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A COMPARATIVE DISTRIBUTION OF MARINE INVERTEBRATES AND FRESHWATER INSECTS OVER AN INTERTIDAL SALTWATER GRADIENT

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ABSTRACT

Insects are arguably the most successful group in the animal kingdom. Their ability to adapt to various environments has enabled them to dominate niches in both terrestrial and freshwater habitats. Although insects are incredibly diverse and successful, we are left with a paradox; why are there no fully marine insects? One explanation is that freshwater insects may simply be ill-adapted to survive saltwater conditions. We investigated a series of tide pools exhibiting a gradient from fresh to hyper-saline conditions. Within our five transects there were tide pools that continually received fresh seawater with every wave (fully marine), there were pools in which evaporation outpaced replacement (hyper-saline), and there were also pools that contained only fresh rainwater. We measured physical parameters of these pools and characterized the invertebrate diversity found within them. We found insects and insect larvae dominating both freshwater and (surprisingly) the most hyper-saline pools. These findings suggest that insects are not necessarily ill-adapted to marine habitats. Conversely, marine invertebrates may be less able to tolerate the more extreme hyper-saline environments, leaving these niches available for exploitation by insects.

INTRODUCTION

Insects are the most successful group within the animal kingdom. They have adapted to and thrive in a variety of conditions. This group comprises approximately 750,000 known species (Pagel, 2002). It is expected, however, that actual numbers may be in the millions. Insect fossils date from about 400 million years ago during the Devonian. Modern insects radiated to become highly diverse about 300 million years ago during the Late Carboniferous period. There is controversy over whether their ancestors were myriapods or crustaceans, with modern molecular evidence supporting the latter view.

Regardless of which lineage they evolved from, it seems clear that the Insecta evolved from terrestrial arthropods since the most ancient fossil insects (and the most primitive of modern forms) are terrestrial (Brusca & Brusca, 2003). Invasion of aquatic habitats was secondary. Nevertheless, many aspects of insect anatomy and physiology seem well adapted for a life in water. A waxy cuticle that prevents water loss in arid conditions can also protect internal tissues from osmotic problems associated with fresh or saltwater environments. Freshwater insects have also evolved an array of respiratory adaptations, including tracheal extensions, gills, or plastrons which have allowed them full range of freshwater habitats. Most aquatic insects have an aquatic larval stage and a terrestrial adult stage. During the different stages of an insect's life they can occupy different niches, thereby avoiding intraspecific competition between age classes. There are still many insects in which both larval and adult stages are aquatic.

With the apparent ease with which insects have adapted to fresh water habitats, we are left with a paradox. There are incredibly few insects that spend their life on the ocean and there are no known insects that are considered to be fully marine. There are approximately five species of sea skaters *Halobates* that spend their life on the surface of the open ocean (Andersen & Weir, 2003). Other insects that have been noted in inter-tidal or coastal regions are found close to land since they depend on a terrestrial environment for part of their life cycle. The species of sea skaters that inhabit the open ocean have their own adaptations to assist them to survive in the open ocean. The ocean species are darker than those found near the coast to protect them from UV radiation. Marine sea skaters have lost their ability to fly and no longer have wings; however, freshwater skaters have retained their wings because of the landlocked, isolated nature of such a body of water (Anderson, 1999). In short, those insects associated with marine environments exist on its surface or its shoreline sediments, and none have adapted to a fully marine existence.

How is it that such a diverse and successful group of organisms with an amazing ability to compete and adapt has not found its way into the ocean, which covers about 75% of the globe? One theory is that insects, having adapted first to terrestrial and second to freshwater habitats, may be ill-adapted physiologically to survive the salinity of the ocean. There is evidence supporting this view. Ocean water generally contains 35 ppt of salt. Salinity above 8 ppt, which is found in brackish water, has been shown to inhibit larval growth of many insect species (Smith & Smith, 1995).

