FACTORS CONTROLLING MARINE INVASION INTO FLORIDA FRESH WATERS

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ABSTRACT

Survey of the pattern of chlorinity and inland distribution of marine organisms in Florida suggests that Pleistocene sea level changes have been responsible for extensive areas of oligohaline water (100-1000 ppm Cl) and nearly oligohaline water (25—100 ppm Cl) on the peninsula accompanied by extensive invasions of blue crabs and marine fish. Transplantation experiments in nature indicate that sodium chloride in the oligohaline concentration range is important to survival. These experiments and a series of natural experiments support the idea that oligohaline waters and distance from brackish water determine the distribution of blue crabs and other marine forms in fresh water. The range and extent of osmoregulation for the blue crab is shown by blood analyses to account for their ability to make inland invasions. Evidence exists supporting the idea that oligohaline waters of the world are zones of evolutionary adaptive exchange between fresh and salt water. Such waters occur on porous land below 25 ft. elevation, in volcanic areas, and in arid regions with outlets to the sea.

In the unique and varied waters of the Florida penninsula a combination of geological circumstances has produced an unusual distribution of salt and extensive invasions of fresh waters by marine fish and crabs. These two phenomena seem to be related. Because of the geochemical distribution of the chlorides in the sediments an extensive series of lakes and streams exists which are not brackish but can hardly be classed as typically fresh either. These waters with chlorinities between .1 and 1 part per thousand (100 to 1000 ppm or .5 to 5% of full sea water) are best termed oligohaline as named by Redeke in 1922 (Hedgpeth, 1951). These waters lack the sharp fluctuations of estuarine waters. A study of these patterns in relation to the physiology of marine animals suggests new ways of considering how marine organisms are distributed inland and how the evolution of adaptations to aquatic environments has occurred.

GEOCHEMISTRY OF SALT IN FLORIDA FRESH WATERS

Normally, the sodium chloride content of fresh waters is small, the chlorinity ranging from one to 10 parts per million. This chloride content is primarily the chloride content of the rain and decreases markedly with distance from the sea (Clarke, 1924). Many authors have found varying chlorinities of this magnitude in rains of different types and in different areas. Larger chloride contents are found in natural waters under the following circumstances:

First, if the water passes over strata containing salt deposits or if it receives ground water contribution derived from salt laden strata, a much higher salt concentration may occur.

Second, water receiving components from volcanic areas especially those containing hot springs may contain high salt content.

Third, the concentration of waters by evaporation in the closed basins of arid regions and to some extent in the lower reaches of rivers in semi-arid areas may produce high salt contents. The ocean is a case of accumulation of salt in a closed basin.

Fourth, some chloride may be added to natural waters by pollution from sewage or industrial wastes.

Examples of these circumstances and summary of knowledge on the geochemistry of chlorine are available in Rankama and Sahama (1950).

In Florida it is primarily the salt deposits held in the sediments which have produced a pattern of high chlorinity in the fresh waters. Geologically, Florida is a dome of Tertiary sediments, mostly limestone, which is flat and scarcely elevated above the sea. The relative absence of impermeable strata has permitted extensive artesian aquifers to develop that cut across the formations of different age. The whole peninsula behaves like a sponge in which water is poured on top and flows out the sides through springs and ground water flow into the surface streams. Recent studies by Ferguson, Lingham, Love, and Vernon (1947), Cooper and Stringfield (1950), Black, Brown, and Pearce (1953) have established much about the nature and behavior of Florida ground waters.

Figure 1 is a simplified elevation may of Florida with 20, 50 and 100 ft. contours drawn. The areas below 20 feet in elevation are shown with wave-like shading to emphasize their position. There is abundant evidence (Flint, 1947) that at times in the late Pleistocene during warmer times the ocean level has been higher than at present. A distinct strand line about 25 ft. above present sea level is known as the Suffolk scarp and is marked by sand dunes known as the Pamlico formation. The 20 ft. contour line in Figure 1 corresponds roughly to a map of the Pamlico shore line by Cooke (1945).

Under conditions thus estimated to exist in the late Pleistocene, marine seas would have existed in the wave-like shaded areas of

FIGURE 1. Topographic map of peninsular Florida showing 20 ft., 50 ft., and 100 ft. contours. The area with wave-like horizontal shading below 20 ft. in altitude was submerged in Pamlico times and now tends to have higher chlorinities and marine invasion.

Figure 1 and the porous sediments beneath would have become infiltrated with salt water.[1]

At present fresh water extends downward in central Florida several thousand feet since a foot of fresh water above sea level can support a displacement of the salt water—fresh water boundary downward 40 feet according to the Ghyben-Herzberg approximation. Under the

[1]A suggestion made at the Fla. Acad. of Sci. meeting in 1951, at Amer. Soc. of Limn. and Ocean. meeting in 1952 but independently by Black, Brown and Pearce (1953).

circumstances shown in Figure 1 there could neither be fresh water in the sediments below the salt water sea areas nor artesian outflows that could wash out salt deposits already existing in the buried sediments.

Cooper and Springfield (1950) published a map showing the present distribution of salt in the ground waters in Florida. The areas of ground water salt greater than 100 ppm correspond almost exactly to the low areas of the peninsula shown as submerged in Figure 1. This suggests that the high salt content of the ground waters has relatively recently been left in the sediments perhaps during Pamlico time. The area of salty ground water cannot have been long raised and still contain salty ground water, for cores do not show corresponding reservoir beds of salt or evaporite deposits of arid climate in the recent rocks which underlie these salty areas. Furthermore the distribution of this salty water does not correspond to geological formations. The lack of extensive salt inside of the 20 foot contour suggests that a considerable time lapse occurred between times of higher sea levels and the time of the Suffolk Scarp.

The salt is working out at a rapid rate and the following calculation suggests that the rate of flushing out of salt is consistent with a hypothesis of Pleistocene salt deposition.

From a drainage basin of about 3000 square miles of the St. Johns river, the average runoff is 14.0 inches. If the runoff is assumed to contain in addition to cyclic salt 100 ppm chloride, a reasonable minimum value as shown in Figure 2, then 3.5 grams chloride per square centimeter per 1000 years is found to be flushed out of the area. If the pore spaces in the mainly limestone sediments are assumed to be 1% as a lower extreme and if these spaces are assumed to have been permeated with salt with a chlorinity of 19 parts per thousand, then 610 ft. of sediments would be flushed out on the average every 1000 years. For a porosity of 10%, 61 feet would be flushed out. Possibly the correct value for relatively unconsolidated limestones lies in between (Imbt, 1950). If porosities are higher, correspondingly longer times are required to remove the salt.

