is a very short planktonic larval stage, at most.

The animal seems to be well-suited for the particular habitat in which it lives. It is quite eurytopic, being able to withstand long periods of exposure, high temperatures, and wide ranges in salinity. (McLean 1960)

Ocenebra japonica (Dunker)

(= Tritonalia japonica)

This carnivorous gastropod has become common in many oyster-growing areas in Washington, having been introduced from Japan. It has become such an important predator on Crassostrea that several culturing areas in Puget Sound have been abandoned, and regulations requiring the close inspection of imported spat have been enacted. (Hanna 1966)

In the field, the animals are generally found on sòlid objects resting on the substratum in the middle and lower intertidal. However, they are apparently capable of movement across the soft substratum, as well.

This species seems to prey upon its victims in much the manner as do the native species of the genus Thais. As well as preying upon Crassostrea, the animal is also able to attack a number of other organisms. The shells of Venerupis japonica have been found bored in the field, and in aquaria, the species was observed to attack Batillaria, Protothaca, Crepidula, and, perhaps preferentially, Balanus glandula.

Fortunately for oystermen, this species does not have have a planktonic stage in its life cycle. The yellow, grainlike egg-cases, similar to those of Thais, ane common on solid objects on the tideflats in the spring, the young hatching out as miniature adults.

As this species seems to be rather similar in form and habit to the native Thais species, it might be interesting to try to determine if there is really any interactions taking place between the two forms. The writer knows of no situation where the two species co-occur, it is concievable that O. japonica and T. lamellosa might co-occur in some areas in the Puget Sound region.

Crepidula fornicata (Linnaeus)

This species is common is some areas of southern Puget Sound and in Willipa Bay, Washington, into which it was apparently introduced from the Atlantic Coast sometime in the late 1800's. (Hanna 1966) It is generally found attached to solid objects resting on the substratum, or in loose "stacks" of individuals. Specimens brooding egg-masses are common in the spring.

The animal has a rather unusual life-mode for a gastropod, that of a nearly sessile muco-ciliary feeder upon plankton. Thus the species could concievably be a competitor for food as well as space with other epibenthic forms, such as oysters. The species has also been introduced into European waters, where it has become abundant in some areas and a nuisance to oystermen.

Crepidula convexa Say
(= C. glauca Say)

This small slipper shell, native to the Atlantic Coast, is noted by Hanna (1966) to occur only in the San Francisco Bay area. However, the writer has found the species also to occur in northern Puget Sound,(Padilla Bay), and Willipa Bay, Washington.

This species is generally found attached to solid objects in the lower intertidal. It resembles somewhat a small C. fornicata, but never attains a size greater than about a centimeter and a half, and never occurs in stacks of several, nested individuals. In Padilla Bay, Washington, this species seems to occur most commonly on the body-whorl of Batillaria. It is not known whether this is a real association, or merely due to the fact that the snail forms most of the solid substrate to be found on the mudflats in this area.

It seems rather puzzling that this species should be as localized as it seems to be, presuming that it, like C. fornicata, has a planktonic stage in the life-cycle.

Crepidula plana Say

This slipper shell, also a native of the Atlantic Coast, is said to occur in Puget Sound and Willipa Bay, Washington. (Ricketts et al 1968, Hanna 1966) The species is common on commercial oysters in the latter area. It appears very similar to the native species, C. nummaria, which seems to be a form more typical of semi-exposed rocky shores.

Nassarius obsoletus
(= Ilyanassa obsoleta (Say))

This snail, native to the Atlantic Coast, has become common in Willipa Bay, Washington (Hanna 1966), where it dwells on sand, mud, or muddy-gravel flats, in the middle and lower intertidal, crawling about on the surface or just below the surface of the substratum. Although several N. species are native to our area, none seems to occur in Willipa bay to compete with N. obsoletus.

R. S. Scheltema has produced several papers concerning the biology and ecology of this species on the Atlantic Coast in the last decade. According to him, this species, unlike most in the genus, is primarily a herbivore upon microflora and only secondarily a scavenger upon carrion.(Scheltema 1964)

The characteristically spiny egg-capsules of this species have been noted common on oyster shells, eelgrass and other solid objects on the tideflats of Willipa Bay in the spring.