We set out to examine the invertebrate communities that inhabit a series of tide pools on Man Head Cay, located in Rice Bay along the northeastern coast of San Salvador Island. This small Cay is littered with numerous tide pools that constitute a salinity gradient. Some pools close to the ocean's edge receive a continual exchange of fresh seawater with every wave, even at low tide. Others are out of reach of the tide and are filled with fresh rainwater. Still others receive occasional splashes from the high tide followed by evaporation, resulting in hyper-saline conditions. The results of our survey were surprising.

MATERIALS AND METHODS

During January 2003, two transects perpendicular to the shoreline were set up on the north (ocean-ward) side of Man Head Cay. Transect one contained seven tide pools and transect two contained six. In each transect, the pools were labeled so that pool A was closest to sea level. We chose the pools so that elevation (height above sea level) increased as distance from the shore increased. Each tide pool was sketched and the length, width, and depth of each were determined for transects 1 and 2. All pools were elliptical with many irregularities in their shape. Pools generally became smaller in size and shallower as they lay further from the ocean. Finally, the organisms in each tide pool were surveyed and water chemistry measurements were taken. This same area was re-visited in February 2005 (transect 3) and again in June 2005 (transects 4 and 5), producing a total of five transects. Each time, pools in this area were treated as independent observations, given that exact identification of individual pools proved problematic. Water chemistry measurements and invertebrate surveys were repeated.

Using the Quanta Probe®, we measured temperature, pH, salinity, and percent saturation of dissolved oxygen (DO). Water chemistry readings were taken on two different days soon after low tide. Low tide was at 1519 hr on 20 January 2003 and at 1602 hr on 21 January 2003. Water chemistry readings were taken four times in each pool (every half hour for 2 hr) on 20 January, and two times (every half hour for 1 hr) on 21 January. Averages of these readings were calculated and used for graphical representation. When calculating and graphing dissolved oxygen concentration in each pond, the percent maximum value of the percent saturation was calculated.

Organisms inhabiting tide pools were sketched, photographed, or a sample was taken. Samples were identified using field guides and specimens in the repository at the Gerace Research Center.

RESULTS

In all pools, temperatures stayed within the range of 22.0-27.9°C during January 2003. However, during June 2005, water temperatures were between 29-40°C. Temperature readings were not taken in February 2005 (transect 3); however, some pools were in the shade while others were in complete sun.

Salinity was fairly constant over time in each individual pool, but varied considerably between pools (Figure 1). An average was taken of the four salinity readings that were obtained for each pool. Transects 1 and 2 exhibited similar salinity gradients. The pools closest to the ocean exhibited saline conditions, close to that of the ocean. As the pools lay further from the ocean their salinity increased. Finally, salinity seemed to peak at pool F and rapidly decreased in the next pool to become that of freshwater. Transect 3 exhibited a different trend. The first seven pools had salinity readings close to that of seawater. Pool H was fresh water and the furthest from shore was hyper-saline. These variations no doubt reflected differences in seawater splash patterns at the highest reaches of the incoming tide.

Transects 4 and 5 exhibited a curious phenomenon. The pools nearest to the ocean, as expected, had salinity close to that of the ocean. The upper-most pools within these transects showed low salinity, yet salt crystals were visible on the bottom of the pools, suggesting that a layer of freshwater was floating over intensely hyper-saline material. This observation points to some interesting problems regarding the dynamics of salinity in some of these pools. It also raises some interesting questions regarding how invertebrates respond to such extreme haloclines.

Oxygen levels exhibited similar trends in most of our transects (Figure 2). Again, four readings were taken for each pool within transects 1 and 2 and results were based on the average. As the pools increased in distance from shore (and in their salinity), the dissolved oxygen levels also increased (Figure 2).

All transects exhibited the same general trend in pH levels. As pools increased in distance from the shore, water became more alkaline (Figure 3). In transects 4 and 5, spikes in pH corresponded with heightened dissolved oxygen levels. Results of pH for pools within transect 1 and 2 were based on an average of four readings and the pH of pools in transects 3, 4, and 5 were based on single readings.