The water being flushed out has its ions in ratios different from those of sea water. As pointed out by Matson and Sanford in 1913 (Black, Brown, and Pearce, 1953), there is a higher calcium concentration than magnesium concentration which can be accounted for by an hypothesis of dilution of the original salts and solution of additional calcium. Similarly the strontium: calcium ratio is lower than in sea water. Six unpublished analyses by Odum and Parrish indicate that there is a lower B/C1 ratio than in sea water thus suggesting that there have been other types of modifications. Black, Brown, and Pearce (1935) in their detailed account of salt water intrusion have made a careful analysis of ionic ratios in Florida ground waters. They call the ground waters with lower salinities than sea water "residual" using the name "connate" for water supposedly originally trapped and of higher salinity than sea water. But it seems possible that the presence of higher salinities than sea water may be associated with definite crystalline salt deposits or depositions under conditions of higher salinity than now exist in or around Florida. These higher salinity waters are mostly in deep or non-artesion strata and do not affect the surface pattern of oligohaline waters. The concentration of ground water salt should be helpful in constructing a paleo-climatic scale for the excess of precipitation over evaporation.

250 new analyses of chloride by the Mohr method in Florida surface waters made during summer 1952 have been combined with 230 analyses summarized from the literature by Black and Brown (1950) as the data upon which Figure 2 is based. Black Laboratories, Gainesville, Fla. and E. Chamberlain, Fla. Game and Fresh Water Fish Commission have other C1 data not used here. Because of limitations of space the raw data and the maps by river systems with the plotted chloride figures are not included but are filed and catalogued in the Dept. of Biology library, Univ. of Florida, Gainesville, Florida. By river systems this C1 data is summarized briefly as follows:

The St. Johns River at its headwaters has 31 ppm increasing to between 150 and 200 ppm between Lake Washington and Lake Harney becoming 227 ppm in Lake Monroe, 98 ppm just south of Lake George,. 100-200 ppm northward to Palatka being less than 300 ppm to Jacksonville at times with values to 900 ppm at other times at Green Cove Springs and northward. Tributaries from the west off higher ground have chlorides less than 12 ppm such as the Oklawaha (except values of 50 ppm in lower east west section), Black Creek, and the Econlochatchee. The most extensive marine invasions occur in the St. Johns system apparently due to the salty springs which add salt such as Salt Springs, Silver Glen Springs, Ponce De Leon Springs of Volusia Co., Blue Springs at Orange City, Alexander Springs, and many salty artesian wells. For locations see Ferguson, Lingham, Love, and Vernon (1947).

The south Florida canals leading out of Lake Okeechobee have about 35 to 100 ppm Cl. The rainwater of the central Tamiami Canal is lower being 13 ppm. Cl running north from the town of Everglades in the Rt. 29 canal decreases to 945 ppm at Rt. 41 junction, 116 ppm 4 miles north of this and 38 ppm 10 miles north of the junction. Lake Okeechobee varies 16 to 60 ppm as do the main

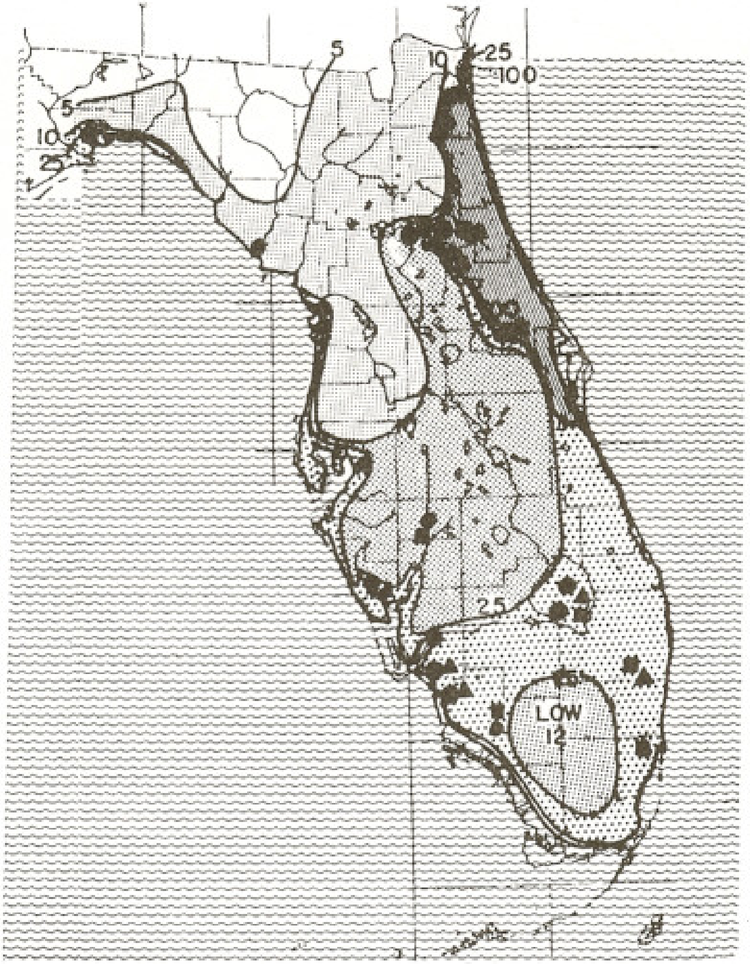

FIGURE 2. Surface chlorinities in lakes, streams, and canals given in parts per million. Somewhat smoothed isochlor lines (5, 10, 25, 100, and 1000 ppm) are drawn on the basis of 480 analyses scattered over Florida: Small stippling, 5—10 ppm; medium stippling, 10-25 ppm; large stippling, 25—100 ppm; vertical hatching, 100—1000 ppm; horizontal wavy shading, greater than 1000 ppm. Places of marine invasion are indicated for 4 indicator species: Blue crabs, solid circles; snook, squares; tarpon, triangles; sting ray, dot in circle.

outflows through the St. Lucie canal and the Caloosahatchee River Estero and Imperial Rivers south of Ft. Meyers have more than 1000 ppm apparently of ground water origin. The drainage into Lake Okeechobee from the north through the Kissimmee, Indian Prairie Canal and Fish Eating Creeks has less than 23 ppm.