Nassarius fraterculus (Dunker)
(= Retinassa fratercula)

This snail, apparently introduced from Japan with oysters, was first reported on our coast in Padilla Bay, Washington, in 1960,(Duggan 1963), and has become quite common on several tideflat areas in the northern Puget Sound area. (Hanna 1966)

Like many members of the genus, this species is apparently a scavenger and feeder upom carrion. The animal can be found roving freely over the surface of the substratum, buried just beneath the surface, or under solid objects. Egg-cases are common on algae and other solid objects on the tideflats in the late spring.

This species is rather similar to the native species, Nassarius mendicus in form and habit. Both species come close to co-occurring in some areas of northern Puget Sound, but N. mendicus seems to occur in situations of rather clean sand substrates and eelgrass, whereas N. fraterculus seems generally to occur in muddier and perhaps more brackish situations.

N. fraterculus may serve as a food item for some sorts of shore birds, as feces containing the cruched shells of the species have been found in some of those localities where it occurs.

Urosalpinx cinerea (Say)

This carnivorous snail was introduced quite early into Pacific Coast waters, and now occurs in Willipa Bay, southern Puget Sound, and extreme southern British Columbia. (Hanna 1966, Quayle 1964) Quayle reports that the British Cloumbia populations seem to be slowly declining, and are perhaps in a marginal habitat there. Medcof and Thomas (1969) note that U. cinerea is also apparently disappearing from the oyster beds of the St. Lawrence estuary in eastern Canada, and may be in a marginal habitat there as well. The species has also been introduced into European waters, where it is a serious oyster pest in some areas. (Purcheon 1968)

Phytia myosotis (Draparnaud)
Cecina manchurica A. Adams

These two high-intertidal dwelling snails have become quite common in some areas of northern Washington. P. myosotis was first noted in California waters in the latter 1800's, having apparently been introduced from the Atlantic Coast. C. manchurica was first noted in 1961, having apparently been introduced from Asian waters. The two species apparently quite often co-occur in our area, and can be found under beach-drift, rocks, and other debris high on the beach in protected waters. They also occur in Willipa Bay, Washington (Hanna 1966), and the writer has noted P. myosotis to occur under rocks in the Salicornia zone on South Slough at the Charleston Bridge, in Coos Bay. MacDonald (1968, 1969) also noted the species in Pony Slough as well.

Corbicula fluminea (Müller)

Although not strictly a marine organism, this brackish- and freshwater-clam, native to eastern Asia and first noted in this country near the mouth of the Columbia River in 1938, has become abundant to the point of being a pest in many river drainages and irrigation projects in the western United States and in the western part of the Appalachians. (Hanna 1966)

In a study of the form in the Tennessee River, Sinclair and Isom (1963) have noted that the animal is of rather general substrate preference, and can tolerate marked fluctuations in water quality. They are apparently a food item for various fishes in the Tennessee and Columbia Rivers, and in East Asia are of commercial importance as human food. They may also serve as a food source for some birds or mammals along the lower Columbia River as well, as piles of their broken shells can be found on the river banks and drift logs in that area.

There are several other introduced species of marine mollusks known from the waters of Washington and Oregon, but with which the writer is not familiar and concerning which there is not much information available. The tideflat mussel <u>Modiolus senhousi</u>, native to Japan, is said to be common in some bays in the northern Puget Sound area. (Hanna 1966, Ricketts etal 1968) The shipworm, <u>Teredo navalis</u>, occurs in Willipa Bay and southern British Columbia, according to Quayle (1964). The small clam, <u>Gemma gemma</u>, native to the Atlantic Coast, is said to range from San Diego to Puget Sound.(Hanna 1966) Unfortunately this species probably rather closely resembles the native species, <u>Transenella tantilla</u>, and the writer has not yet been able to find suitable descriptions or illustrations by which to distinguish the two forms.

Although this paper deals solely with exotic mollusks to be found in our area, it might be well to point that a number of other types of animals have been able to establish themselves in our Pacific Coast waters as well. Several arthropods, a tunicate, and even an alga have been introduced and established. (Ricketts et al 1968, Scagel 1956)

It should also be pointed out that for all the species that have become established, there are probably a good many more that were introduced into our waters, but which, for some reason were unable to survive. Hanna (1966) gives long lists of molluscan species that have been found in specific shipments of shell-fish destined for introduction into Pacific Coast waters, only a few of which turn out to be well-known, established exotic species. No sources go into detail concerning the exact process by which a species happens to find itself introduced, but presumably those life-support measures that are taken to keep oysters and spat in good health during transit would also serve to keep any other stow-away organisms viable as well.