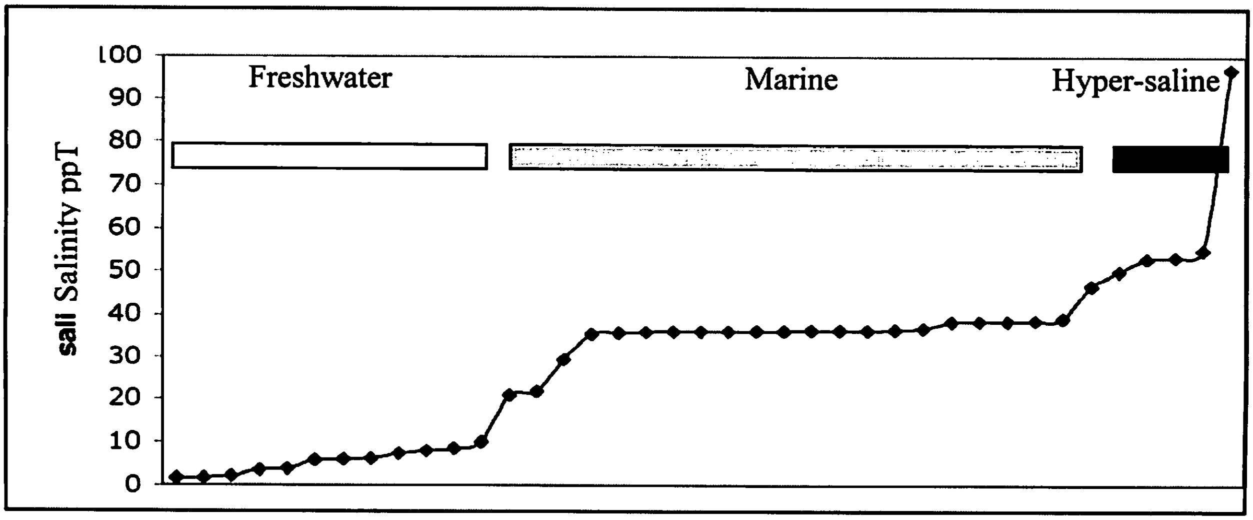


Figure 1. Salinity measurements for a series of tide pools on Man Head Cay. There are three groups of pools based on salinity: freshwater (0-10 ppT), marine water (35-37 ppT), and hyper-saline (50 + ppT). Pools are arranged here by increasing salinity.

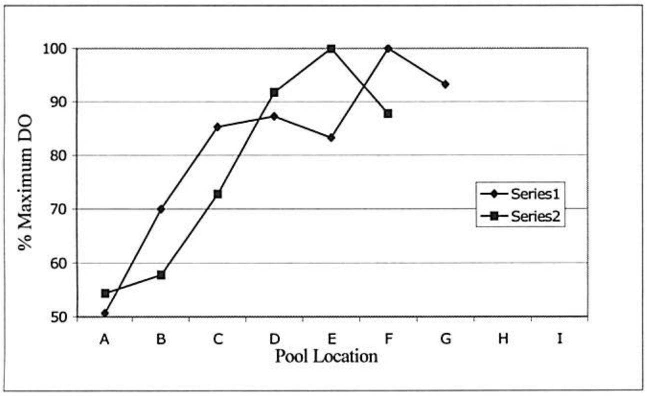


Figure 2. Percent maximum dissolved oxygen in two representative transects (transects 1 and 2). Pool A is closest to the ocean, pool G is furthest.

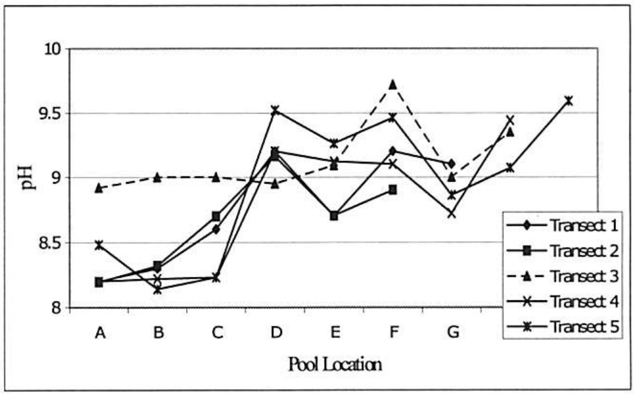


Figure 3. pH measurements for tide pools in each transect. Pool A is closest to the ocean, H is furthest.