The Peace River system is low in Cl generally 16 ppm or less. The small rivers with mouths on Tampa bay are less than 12 ppm in headwaters increasing to 30 ppm 5 to 10 miles from the mouth. The Withlacoochee river draining central Florida is low, 13 ppm or less. The group of spring runs opening separately on the West coast is described below.

The Suwanee-Sante Fe system is low in chloride being generally 8 ppm or less. Similar low values characterize the pan handle rivers except where the small streams pass over low ground in the last 5 miles.

Estuaries throughout the State are typically 1000 ppm or over including 11,000 ppm in the Indian River and 15,700 ppm among the mangrove islands and lakes of the lower everglades region.

The map in Figure 2 is a smoothed summary. Clearly the chloride content of surface waters reflects the chloride content of the ground waters as observed in a comparison of Figures 1 and 2. The contrasts between low and high salty regions are especially prominent between streams entering the west and east sides of the lower (northern) St. Johns river. Single analyses of streams can be compared with some validity where there are sharp contrasts in chloride content, although it must be kept in mind that the chloride content of a stream may vary markedly with the season. The low chloride surface waters of north central Florida and the central everglades are mostly rainwater. Woodcock (1952) collected rain from south Florida with chlorinities from 1 to 10 ppm inversely depending on the intensity of the rain.

Although the evaporation rate in Florida is high, the accompanying high rainfall prevents the evaporation from producing any large concentrating effects. The role of evaporation increasing the salt content depends on the percent turnover of the body of water. Mr. A. O. Patterson, District Engineer, Surface Water Branch of the U. S. Geological Survey at Ocala, Fla. has furnished evaporation data from their records on the large Lake Okeechobee. Between 1940 and 1946 there was an evaporation of 52 inches per year. A lake with no inflow other than rain and in a region with about 48 inches rain (Moorehaven 1940-1946, Records of Florida State Board of Conservation) would have the chloride of the rain concentrated many times. Most of the Florida fresh waters have inflows, and the greater the inflow due to streams the less would be this concentration. The chloride figures give in Figure 2 suggest that concentrations of 1 to 10 times may occur. In Lake Okeechobee there is apparently a concentration in passage through the lake of not over 1-2 times on the average because the inflow and rain together much exceed the evaporation. However, rainfall variations from year to year range from 30″ to 75″ so that the action of evaporation is subject to extreme annual variations.

Because of the low elevation, tidal waves move as much as 60 miles up some of Florida's canals and streams. However the actual transport of salt of immediate marine origin does not proceed such a distance for the tide causes only a pulse but not a reversal of current direction. Good examples can be observed in Weekiwachee or Chassahowitzka Springs rivers. The oligohaline water far up the rivers and canals derives its salt from the ground water. How far marine salt comes upstream as wedges of bottom water in the St. Johns river is not yet known.

Invasion of Marine Fauna into Florida Fresh Waters

That many marine fishes and blue crabs come regularly up streams and springs in Florida for a much as 180 miles is common knowledge in the hundreds of fish camps throughout Florida. In the scientific literature numerous references to this invasion have been made, such as by Carr (1937) and Gunter (1942). Sixteen species of marine fishes were recorded from oligohaline Homosassa Springs by Herald and Strickland (1949). Members of the biology department of the University of Florida have gradually been establishing a detailed pattern of the distribution of marine invasion although the difficulty of the task makes it a long term project. Crab occurrence records are given for Florida by Rathbun (1930).

Without waiting for careful icthyological survey of all the State's waters it is possible to establish roughly the distributional pattern of some indicator species in order to compare with the distribution of oligohaline water. Data on marine invasion is derived from personal observations in springs, interviews throughout Florida during June 1952, Herald and Strickland (1949), Dequine (1953), and records of fishes and crabs held by the U. S. National Museum especially due to collections of E. S. Herald, now curator, Steinhart Aquarium, San Francisco, California.

Symbols representing 4 species (*Callinectes sapidus, Tarpon atlanticus, Centropomis sp.*, and *Dasyatis sp.*) in Figure 2 indicate the similarity in the distribution of marine invaders and oligohaline or nearly oligohaline waters. It is difficult to distinguish between sporadic and frequent occurrence but only occurrences reported several times are included. Quantitative data on fish catches in oligohaline Lake George and nearly oligohaline Lake Okeechobee (Dequine. 1953) indicate that the number of marine fish present is considerable. For example, 1,602 lbs. of croakers (*Micropogon*) and 7,911 lbs. of sting rays (*Dasyatis*) were harvested from Lake George in 1952 and 1,556 lbs. of tarpon (*Tarpon*) from Lake Okeechobee.

Over most of Florida, apparently no chloride limit exists for the following species: mullet (*Mugil cephalus*), 3 ppm in Ponce De Leon Springs, Holmes Co.; needlefish (*Strongylura marina*) 5 ppm in Weekiwachee Springs; and sole (*Trinectes maculatus*), 5 ppm in Ichatucknee Springs.

Other species seem to be limited in their inland distribution to oligohaline or nearly oligohaline water. Listed below for each species is the lowest chlorinity observed where frequent occurrence was reported. Snook (*Centropomis sp.*), 25 ppm in Hillsborough River, L. Okeechobee and the N. New River Canal, 12 ppm in the high sulfate Peace River; blue crab (*Callinectes sapidus*), 25 ppm in Alafia River and Oklawaha River, 12 ppm in the Peace River; tarpon (*Tarpon atlanticus*), 35 ppm in the North New River Canal and Lake Okeechobee; sheepshead (*Archosargus probatocephalus*), 30 ppm in middle Weekiwachee River; mangrove snapper, (*Lutjanus griseus*), 50 ppm in Chassahowitzka Springs; channel bass (*Sciaenops ocellata*), 100 ppm in Crescent Lake; croaker (*Micropogon undulatus*), 150 ppm in the St. Johns River; sting ray (*Dasyatis sp*), 150 ppm in upper St. Johns River; peneid shrimp (?), 150 ppm in central St. Johns River; snapper (*Lutjanus sp.*), 570 ppm in Homosassa Springs; sea trout (*Cynoscion nebulosus*), 570 ppm in Homosassa Springs; hydroid (sp.) reported by C. F. Byers from Homosassa Springs; barnacles (sp.?), 900 ppm at Green Cove Springs on the St. Johns River (larvae possibly released from ship bottoms); marine amphipods, 900 ppm in Chassahowitzka River.