Discussion

As the exotic marine mollusks found in our waters are almost all dwellers of protected bays and estuaries, it might be well for one to discuss briefly some of the general characteristics of the estuarine environment, and its possible effects on the biota. I found Lauff (1967) and the chapter by Emery, Stevenson and Hedgpeth in Hedgpeth (1957) very useful in terms of general information on this subject.

An estuary is a very unique sort of aquatic habitat. Being the region of intermingling of purely marine and freshwaters, the estuary is generally looked upon as a distinct region, in terms of the biota present and the environmental factors to which they are exposed. From the standpoint of purely physical environmental factors, the estuary would appear to be a rather rigorous habitat. In estuaries, salinity can fluctuate greatly with the cycle of the tide and year. Sedimentation is usually rapid, and the production of large intertidal flats creates an environment exposed for long periods of time to the vicissitudes of the terrestrial environment; sun, wind and desiccation, and temperature. Often, these wide tideflats, being of very gradual slope and of fine-grained sediments, are poorly drained and oxygenated at depth, so that anaerobic conditions may exist up to very near the surface of the substratum. All of these are stresses to be faced by any prospective estuarine organism.

Although the physical conditions to which an estuarine organism is exposed are relatively extreme, the potential for productivity and an ample food source for a variety of organisms is quite high, as the estuary seems to be benefited by a good supply of nutrients from a number of sources. Although the waters of estuaries are often rather turbid, due to river runoff and turbulence, it should be pointed out that this very runoff, along with the fact that the entire bottom of an estuary is often in the photic zone due to the shallowness of the water, contributes greatly to the potential productivity of the estuary. Along with the nutrient materials brought into the estuary from the terrestrial hinterlands by streams, the broad, protected expanses of tideflats characteristic of such situations seem to be a suitable habitat for benthic plants of all sorts, from diatoms and algae on up to the rooted, aquatic angiosperms such as <u>Zostera</u>, all of which are capable of fixing an enormous amount of carbon, converting it to a form that can be used by the higher trophic levels of organisms, both is the living and detrital form. The higher tidal marshes, with their dense stands of plants, may be equally important in providing nutrients for the estuarine community.

The biota of estuaries can generally be characterized by relatively low diversity, high numbers, and greater or lesser developement of eurytopism. (Emery et al in Hedgpeth 1957) Tolerance of a wide range of environmental conditions would obviously be advantageous for a prospective estuarine organism, based on what was said earlier concerning the physical condition to be found there. Many diff rent and interesting methods for survival in the estuary, and in soft-bottom habitats in gener l have been described.

There are probably several reasons why estuaries do, in fact have a low biotic diversity. That this should be so might seem rather puzzling at first, for it would seem that through geologic time, as long as there has been land and sea, there should have been estuaries. One might think that over this length of time, the biotic reserviors of the land, sea, and fresh-watees would have stocked the estuaries with fully as many species as are found in other habitats.

It may be that the harshness and fluctuations in physical factors in the estuarine environoment are simply and basically too marked for more than a mere handful of organisms to have adapted to, even over the long history of life. These organisms may have either evolved and adapted their way into the estuary in order to exploit the relatively unused resources to be found there, or they may have, in effect, retreated into the estuary in the face of species interactions taking place in adjacent habitats.

In many places in the world, estuarine habitats are of rather discontinuous distribution, such as on the Oregon Coast, where the several river estuaries are seperated by greater or lesser distances of fully marine, exposed coast conditions. These conditions would not seem to be well suited for the survival of organisms adapted to an estuarine existence. Thus given the conditions of wide variation in physical factors, plus semi-isolation, one could concieve of "catastrophes" in the marine environment, conditions which might produce mass mortalities or local extinctions. If this were to happen, effected estuaries might no be repopulated for some time. Climatic changes, for example, could cause extinctions of existing populations, and repopulation would require either larval recruitment from distant uneffected areas, ar a re-evolution and adaptation of new estuarine forms in situ. Until one or the other of these happened, the resources that remained in the effected estuaries would lie unexploited.