A comparison of the number of species of marine invertebrates, freshwater insects, and marine vertebrates within each type of tide pool is shown in Figure 4. Marine invertebrates were present throughout each transect with the fewest species in the freshwater and hyper-saline pools. Marine vertebrates were only present in the pools that were closest to the ocean and hence, marine. Freshwater insects were present in the uppermostpools, those containing either fresh water or hyper-saline containing either fresh water or hyper-saline conditions. Table 1 contains a list of organisms found in each pool. Figure 5 shows some representative pool inhabitants.

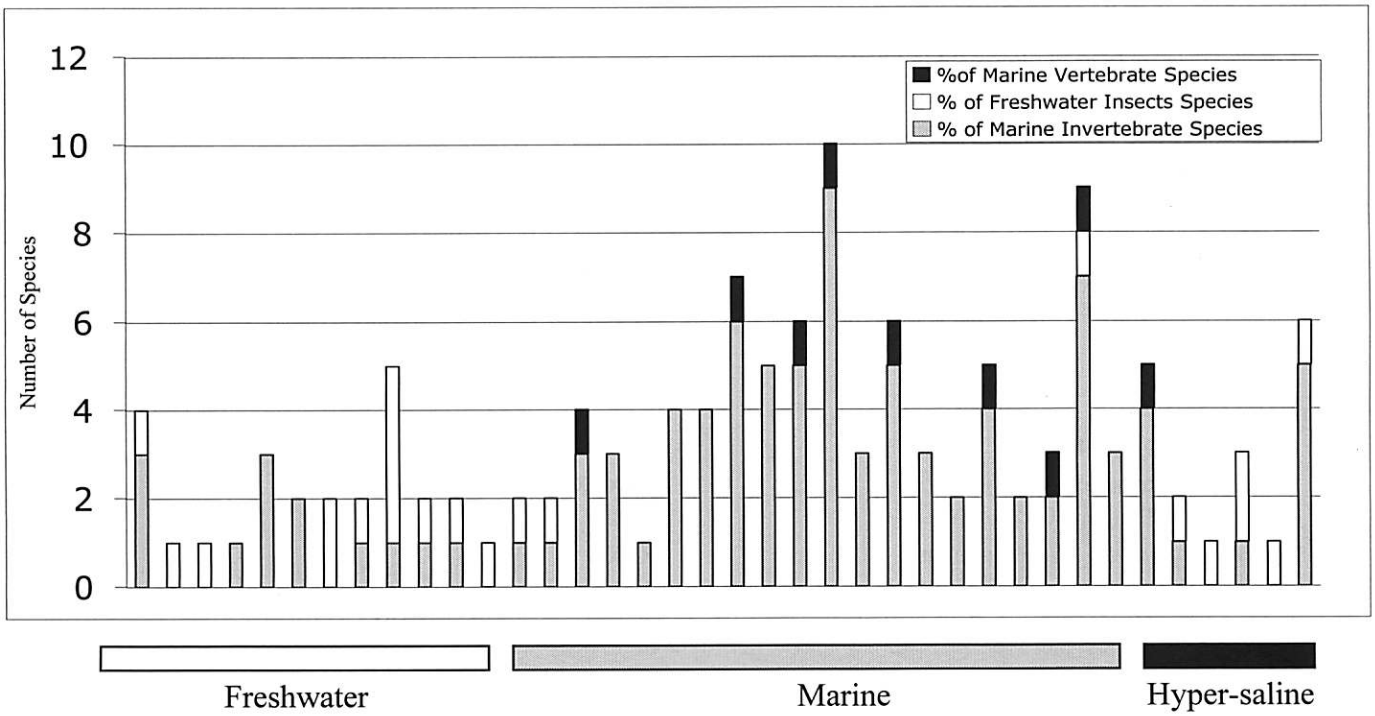
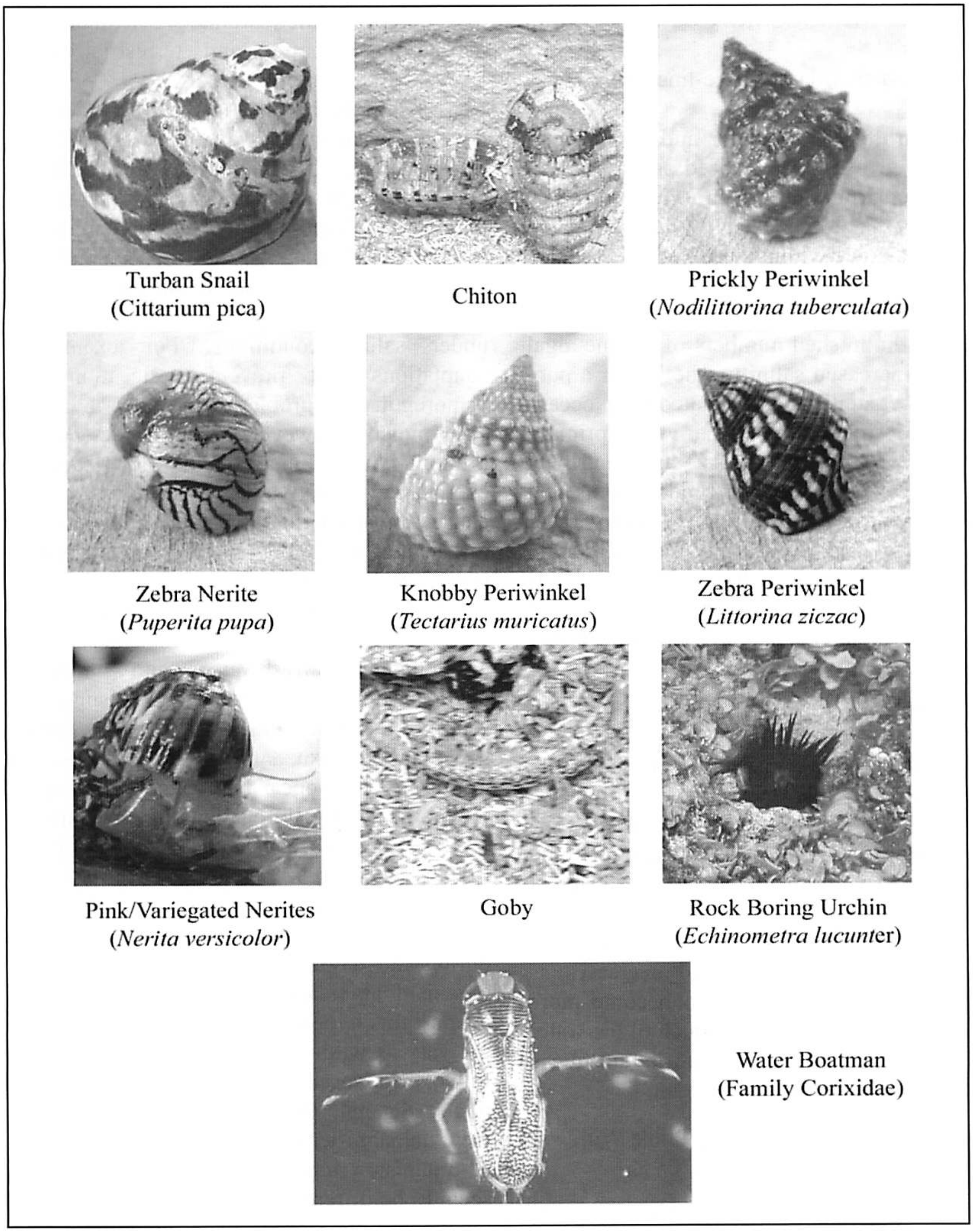


Figure 4: A comparison of the number of marine vertebrate species, marine invertebrate species and species of freshwater insects within each pool of transect 1, 2, and 3 over a salinity gradient (same salinity distribution shown in Figure 1).