Additional fish species occurring more sporadically are recorded in Herald and Strickland (1949), Dequine (1953), and will be in Carr and Goin's forthcoming *Guide to the Reptiles, Amphibians, and Freshwater Fishes of Florida*.

For the blue crab where the most observational data are available the following minimum chlorinities were recorded for invasion into various bodies of fresh and oligohaline water: Trout creek, 220 ppm; St. Johns River, 150 ppm; Crescent Lake, 96 ppm; Chassahowitzka Springs, 53 ppm; Lake Okeechobee, 35 ppm; Tamiami Canal, 35 ppm; Wakulla River (lower) 30 ppm; Crystal River, 25 ppm; Alafia River 25 ppm; Miami Canal, 24 ppm; Oklawaha River, 15 ppm; Peace River (high sulfate), 12 ppm; Weekiwachee Run, 12 ppm; Wekiva Spring River, Orange Co., 10 ppm; Green Cove Springs (100 yds from high salt) 5 ppm.

It seems clear from the field data that blue crabs will move very short distances into water with little chloride but occur frequently and abundantly only with 25—100 ppm C1 or more. Current and elevation may effect this migration but are apparently not the main factors in Florida as discussed below in numbered paragraph 3.

Natural Experiments which Relate the Distribution of Marine Invaders and Especially the Blue Crab to the Distribution of Oligohaline Waters

A number of distributional patterns are described below which help one to understand Florida marine invasion.

1. Blue crabs (*Callinectes sapidus*), especially males but not exclusively males move up into fresh waters from both the Atlantic and Gulf coasts. As observed during 1951-52 in Homosassa Springs and reported in other parts of the State, the maximum invasion is in the summer. Hay (1904) and Pearson (1948) find this to be the case in the Chesapeake Bay estuaries also. It is interesting that this seasonal pattern exists in Homosassa Springs in spite of the constant temperature of the spring. Florida crabs in commercial quantities range over 100 miles up the St. Johns River with its high content of salt which originates from ground water. At intervals of 25 miles or so there are large high chlorinity springs where the crabs may tank up much as an automobile enroute. The high density of marine forms in Homosassa Springs (570-800 ppm C1) may be due to the pausing of the fish and crabs in the boils to tank up on salt, since they may be losing salt in the large broad feeding areas of the run immediately adjacent where chlorinities are somewhat lower (300 ppm C1).

2. The tendency for crabs and fish to move most readily into oligohaline waters but to penetrate only short distances in the lowest chlor-

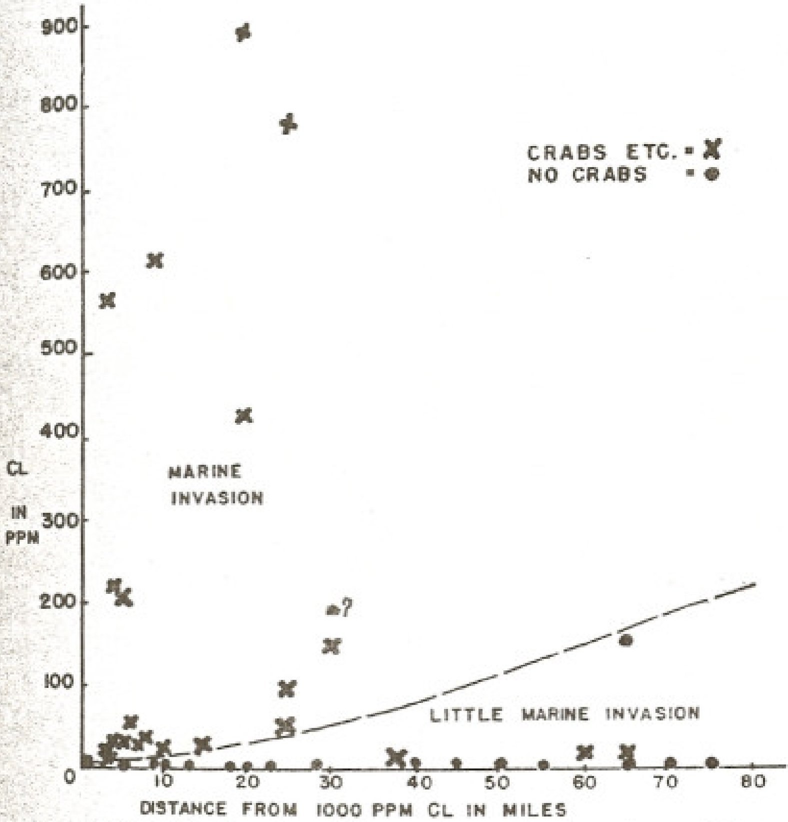

FIGURE 3. Bodies of fresh water which receive marine invasion and those which do not are plotted on a graph of chlorinity and distance from places of high chlorinity. Little marine invasion is associated with that part of the graph with lowest chlorinities and greatest distance from brackish water below the slanting line.

inity waters is demonstrated in Figure 3. Localities known to receive marine invasions or known rarely to receive them are plotted on coordinates of chlorinity and distance from chlorinities of 1000 ppm. It is possible roughly to divide these two types of localities by a slanting line that indicates that as distances from high salt become greater marine invasion requires higher oligohaline chlorinities. Four exceptions include a few crab records for Wekiva River, Oklawaha River, and Peace River discussed below and uncertain status of Alexander Springs.

3. In contrast to the St. Johns River the Suwannee-Santa Fe Rivers, which contain mainly the salt of rain water, do not contain many if any

crabs above the delta area. Low elevation and slight current are concurrent factors here probably favoring marine invasion in the St. Johns River or any other sluggish stream but are not definitive since some crabs go far up the fairly swift Peace River. They seem to be generally absent in the central Tamiami canal which is very flat. Currents are generally weak in the streams of peninsular Florida.