Estuaries are looked upon by some as an intermediate seral stage in the successional sequence between a shallow-water marine environment in an area of rapid sedimentation, and a low-lying terrestrial environment. The process of natural "reclamation" of marine tideflats into semi-terrestrial environments by the plants comprising salt-marsh floras can be seen in most estuaries. Thus it would seem that estuaries are probably fairly transient phenomena, viewed over geologic time. Such transience would not seem to promote the evolution of a very complex marine community in any particular locality. In any case, the fact that a transition from a marine situation to a terrestrial one involves such steep gradients in terms of physical factors and physiological requirements, it would seem that this sea-to-land successional sequence is not immediately comparable to the standard terrestrial successional sequences, in terms of changes in diversity, etc.

Considering the fauna of an estuary, larval behavior is very important in the manitainence of populations. As pointed out by Quayle (1964), the larvae and larval portions of the life-cycle of an estuarine organism are constantly being acted upon by two opposing tendencies; the tendency to concentrate versus the tendency to disperse. There are clear advantages to both, and the survival of an estuarine organism may depend upon the relative emphasis that is placed on each in its energetic strategy. Clearly the patchy distribution of the estuarine habitat over space makes the ability to concentrate and "conserve" larvae in the proper areas advantageous, and yet, because of the transience of any particular estuarine situation and the chances of mortality through large fluctuations in environmental factors, it is also clearly advantageous to have some sort of means of dispersal over space as well.

Carriker, (in Lauff 1967), discusses various means by which the larvae of estuarine organisms might be retained in the estuary. It seems, for example, that for organisms such as *Venus*, spawning is somehow timed to occur at low tide, during neap tides, and during the summer, all conditions which would minimize the loss of larvae through the seaward end of an estuary. It has also been found for such organisms as *Crassostrea* and *Balanus*, the developing larvae use the natural circulation of the estuary to stay within it. As the larvae mature, they drop toward the bottom and are transported up the estuary by the landward bottom drift, a characteristic of many sufficiently un-mixed estuaries. Thus the larvae are retained in the estuary, and often transported even farther landward than their parents. Carriker goes on to state that there may be a natural selection for more extreme eurytopy in larvae than is eventually experienced in adult stages, to allow the larvae to be able to disperse from one estuary to another through the intervening, more oceanic conditions that often occur. The problem of over-dispersal is, of course, greatly reduced in those species which lack a planktonic larval stage in their life-cycle. These species, including the carnivorous gastropods *Ocenebra* and *Urosalpinx*, have apparently chosen an energetic strategy whereby larvae are concentrated around the immediate habitat of the adults, perhaps in response to the rather patchy distribution that the potential prey items, mainly epibenthic forms such as oysters, might assume in the mostly soft-bottomed estuary. Those forms with planktonic larvae seem to be themselves mostly plankton-feeders, and thus have a food source that is of as general a distribution in an estuary as the water upon which it is borne. Forms with non-planktonic larvae, such as the carnivorous snails mentioned earlier, prey on food items that might not be of so general an occurence in the estuarine habitat. Also, for these forms, just as their dispersal methods are limited, so ~~are~~ is their ability to colonize and recolonize habitats in the time sense.

Given the physical and biotic factors influencing life in bays and estuaries, of how much significance might be a study of introduced species in these environments?

The introduction of organisms into new environments can be concieved of as large scale experiments in evolution, as C. H. Waddington points out in Stebbins (1965). With the introduction of an exotic species into an alien environment, one is both blessed with having a natural system within which to study, and cursed by the fact that often the natural system into which the species was introduced is probably not perfectly known in the first place, so that any observations made of effects on the system are of somewhat less value.

Unfortunately, the "experiment" of introducing exotic mollusks into our waters has been a rather sloppy one at best. It would have been desirable to know what was being introduced where, at what time and in what amounts under what conditions, but unfortunately, this is never fully known. Full knowledge and accurate records of the movements of even the commercially important species are either non-existent or inaccessible in many cases. As a result, the important initial stages of colonization of these exotic species in our native habitats will probably never be known, most of the exotic mollusks having been noticed only after they had become well-naturalized.