Table 1. Species diversity in tide pools with varying salinity. Each "X" indicates a sighting for a species in a pool with the given salinity.

Organism	Freshwater	Marine	Hyper-saline
Algae			
Padina gymnospora (Brown Algae)		X	
Chondria tenuissima (Red Algae)		X	
Cladophora prolifera (Green Algae)		XX	
Derbisia sp. (Green Algae)		X	
Dictyota menstualis (Green Algae)		XX	
Unidentified Green Algae		X	
Annelida			
Serpulidae (Calcarious Tubeworms)		X	
Mollusca			
Polyplacophora (Chitin)		XXXXX	
Gastropoda			
Turbinidae			
Cittarium pica (Turban Snail.Magpie Shell)		XXXXXX	
Fissurellidae			
Diadora (Keyhole Limpit)		XXX	
Neritidae			
Nerita tessellata (Checkerboard Nerites Snail)		XXX	
Nerita versicolor (Pink/Varigated Nerites Snail)		XXX	X
Puperita pupa (Zebra Nerites Snail)		XX	X
Littorinidae			
Littorina mespillioum (Dwarf Periwinkle Snail)			X
Littorina ziczac (ZigZag Periwinkle Snail)	X	XXXXX	X
Pectarius murica (Beaded Periwinkle Snail)	XXXXX	XX	XX
Nodilittorina tuberculata (Common Prickly Periwinkle)	XXXXXXXXXX	XXXXX	X
Arthropoda			
Crustacea			
Paguridae			
Pagurus pollicaris (Hermit Crab)		X	
(Cancer Crab)		X	
Fast Isopod	X	X	X
Slow Isopod	X	X	
Insecta			
Chironomidae (Fly Larvae)	X		
Culicidae (Mosquito Larvae)	XXXXXXXXXX	X	X
Libellulidae (Dragonfly Larvae)	X		
Sigara atropodonta (Waterboatman)	XXXX		XXX
Echinodermata			
Echinometra lucunter (Rock Boring Urchin)		XX	
Vertebrata			
Goby sp.		XXXXXXX	X



Turban Snail
(Cittarium pica)

Chiton

Prickly Periwinkel
(*Nodilittorina tuberculata*)

Zebra Nerite
(*Puperita pupa*)

Knobby Periwinkel
(*Tectarius muricatus*)

Zebra Periwinkel
(*Littorina ziczac*)

Pink/Variegated Nerites
(*Nerita versicolor*)

Goby

Rock Boring Urchin
(*Echinometra lucunt*er)

Water Boatman
(Family Corixidae)

Figure 5. Some representative shore-line pool inhabitants from Man Head Cay, San Salvador Island, Bahamas. The water boatman was the most common insect during January in freshwater and hyper-saline pools.

DISCUSSION

The Oxygenation of Shore-line Pools

Within transects 1 and 2 and as a general trend, dissolved oxygen increased as pools were located further from the ocean (Figure 2). We hypothesize that this was due to the photosynthetic algae within these pools. It seemed that, in general, as salinity increased, algal cover increased, and so too did dissolved oxygen. This could reflect diminished numbers of marine algal grazers with increased salinity. The longer a pool sits under direct sunlight and isolated from ocean-turnover, the more time that the primary producers have to photosynthesize and contribute to rising oxygen levels within a pool. Pools that exhibited freshwater conditions had lower amounts of algae and lower oxygen levels. Within the pools that contained salt crystals there was also a low amount of algal growth and a low level of dissolved oxygen. This correlation begs further study.

The pH of Shore-line Pools

In all five transects, pH generally increased as the pools moved away from the shoreline (Figure 3). This trend can also be explained by the relationship between pH and levels of photosynthesis occurring in different pools. As photosynthesis increases, the amount of carbon dioxide dissolved in the water decreases. As CO_2 decreases, carbonic acid decreases as well. This can cause the water to become more alkaline (Wetzel, 2001). Hence, much of the water chemistry in these pools can be attributed to the biotic activity of resident algae.