4. The crabs found up the Peace River as far as 50 miles from any salt other than rain water salt may be an exception due possibly to the strange chemical composition of this often polluted river with its high sulfate (64 ppm) and high phosphates (5 ppm). Over the earth high sulfate waters without high chlorides are rare so that even if sulfate can substitute for chloride it will rarely occur. Mr. Ellis Landquist from his interviews and collections along the Peace River in his study of pollution states that there is evidence that the crab invasion is a recent change. Crabs move into water with very low chlorinities in the Oklawaha and Wekiva River (Orange Co.). In the other waters of the State 25 ppm chloride seems to be a boundary for frequent occurrence and 100 ppm chloride for really abundant presence depending on the distance from even higher chlorinites. Most of these waters are hard with 40 ppm calcium or more so that chloride is the main variable, although magnesium and sulfate tend to be higher when the chloride is very high. Where waters are both soft and low in chloride as in many lakes and headwater streams there is no crab invasion as in the Tamiami canal. Even widely ranging species such as mullet are scarce in such waters. Thus the calcium and the corresponding alkalinity are probably factors here as reported in the literature (Krogh, 1939) although in most springs and stream waters the calcium is relatively constant (10-60 ppm) compared to the range of sodium chloride (5-2000 ppm).

5. That crabs are regulated in their distribution by the stimulus of the sodium chloride content as well as the tolerance is suggested by the crab distribution in Chassahowitzka Springs boil area. Although crabs were able to live 10-20 days in cages in the main boil with a chloride content of 50 ppm as described below, and although this boil area contains a dock from which fish heads are tossed as boats unload, crabs are only rarely observed to enter this area. In contrast crabs are abundant a few hundred feet down stream where a second spring with chlorinity of 730 ppm mixes with the first boil water. Thus this natural situation suggests that the sodium chloride is both a stimulus to selection of water in a gradient and physiological re-

quirement. It seems that in these low ranges, the sodium chloride is important qualitatively as well as in a role of increasing total osmotic pressure. The difference between 10 and 50 ppm chloride in water with 250 ppm total salts is not great as total solute but is clearly important to the distribution of marine invasion.

6. Perhaps the clearest demonstration of the salt role in marine invasion by the natural experiment method is a comparison of 4 spring runs: Weekiwachee, Chassahowitzka, Homosassa and Wakulla on the west coast of Florida. Each run is about 8 miles long gradually becoming an estuary in the lower parts. The calcium contents are almost identical at about 50 ppm. By coincidence the constant chlorides of the first three are respectively 5, 53 and 570 ppm. The distribution of marine invasion is similarly striking. Weekiwachee regularly has only the mullet, sole, and needlefish; Chassahowitzka has mangrove snappers and crabs up to the boil; Homosassa always has 500 or more individuals of 5—15 marine species milling around the boil. The Wakulla River begins as a low chlorinity spring without the oligohaline species but as it passes downstream and passes the 25 foot altitude and the Pamlico scarp, additional springs raise the chlorinity to 30 ppm. At this point blue crabs, fiddlers, *Potomogeton pectinatus* and other oligohaline forms appear.

7. It is possible that spring waters by their clearness and lack of organic matter attract marine invasion. If there is a tendency to respond to water of low turbidity and organic content, marine organisms might respond to spring waters and marine waters which tend to be similar in this respect.

8. In a personal communication, Harold Humm of the Oceanographic Institute, Florida State University, describes an extensively used procedure for killing blue crabs in a limp position by placing them in fresh water. He describes the complete failure of this procedure at Beaufort, N. C., Duke University Marine Station using local fresh well water. The crabs did not die. This may have been another example of the effect of small sodium chloride content.

9. In these discussions, a clear distinction should be made between marine species which invade fresh waters and those species of marine affinity completely adapted to permanent life in fresh water. Thus there are species of fresh water crabs in rivers throughout the world in waters with only the chloride content of rain water, such as the Blue Nile (Flower, 1931). A. M. Laessle of the University of Florida

has found a crab species in Jamaica Bromeliads. In Florida there is a small fresh water crab *Rithropanopeus harrisi* Gould (Rathbun, 1930) which is recorded a number of time from oligohaline waters in the St. Johns River. The osmoregulation is discussed below. The saber crab *Platychirograpsis typicus* which was described by Marchand (1946) as possibly introduced into the Hillsborough River near Tampa, Florida may be another oligohaline crab. It is at present distributed in the lower Hillsborough River and Sulfur Springs where the chlorinities are high for fresh waters. A specimen of *Sesarma sp.* was collected in Silver Springs in September, 1953. It is obvious that not all marine invaders are chlorinity sensitive since a few species of fish are found long distances up low chlorinity rivers like the Mississippi and the Amazon. (Gunter 1942).

Crab Survival Experiments

To test the abilities of Blue crabs to move into oligohaline waters some transplantation experiments were made both in Florida and at Woods Hole, Mass. Crabs were transported by car and were out of the water less than 2 hours in all experiments. In the Florida experiments sudden transfers from brackish water were made into hardware cloth cages in constant temperature springs. In the Woods Hole experiments crabs in 30 parts per thousand salinity were conditioned in 1/10 sea water for 24 hours before transferring to cages in ponds. Experiments on osmoregulation in crabs following sudden transfers summarized in Prosser (1950) suggest that 1-2 days are usually required for internal salt concentrations to reach a new equilibrium.

The results in Table 1 indicate that crabs can live longer in those freshwaters with higher chlorinities especially in the oligohaline range (.1 to 1.0 parts per thousand). In the Florida transfers the ability to survive is correlated with the natural presence of blue crabs in the springs used for the experiments. The crabs in the Woods Hole area have a similar ability to live some time in oligohaline water although such waters are scarce in the northeast. The ability of the Woods Hole crabs to survive in oligohaline waters of low alkalinity suggests that calcium is not a major factor.