As interesting as this information might have been to have, it is by no means all that one might find useful from a study of our introduced species. As the naturalized populations are wholly cut off from the main body of the population of the species in its native habitat, there is a myriad of interesting studies that might be attempted concerning the structure and genetics of out-lying populations, using these naturalized populations of exotics, many of which are still fairly discrete units in the native environment, spatially. Observations might be made of the rapidity of race formation, the divergence upon isolation that is said to lead the way to speciation, or on the phenomenon of phenotypic and physiological plasticity in the face of a unfamiliar set of environmental conditions. For many of our exotic species, nearly a hundred years have elapsed since the first populations became naturalized. This may have been enough time for our populations to have diverged enough so that some useful observations of these sorts could be made.

As was hinted at throughout the discussion of specific exotic mollusks to be found in our waters, there seems to be a good deal of potentially valuable work that could be done in studies of the ecological ramifications of the establishment of these species in our marine environments. That these species have, in many cases, succeeded to such an amazing degree, and have spread so rapidly through the native suitable habitats is part of the reason why I chose this particular topic for my work, and I will now set down some of my own ideas as to why this should have happened.

In the over-all view of our naturalized exotic mollusks, one comes to the conclusion that in the majority of cases the exotic species are occupying niches in the native ecosystem that were previously unoccupied or unexploited, for some reason. At the risk of being overly simplistic, I will, for my present purposes, define "niche" simply as a potential functional role that can be assumed by an organism in the community. Some might also argue against using the the term "community" to describe our soft-bottom, quiet-water marine biotic assemblages, however I feel that there must be some significance to the general similarity between assemblages of organisms from similar physical habitats at similar latitudes. Although the estuary is probably mostly aptly described as a physically-controlled situation, there are indeed species interactions occuring, and I feel that these are often well-defined and specific enough to allow the assemblage to indeed be termed a community, the biotic whole being greater than the mere sum of the parts.

Be this as it may, perhaps some more concrete examples of what appear to have been previously unfilled niches are in order. For example, the native estuarine fauna of Washington and Oregon seems to include few gastropods other than opisthobranchs, with some naticids occuring in more saline situations, along with one nassariid, and the upper intertidal littorines. Thus have such species as Batillaria, Nassarius fraterculus, and N. obsoletus been able to establish themselves in the middle and lower intertidal, and Phytia and Cecina in the upper interidal. Interestingly, Southern California waters have a snail, Cerithidea californica, which is quite similar to Batillaria in form and habit. (McLean 1960, Ricketts et al 1968, MacDonald 1969, Warme 1971) These two species seem to overlap in range in the San Francisco Bay region, and it would be of prime interest to see the degree to which they might competitvely interact. So far no information concerning this has been published, to the best of my knowledge. In his short section on ecological equivalents, MacDonald (1969) also suggests that the snail Phytia is ecologically replaced in southern California by the snail, Melampus olivaceus.

For another example, the native estuarine biota of the Pacific Northwest seems to have no widespread muco-ciliary-feeding gastropods, such as Crepidula. Thus have the exotic species, C. fornicata, C. convexa, and C. plana become established in many areas. It should be noted, however, that the small calyptraeid gastropod, Crepipatella lingulata, co-occurs in some areas of Puget Sound with Crepidula fornicata, although it can also be found onerocky shores both in Puget Sound and on the exposed, outer coast. In any event, Southern California waters seem to have an ecological equivalent in the species Crepidula onyx, which seems to adopt a life-mode very similar to that of the exotic species. (MacGinitie and MacGinitie 1968, Ricketts et al 1968) It is not known whether or not there are any localities where the native and exotic species co-occur.

The above examples seem to indicate that unfilled niches, unexploited modes of life, do indeed occur in the soft-bottom quiet-water and estuarine habitats of Washington and Oregon. There are several possible explanations for this. For example it is concievable that, although the physical environmental stimuli might have been comparable over the North Temperate zone, the lines of evolution and adaptation which led to the estuarine communities of the various coasts have not been exactly parallel and perfectly analogous. Thus, due perhaps to chance biological events or perhaps slightly different external stimuli, each semi-isolated region of the North Temperate zone came to have its own somewhat distinct estuarine fauna. Given this situation, the introduction of elements of one or several of these faunas into some suitable region, already possessing its own fauna, could concievably result in the naturalization of some of the exotic elements, which, for some reason had no analogous forms evolve in the native fauna. Thus might a new "hybrid" estuarine biota, with a contingent of exotic species, and thus presumably of greater complexity and perhaps stability, become established.