Invertebrate Diversity Among Pools With Varying Salinities

The tide pools of Man Head Cay provide an excellent laboratory for studying how organisms partition themselves at the interface between fresh and saltwater habitats. Pools range from fully marine to fresh, rain-water catchments, with hyper-saline pools and the curious blended environment in pools with freshwater floating over a hyper-saline (saturated) saltwater. How do marine invertebrates and terrestrial/freshwater insects partition these habitats?

Salinity has been shown to decrease the developmental rate and increase mortality rate of freshwater insects (Chadwick & Feminella, 2001). However, there are various examples of insects that inhabit hyper-saline water (Usinger, 1957; Foster & Treherne, 1976; Smith & Smith, 1995). Terrestrial insects come equipped with various mechanisms that would aid them in their survival under saline conditions. For example, the adaptations that prevent desiccation aid in osmoregulatory problems within a hyper-saline environment. However, despite these adaptations, utilizing these mechanisms for survival is energetically costly. With an extra output of energy toward regulation of ions it is possible that insects become more vulnerable to competition (Foster & Treherne, 1976).

Despite these limitations, we found that insects dominated the two most extreme environments, freshwater and hyper-saline habitats (Figure 4, Table 1). This suggests that salinity is not necessarily a limiting factor for these insect taxa, and in fact, it is marine organisms that appear less capable of adapting to the more osmotically-challenging environments.

When we began our tide pool study, we initially hypothesized that as we moved from unstressed (ocean-like conditions) to stressed conditions (fluctuating salinity and temperature during the day), there would be a decrease in organism abundance. Our observations did not support this hypothesis. First, water chemistry did not vary as wildly over the course of a day as we initially supposed, even in the most isolated tide pools. Second, the most highly stressed pools were not significantly impoverished in the number of organisms they contained. However, there did seem to be differences in the types of species that inhabited the ocean-like conditions versus freshwater conditions. The pools in the zone closest to the shoreline (ocean-like) contained more traditional tide pool organisms, such as snails, chitons, hermit crabs, and gobies (Table 1). The pools in the zone farthest from the shoreline (freshwater) contained organisms such as fly larvae, dragonfly larvae, and water boatmen (Table 1).

The most striking finding was that insects dominated both freshwater and hyper-saline pools. This suggests that insects are not physiologically precluded from living in saltwater environments, and in fact, may do better than their marine counterparts. It is conceivable that adaptation for a terrestrial (dessicating) environment has actually pre-adapted insects to be more euryhaline than marine invertebrates.

The Marine Insect Paradox

As mentioned, it has long puzzled biologists that insects are seemingly excluded from the marine habitats. Some researchers have proposed that adaptation primarily to a terrestrial environment, and secondarily to freshwater habitats, may have physiologically restricted insects in their tolerance of saltwater conditions. Our findings suggest that no such barrier exists. We found insects in all ranges of water salinity, but insects clearly dominated the extremes, both fresh water and hyper-saline pools. These findings lend support to another theory to explain why there are no fully marine (pelagic) insects. When insects emerged in evolutionary history, they may have found the marine environments already full of highly adapted invertebrates. Usinger first proposed this hypothesis in 1957, suggesting that crustaceans became well established in the fully marine environments and that their competition and predation could have limited the invasion of marine habitats by insects (Cheng, 1976). According to Usinger's theory, insects avoided the competition in the ocean and during the time of their evolution inhabited the available niches on land and freshwater.

This finding has parallels in other contexts. Within a study on caddis flies in saline waters of Death Valley, Colburn (1988) found that, despite the physiological stress, caddis flies were more successful in the hyper-saline bodies of water than in freshwater. This seemed to be due to less competition in this type of habitat.

Vermeij & Dudley (2000) made similar conjectures when they found that molluscs and crustaceans, typically aquatic groups, were absent from salt lakes, suggesting that highly adapted native species prevent invaders from the land moving to these lakes.

Our findings demonstrate that insects are fully capable of occupying saltwater habitats and, in fact, may be better adapted to extreme salt environments than their marine counterparts.

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