Physiological Basis of Crab Invasions

Extensive series of experiments by many workers on many species of marine animals which can move with varying degrees into brackish water have permitted a general scheme to be established as to the

TABLE 1

TRANSPLANTATION EXPERIMENTS WITH BLUE CRABS

Crab Source, Date	*Cl ppm*	*Number of Crabs*	*Place of Experiment*	*Ca ppm*	*Temp. Deg. F.*	*Cl ppm*	*Days Survival*
IN FLORIDA SPRINGS, 1952:							
Bayport estuary, Feb. 4	3300.	7	Homosassa	50	75	570.	>14
Bayport estuary, Feb. 4	3300.	5	Chassahowitzka	49	74	53.	7-18
Salt Springs, Aug. 7	2800.	8	Silver	70	73	8.	5
Bayport estuary, Feb. 4	3300.	4	Weekiwachee	49	74	5.	1½
Bayport estuary, Feb. 5	3300.	4	Weekiwachee	49	74	5.	1
Chassahowitzka run, Aug. 22	730.	7	Rainbow	21	74	4.	1-2
PONDS AT WOODS HOLE, MASS., 1953:							
24 hours in lab., Aug. 13	1680.	3	Nobsca pond	9*	70-80	475.	9->18
24 hours in lab., Aug. 13	1680.	3	Rain pool at golf course	5*	70-80	11.	1

*Calcium values at Woods Hole inferred as .4 of Methyl Orange alkalinity variation of internal salt with external salt. According to the sha[pe] these curves Krogh (1939) and Prosser (1950) have summa[rized] this data into types.

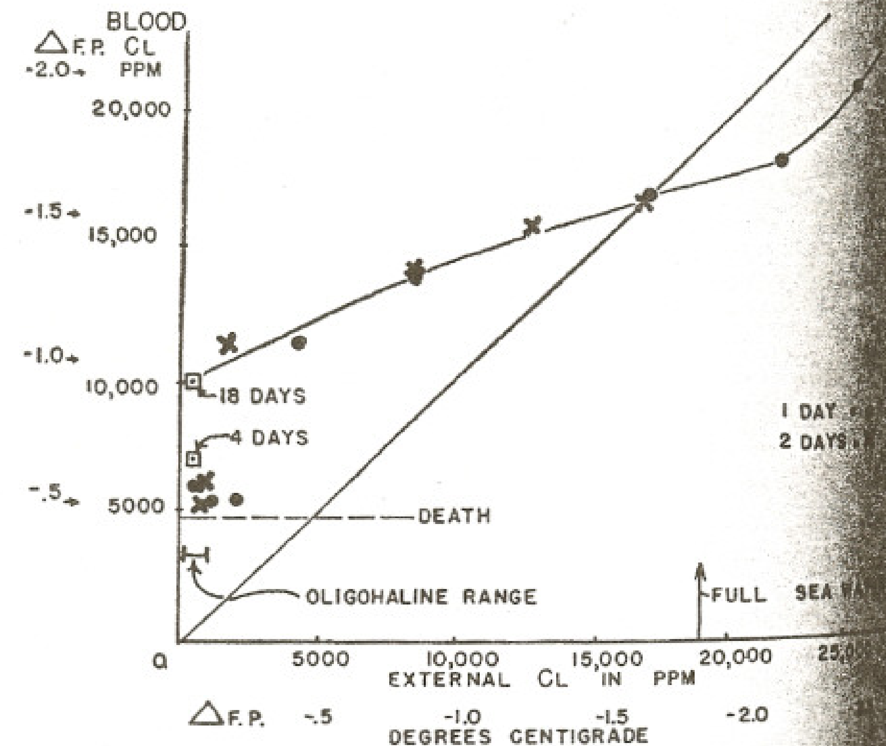

FIGURE 4. Internal blood chlorinity as a function of external chlorinity [of] blue crab (*Callinectes sapidus*) at Woods Hole, Mass., August. A roughly equivalent scale for lowering of the freezing point in degrees centigrade. The time lapse between start of each [experi]ment and the measurement of blood chlorinity is indicated.

To check the characteristics of the osmoregulation of the blue [crab] a few measurements were made of blood chlorinity as a functi[on of] external chlorinity after 24 and 48 hours dilution. These experi[ments] were made with crabs collected near Woods Hole, Mass., and in frequently renewed containers. Figure 4 shows the general of this curve is somewhat similar to the one for the Chinese handling crab *Eriocheir sinensis* that has a similar ecological dis[tribu]tion in the low country of Europe. Scholles (Prosser, 1950) Krogh (1939) indicated that *Eriocheir* regulates like a fresh organism while it is up in the rivers. The blue crab belongs wi[th] group that is more or less isotonic at full sea water salinities but regulates at lower or higher salinities. The blue crab is isotonic at somewhat less than full sea water. If crabs are placed suddenly from 19,000 ppm into the very low chlorinities of the oligohaline range (450 ppm), they lose salt rapidly until death occurs at 5000 ppm blood chlorinity. If however crabs are acclimated one day in brackish water (2000 ppm) before introducing into the oligohaline water the regulation after an adjustment period is continued even at this low external chlorinity. A crab kept 2 weeks in 450 ppm chlorinity had an internal blood chlorinity in line with the slanting curve in Figure 4. Figure 4 includes blood analyses from individuals in the process of losing salt rapidly as well as those which were regulating. It seems likely that crabs can recover from some loss of chloride below their regulation levels following fairly sudden changes since they maintain considerable activity as long as chloride levels do not fall below 5000 ppm. A crab was active in one case with low internal chlorinity (6930 ppm) 4½ days after sudden shift to oligohaline water. Huf (1933) found 7000 ppm Cl in *Potamobius* blood from fresh water.

A curve of internal osmotic pressure against external osmotic pressure obtained by Jones (1941) for *Rithropanopeus harrisi* from low salinity waters in San Francisco indicates that the crabs can survive for some time with internal blood salts below the level of regulation. *Rithropanopeus harrisi* does not regulate as much as the blue crab.

Evolutionary Implications of the Oligohaline Range

The remarkable distribution of blue crabs and possibly other marine organisms in Florida fresh waters seems to be an ecological manifestation of the physiological phenomena described above and the extensive oligohaline waters. From the data at hand it seems likely that as an intermediate between typically freshwater and marine forms, the blue crab belongs to a class of organisms which can exist in fresh water only if they can obtain sufficient salt to compensate for that lost. Apparently the chlorinity range from 10 to 500 ppm is important for these organisms. As intermediates physiologically and ecologically these oligohaline organisms may represent intermediates in the evolutionary shift of species from freshwater to saltwater.