The presence of obviously unfilled ecological roles in the estuaries of the Pacific Northwest may also be, in part, a reflection of a lack of time for them to have been ~~resqlon-~~ recolon-ized after the marked climatological events of the Pleistocene.

There may be some evidence for this in the recolonization of northern temperate waters by *Mya arenaria* that has taken place in the last few centuries. From the fossil record of the Pleistocene, it can be shown that *M. arenaria* occurred in both European and North American waters during the last warm interglacial period. When the glaciers advanced the last time, *Mya* was exterminated in the more northerly parts of its range, and became extinct in Europe. When the glaciers then retreated, the habitat that *Mya* had formerly occupied remained unfilled, with no source of recruitment being within the range of dispersal of the larvae, and evolutionary rates being so slow that no new species ~~appeared~~ appeared to fill the niche *in situ*. Thus when *M. arenaria*, relatively unchanged from the Pleistocene, was reintroduced into European waters in the 1500's, it was able to quickly take hold become established, perhaps simply refilling the empty niche that it had just recently occupied, geologically speaking. The species is now known from northern Norway to the Black Sea in European waters. (Foster 1946) As for the species's rapid spread along our coast, assuming it is exotic, it is concievable that an analogous situation occurred in the Pacific, with the species being exterminated on the eastern side of the ocean basin, but being able to survive the glaciation on the western side, although, of course, the initial introduced populations were of Atlantic rather than Pacific origin.

In further reference to the paleobiogeography of the Pacific Coast, Valentine (1961) has attempted to work out the climatic conditions of the Pleistocene of California by studying the molluscan faunas preserved in the many raised-beach deposits to be found in that area, the great majority of which contain assemblages which are composed of species~~, the great majority of which are still~~ still to be found in our waters. This is a very fortuitous circumstance for the paleoecologist, and makes uniformitarian inferences a good deal easier to make. Thus Valentine's study is probably a fairly good account of the Pleistocene events in California, an area that was somewhat south of the main continental ice-sheets. Although raised-beach deposits also occur in Washington and Oregon, there seems to have been no attempt to study them in a similar light, to work out details of the Pleistocene climate and biogeography of our area. Such a study would be useful in determining to what extent the molluscan faunas of our estuaries were modiefied or denuded in the Pleistocene advances of the glaciers. If such a denudation did in fact occur, it is concievable that the dispersal mechanisms and evolutionary rates of the surviving native fauna has not been sufficient to fully recolonize the estuaries of our area, given our regimes of climate, geography and selective pressures. However, I would perhaps hesitate to use a denudation theory in explaining the degree to which exotic species have been able to establish themselves in relatively unglaciated areas, sutch as San Francisco Bay.

Whatever the agency of naturalization, it is apparent that the establishment of exotic marine mollusks has substantially increased the diversity in many bays and estuaries of the West Coast, and in some areas, the molluscan fauna may be dominated by exotic forms. Due to the great dispersal capabilities of some of these species, there may no such areas in Washiington or Oregon that are populated by only native species. As these exotic species increase the diversity and food-web complexity of the estuary, it would seem that they might also be contributing to a greater degree of stability in the estuarine community. (Margalef 1969) Some species, such as the oysters, add an element of structural or topographic complexity to the otherwise rather homogeneous tideflat, and thus provide an abundant source of solid substrate for other epibenthic organisms, and thus affording a still greater increase in biotic diversity. I believe that the further study of marine communities with contingents of established exotic species will shed a good deal more light on the structure and behavior of communities in general, as well as their component parts, and can be used to note changes that take place with changes in diversity and the level of interspecific interactions. As yet, there seems to have been little work done in this direction with respect to marine communities, although terrestrial situations of this kind seem to have been studied for some time.

Summary

A significant number of species of marine mollusks native to Japan and the Atlantic Coast of the United States have become established in the bays and estuaries of Washington and Oregon in the last century, for the most part due to the process of establishing and maintaining the local oyster industry. The establishment of such forms would seem to afford an opportunity to study the mechanics of colonization of new habitats by organisms, speciation and the genetics of isolated populations, and perhaps to study something of the structure and maintainence of the estuarine biocoenose in our area, as well.

The following exotic mollusks have become at least locally naturalized to some areas in the marine environment of the

Pacific Northwest: from the Atlantic Coast; *Mya arenaria*, *Petricola pholadiformis*, *Gemma gemma*, *Teredo navalis*, *Crepidula fornicata*, *C. convexa*, *C. plana*, *Nassarius obsoletus*, *Urosalpinx cinerea*, and *Phytia myosotis*; from the Eastern Pacific region: *Crassostrea gigas*, *Venerupis japonica*, *Corbicula fluminea*, *Modiolus senhousei*, *Batillaria zonalis*, *Ocenebra japonica*, *Nassarius fraterculus*, and *Cecina manchurica*.

The establishment of such a variety of forms seems to demonstrate the presence of many empty ecological niches in the estuaries of the Pacific Coast of North America. This situation may be due to the stresses and transience of the general estuarine habitat, The relative biogeographical isolation of our particular area, or the low rate of evolution and recolonization of the estuaries after the rigors of the Pleistocene glaciations.

References and Literature Cited

Bernard, F. R., 1970, A Distributional Checklist of the Marine Mollusks of British Columbia, Based on Faunistic Surveys since 1950, Syesis, vol. 3, pp. 75-95.

Duggan, E. P., 1963, Report of Non-indigenous Marine Shells Collected in the State of Washington, Veliger, vol. 6 (2), p. 112.

Duval, D. M., 1962, The Biology of Petricola pholadiformis Lamarck (Lamellibranchia; Petricolidae), Proc. of the Malacological Soc. of London, vol. 35: (2), p. 89f.

Foster, R. W., 1946, The Genus Mya in the W. Atlantic, Johnsonia, vol. 2:(20).

Galtsoff, P. S., Introduction of Japanese Oysters into the United States, U. S. Fish and Wildlife Service, Circular 12, 1932.

Glide, J. B., 1964, The Effect of Scoter Duck Predation on a Clam Population in Dabob Bay, Washington, Proc. of the Nat'l Shellfisheries Assoc., vol. 55, pp. 73-86.

Green, J., 1968, The Biology of Estuarine @nimals, 401 pp., U. of Wash. Press, Seattle and London.

Griffith, L. M., 1967, The Intertidal Univalves of British Columbia, B. C. Prov. Mus. Handbook 26, 101 pp.

Habe, T., 1962, Shells of the Western Pacific in Color, Vol. I, Hoikushu, Osaka.

Hall, C. A., 1964, Shallow-Water Marine Climates and Molluscan Provinces, Ecology, vol. 45: (2), pp.226-234.

Hanna, G. D., 1939, Exotic Mollusca in California, Cal. Dept. of Agri., Bull. 28; pp. 300-321.

__________, 1966, Introduced Mollusks of Western North America, Cal. Acad. of Sci., Occasional Pap. 48, 108 pp.

Hedgpeth, J. W., (ed.), 1957, Treatise on Marine Ecology and Paleoecology, Vol. I, Ecology, Mem. 67, Geol. Soc. of Amer., 1296 pp.

Hyman L. H., 1967, The Invertebrates, Vol. VI, Mollusca I, 792 pp., McGraw-Hill.

Lauff, G. H., (ed.), 1967, Estuaries, Amer. Assoc. Adv. Sci., Pub. 83, 757 pp.

Laursen, D., 1966, The Genus Mya in the Arctic Region, Malacologia, vol. 3: (3), pp. 399-418.

Lindsay, C. E., 1961, Pesticide Tests in the Marine Environment in the State of Washington, Proc. Nat'l. Shell. Assoc., Vol. 52, p87f.

McLean, J. H., 1960, Batillaria Cumingi, Introduced Cerithiid in Elkhorn Slough, Veliger, vol. 2: (3), pp. 61-63.

MacDonald, K. B., 1968, Molluscan Faunas of Pacific Coast Salt Marshes and Tidal Creeks, Veliger, vol. 11: (4), pp. 399-405.

_______________, 1969, Quantitative Studies of Salt Marsh Molluscan Faunas from the North American Pacific Coast, Ecol. Monog., vol. 39: (1), pp. 33-60.