The penninsula of Florida is a block of sediments of a type which must have always existed in varying quantities somewhere through geological time. It is a block of sediments which is exposed to oscillations of the sea and a consolidation process. The suggestion is made that in such environment gradual ranges of chlorinity have always existed without the sharp tidal salinity shifts of the usual estuary. Under such conditions it seems reasonable that evolutionary shifts of species from fresh water to salt water and back may have occurred readily. Certainly at present in the St. John's river and in the salt springs there exist fish communities with mixed components. Perhaps the line between fresh and salt has not always been so sharp. The Paleozoic formations containing fossil fishes now long since consolidated may have formed in environments with geochemical properties similar to those of modern Florida.

Marine fauna with a tendency to develop freshwater forms such the Mysid shrimps might be expected to make the transition readily where stable salinity gradients have persisted. It is interesting therefore that Horton Hobbs and Irene Bolick (unpublished) have found Mysids in Wakulla Springs and McLane (1948) found them in the St. Johns River since these two streams have stable oligohaline chlorinity grandients. Carr (1937) described 3 marine relict fish established in freshwater Lake Eustis.[2]

Geographical Implications of the Oligohaline Range

If, as this odd assortment of data suggests, the sodium chloride content of fresh waters is important in controlling the distribution of marine invasion in Florida in the oligohaline range, there are other areas of the world which might be expected to receive similar marine invasion and characteristic faunal associations.

Sedimentary and porous areas peripheral to the Suffolk scarp line of about 25 ft. present elevation may be expected to contribute springs and ground waters of relatively high chlorinity for fresh water and thus to encourage marine invasions.

The Netherlands, Belgium, and North Germany resemble Florida in some respects. Many of the fresh waters from these regions have chlorinities 10—500 ppm (Redeke, 1948). In fact the fresh-salt boundary based on faunal differences as defined by Redeke and Valikangas may have been much affected by the presence of much oligohaline water in their areas. Thienemann (1950) describes some

[2]Two recent papers read at the December 1953 Florida Academy of Science meetings at Rollins College have described additional marine invasion: (1) Wass, M. Two Mysid shrimps, one fresh water and one marine, previously unreported from Florida. (2) McLane, W. N. Notes on the fishes of the St. Johns drainage system.

marine invasion in this part of Europe. The artificially introduced Chinese wollhandling crab is centered in these areas. Other cases of other species are mentioned by this author.

The upper reaches of Lake Pontchartrain in Louisiana may owe its marine invasion (Gunter, 1942) to oligohaline water. In Belmonte, Cuba, Brues (1927) kept *Callinectes ornatus* in "freshwater" three months up Rio Caonao in a pond previously flooded with sea water. The caves of Yucatan whose aquatic fauna is partially marine contain fresh waters with the chlorinity range nearly oligohaline. Pearse (1938; Pearse *et al.*, 1936) who monographed this fauna nevertheless does not think of these low chlorinity waters as important to evolutionary exchange of fauna between freshwater and marine areas as the beaches (Pearse, 1952).

Rivers draining arid regions where evaporation and accumulated salt deposits contribute to the chlorinity should receive considerable marine invasion. Such waters as those in southwest Texas and southernmost California have chlorinities of the range which by this theory should encourage marine invasion. Salton Sea has marine forms and Gunter (1942) describes marine invasion for the Rio Grande. Most of the rivers of the United States that reach the sea however, have chlorinities less than 15 ppm chloride and are not oligohaline. Mansuetti (1952) reports that the penetration of some marine fishes in such low chloride rivers as surround the Chesapeake Bay is not much over 10 miles from tide water and high salinities.

Areas which receive chlorides in part from volcanic waters and hot springs and also are known to receive marine fishes (Herre, 1924) are found in the Phillipines such as Lake Manait, Lake Buhi, Lake Bombom, and Taal Lake with chlorinities of 580 ppm or over (Heise, 1917). Some marine relicts are described in low altitude lakes and the acidotrophic lakes of Japan and the Kuriles (Miyadi, 1933, 1938).

The often repeated idea that tropical waters receive more marine invasion than temperate ones seems open to the alternative suggestion that tropical waters more often contain appreciable oligohaline chlorinity.

Freshwater Invasion of Marine Waters

Most of the data in this paper concerns the invasion of freshwater by marine species but the oligohaline waters should favor the reverse migration also. Ordinarily when brackish water animals adjust to freshwater they move from a sharply fluctuating salinity into a m[illegible] constant environment. For a freshwater species to invade the [illegible] estuary it must adjust to a condition of greater salinity oscilla[illegible] and to a very sudden increase at the fresh-brackish boundary. [illegible] the usual estuary tends to be a barrier to freshwater species.

Gradual oligohaline gradients such as occur at the mouths of s[illegible] of the oligohaline springs and the St. Johns River are much les[illegible] barrier and should favor invasions and evolutionary adaptatio[illegible] freshwater species to marine conditions. William Sloan of the U[illegible]versity of Florida has found evidence for this in his study of the in[illegible] in the spring runs of the west coast of Florida now in progress. Sim[illegible] phenomena may be involved where the snail *Physa* occurs in [illegible] Baltic sea. Davis (1948) found considerable fresh water compo[illegible] in Long Lake in the brackish everglades at 15,000 ppm Cl.

Consider a range of chlorinity from 1.9 ppm Cl such as occu[illegible] some rivers in eastern United States to 19,000 ppm Cl characteri[illegible] of the open sea. What may be important to an organism is the pe[illegible] change. A change from 1 to 10 is as harsh as a change from [illegible] 100 or 100 to 1000. Consider therefore the chlorinity range [illegible] logarithmic scale. The range can thus be divided into 4 cycles [illegible] representing a 10 fold chlorinity change as follows:

No. 1	1.9	to	19.	ppm
No. 2	19.	to	190.	ppm
No. 3	190.	to	1,900.	ppm
No. 4	1,900.	to	19,000.	ppm

An oligohaline salinity gradient such as discussed above has [illegible] complete range represented by considerable areas without sharp [illegible] change. Fresh water organisms dominate the first two cycles. F[illegible] water organisms and marine organisms share the third cycle. [illegible] the fourth cycle is dominated by marine species. In the usual est[illegible] cycles 1, 2, and 3 are mostly absent being represented mainly [illegible] sharply fluctuating boundary zone. Thus where the whole interme[illegible] salinity range is present, it is not correct to say that marine [illegible]ponents dominate the intermediate zones. Certainly the fauna of [illegible] salty springs is more fresh in affinity than marine even though [illegible] salinities are in the brackish range.