MacGinitie, G. E., 1935, Ecological Aspects of a California Marine Estuary, Amer. Midl. Nat. vol. 16: (5), pp. 629-765.

_______________, and N. MacGinitie, 1968, Natural History of Marine Animals, 473 pp., 2nd. ed., McGraw-Hill.

Margalef, R., 1969, Diversity and Stability; A Practical Proposal and a Model of Interdependence, in Brookhaven Symposia in Biology, no. 22, Diversity and Stability in Ecological Systems, pp. 25-37.

Marriage, L. D., 1958, The Bay Clams of Oregon, Fish. Comm. of Ore., Ed. Bull. no. 2.

Matthiessen, G. C., 1960, Obeervations on the Ecology of the Soft Clam, Mya Arenaria, in a Salt Pond, Limnology and Oceanography, vol. 5: (3), pp. 291-300.

Medcof, J. C., and M. L. H. Thomas, 1969, Canadian Atlantic Oyster Drill, Distribution and Industrial Importance, Canada Fisheries Resch. Brd. Journ., vol. 26: (5), pp. 1121-1131.

Miller, R. S., 1969, Competition and Species Diversity, in Brookhaven Symposia in Biology, no. 22, pp. 63-70.

Packard, E. L., 1918, Molluscan Fauna from San Francisco Bay, U. of Cal., Pub. in Zoo., vol. 14: (1), pp 199-452.

Preston, F. W., 1969, Diversity and Stability in the Biological World, in Brookhaven Symposia in Biology, no. 22, pp. 1-12.

Purcheon, R. D., 1968, The Biology of the Mollusca, 560 pp., Pergamon.

Quayle, D. B., 1964, Distribution of Introduced Marine Mollusca in British Columbia Waters, Journn. Fish. Resch. Brd. of Canada, vol. 21; (5), pp. 1155-1181.

_______________, 1970, The Intertidal Bivalves of British Columbia, B. C. Prov. Mus. Handbook no. ~~10~~ 17, 104 pp.

Ricketts, E. F., J. Calvin, and J. W. Hedgepeth, 1968, Between Pacific Tides, 614 pp., 4th. ed., Stanford U. Press.

Sanders, H. L., 1969, Benthic Marine Diversity and the Stability-Time Hypothesis, in Brookhaven Symposia in Biology, no. 22, pp. 71-81.

Scagel, R. F., 1956, Introduction of a Japanese Alga, Sargassum muticum, into the N. E. Pacific, Wash. Dept. of Fish., Resch. Papers, vol. 1: (4).

Scheltema, R. S., 1961, Metamorphosis of the Veliger Larva of Nassarius obsoletus (Gastropoda) in Response to Bottom Sediment, Contrib. 1132, Coll. Reprts. 1961, Woods Hole Ocean. Inst.

______________, 1964, Feeding Habits and Growth in the Mud-Snail, Nassarius obsoletus, Chesapeake Sci. vol. 5: (4), pp. 161-166.

______________, 1965, The Relationship of Salinity to Larval Survival and Developement in Nassarius Obsoletus (Gastropoda), Biol. Bull., vol. 129: (2), pp. 340-354.

______________, 1967, The Relationship of Temperature to Larval Developement of Nassarius Obsoletus (Gastropoda), Biol. Bull., vol. 132: (2), pp. 253-265.

Sinclair, R. M., and W. G. Isom, 1963, Further Studies of the Introduced Asiatic Clam Corbicula in Tennessee, Tenn. Stream Poll. Contr. Bd., Tenn. Bept. of Pub. Health.

Stebbins, G. L., (ed.), 1965, The Genetics of Colonizing Species, Proc. of the 1st. Internat'l Union of Biol. Sci. Symp. on Gen. Biol., 588pp., Academic Press.

Valentine, J. W., 1961, Paleoecologic Molluscan Geography of the California Pleistocene, U. of Cal., Pub. Geol. Sci., vol. 34; (97), pp. 309-442.

Warme, J. E., 1971, Paleoecological Aspects of a Modern Coastal Lagoon, U. of Cal. Pub. in Geol. Sci., Vol. 87.

Wilson, E. O., 1969, The Species Equilibrium, in Brookhaven Symposia in Biology, no. 22, pp. 38-47.