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REFERENCES

BLACK, A. P. AND E. BROWN.
1951. Chemical character of Florida's waters. Division of Water Survey and Research, State Board of Conservation, Water Surv. and Res. Pap. No. 6, 119 pp.

BLACK, A. P., E. BROWN, AND J. M. PEARCE.
1953. Salt water intrusion in Florida—1953. Division of Water Survey and Research, State Board of Conservation, Water Surv. and Res. Paper, No. 9, 38 pp.

BRUES, C. T.
1927. Occurrence of the marine crab *Callinectes ornatus* in brackish and fresh water. Amer. Nat., *61:* 566-568.

CARR, A. F.
1937. A key to the fresh water fishes of Florida. Proc. Fla Acad. Sci., *1*:72—90.

CLARK, F. W.
1924. The data of geochemistry. Bull. U.S. geol. Surv. No. 770. 5th ed. 841 pp.

COOKE, C. W.
1945. Geology of Florida. Bull. Fla geol. Surv. No. 29. 339 pp.

COOPER, H. H, AND V. T. STRINGFIELD.
1950. Ground water in Florida. Inform. Circ. Fla geol. Surv. No. 3, 6 pp.

DAVIS, C. C.
1948. Notes on the plankton of Long Lake, Dade County, Florida, with Descriptions of Two New Copepods. Proc. Fla Acad. Sci., *10:* 79-88.

DEQUINE, J.
1953. Preliminary progress report on Florida's controlled seining program 1 April 1952 through 28 February 1953. Fla. Game and Fresh Water Fish Comm. Tallahassee, Fla. 31 pp.

FERGUSON, G. E., C. W. LINGHAM, S. K. LOVE, AND R. D. VERNON.
1947. Springs of Florida. Bull. Fla geol. Surv. No. 31, 196 pp.

FLINT, R. F.
1947. Glacial Geology and the Pleistocene Epoch. John Wiley. N.Y., 589 pp.

FLOWER, MAJ. S. S.
1931. Freshwater crabs in Egypt, Sinai, Sudan. Proc. zool. Soc. Lond. 1931: 729-735.

GUNTER, G.
1942. A list of fishes of the mainland of North and Middle America recorded from both freshwater and saltwater. Amer. Midl. Nat., 2 305-326.

HAY, W. P.
1904. The life history of the blue crab (*Callinectes sapidus*). Rep. U.S. Comm. Fish., 1904, pp. 347-413.

HEISE, G. W.
1917. The crater lake of Teal Volcano. Phillip. J. Sci., *12*: 247—254.

HERRE, A.W.C.T.
1924. Distribution of the true fresh water fishes in the Philippines. Phil. J. Sci., *24*: 249—308.

HEDGPETH, J. W.
1951. The classification of estuarine and brackish water and the hydrographic climate. Rep. Comm. mar. Ecol. Paleont. No. 11, pp. 49—

HERALD, E. S. AND R. R. STRICKLAND.
1949. An annotated list of the fishes of Homosassa Springs, Fla Proc. Fla Acad. Sci., *11*: 99-109.

HUF, E.
1933. The maintenance of salt content in the fresh water crab (Potamobius Pflüg. Arch. ges. Physiol., *232*: 558—573.
(only an abstract seen)

IMBT, W. C.
1950. Carbonate porosity and permeability. in Trask, P.D. Applied Sedimentation, John Wiley, N.Y., 707 pp.

JONES, L. L.
1941. Osmotic regulation in crabs. J. cell. comp. Physiol., *18*: 79—92.

KROGH, A.
1939. Osmotic regulation in aquatic animals. Cambridge, 237 pp.

MCLANE, W. M.
1947. The seasonal food of the largemouth black bass *Micropterus salmoides floridanus* (Lacépède), in the St. Johns River, Welaka, Florida. Proc. Fla Acad. Sci., *10*: 103-138.

MANSUETTI, R.
1952. Mixing of fresh water and marine fishes in Maryland estuarine waters. Abstract, Atlantic Estuarine Research Society.

MARCHAND, L.
1945. The saber crab *Platychirograpsus typicus* (Rathbun) in Florida; a case of accidental dispersal. Proc. Fla Acad. Sci., *9*: 93—99.

MIYADI, D.
1933. Ecological studies on marine relicts and land locked animals in inland waters of Nippon. Philipp. J. Sci., *65*: 239—247.

1938. Bottom fauna of the lakes in Kunasiri-sima of the south Kurile islands. Int. Rev. Hydrobiol. *37*: 125—163.

PEARSE, A. S. (EDITOR)
1938. Fauna of the caves of Yucatan. Publ. Carneg. Instn No. 491, 301 p[p.]

PEARSE, A. S.
1950. The emigrations of animals from the sea. Sherwood Press, Dryde[n] N.Y. 210 pp.

PEARSE, A. S., E. P. CREASER, AND F. G. HALL
1936. The cenotes of Yucatan. Publ. Carneg. Instn No. 457, 304 pp.

PEARSON, J. C.
1948. Fluctuations in the abundance of the blue crab in Chesapeake Bay Res. Rep. U. S. Fish. Serv. No. 14, 26 pp.

PROSSER, C. L. EDITOR.
1950. Comparative Animal Physiology. Saunders, Philadelphia, 888 pp.

RANKAMA, K. AND TH. G. SAHAMA.
1950. Geochemistry. Univ. of Chicago Press, p. 311, p. 756.

RATHBUN, M.
1930. The cancroid crabs of North America. Bull. U. S. nat. Mus. No. 152.

REDEKE, H. C.
1948. Hydrobiologie van Nederland de Zoete Wateren. D. De boer, Amsterdam, 580 pp.

THIENEMANN, A.
1950. Verbreitungsgeschichte der Susswassertierwelt Europas. Binnengewässer, *18*: 809 pp.

WOODCOCK, A. H.
1952. Atmospheric salt particles and raindrops. J. Met. *9*: 200-212.