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Disarticulation and Dissolution of Crab Remains Across a Depth Gradient in the Bahamas: A Taphonomic Study

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DISARTICULATION AND DISSOLUTION OF CRAB REMAINS ACROSS A DEPTH GRADIENT IN THE BAHAMAS: A TAPHONOMIC STUDY

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ABSTRACT

The fields of Paleontology and Paleoecology would not be complete without taphonomy, the study of the processes affecting organisms between death and fossilization. Taphonomy is important because it allows us to make more complete conjectures about prehistoric organisms and environments, and makes us aware of possible holes and biases in the fossil record due to highly destructive processes or the loss of delicate, non-resistant organisms. Studies on the processes affecting modern organisms have contributed greatly to the understanding of ancient processes; however, most of these studies are near-shore and short-term. What is lacking is information on the effects of these factors over long periods of time, and to depths below 50 meters. To gain more information about long-term effects, the Shelf and Slope Experimental Taphonomy Initiative (SSETI) has deployed sets of crabs, molluscs, urchins, and wood on a variety of substrates at depths from 15 to 300 meters in the Bahamas. Sample groups have been collected every few years for the last six years, and are compared to control sets.

My research focuses specifically on the crabs, species *Callinectes sapidus*, from experimental sites in the Bahamas. The crab remains display a wide range of breakage, dissolution and disarticulation, varying by depth. To determine the

effects of depth and environment on the crab remains, changes in size, mass, and surface condition of each of the specimens was documented and the results were analyzed for trends across a depth gradient. Scanning electron microscope analysis of carapace surface conditions was conducted to determine the degree of dissolution of each specimen.

The crabs were reduced to disarticulated chelipeds, mandibles, and carapace fragments within one year in most environments, and the outer surfaces of the remains show near-complete loss of pigmentation, and microscopic pitting. Although the sample sizes in this experiment are fairly small, a trend of better preservation in the middle depths and worse preservation at shallow and deep sites was found. Since this taphonomic trend exists, the information gleaned from this study may prove to be useful in accurately identifying the depth ranges in which fossil assemblages were created.

INTRODUCTION

The goal of this project is twofold: to describe the degeneration patterns of a set of crabs along two transects in the Bahamas, and to find plausible explanations for those patterns. To accomplish this, I have analyzed the crab remains for taphonomic degeneration in several different ways, and have researched previous experiments of this type, work on crabs in the fossil record, crustacean biology, and relevant marine chemistry data.

PREVIOUS STUDIES IN EXPERIMENTAL TAPHONOMY

Taphonomy has its beginnings as a simple descriptive science, which served to catalogue the ways in which an organism gradually becomes a fossil. In the 1960's, taphonomy developed into a more predictive science (Robison and Teichert, 1979), and the focus of taphonomic studies moved from the fossils themselves to the processes behind their fossilization. Starting in the mid-1980's, a number of studies in experimental taphonomy were conducted both in the lab and in marine settings to investigate the decay of a number of arthropod groups under various conditions of burial, depth, time of exposure, and temperature (Schäfer, 1972; Plotnick, 1986 & 1988; Briggs and Kear, 1994).

It is generally accepted that rapid burial and anoxia are the two main environmental factors that lead to good preservation, protecting fragile organisms from predation, physical weathering, and chemical breakdown (Martin, 1999). The body of study on modern taphonomy, though small, has served to support and supplement our understanding of the basic avenues to exceptional preservation of organisms.

Plotnick (1986) studied the decay of the shrimp *Pandalus danae,* both in the lab and in the field, and found scavenging, burrowing by infauna, and bacterial decomposition to be major factors in the breakdown of the shrimp remains. In a later study conducted with Baumiller and Wetmore (1988), Plotnick enclosed specimens of the crab *Panopeus* in wire mesh cages to restrict predation. The

specimens were then buried in a carbonate environment for periods of up to 10 months; they found that the crabs remained fairly well-preserved, and attributed this to an environment with fewer infaual burrowers and a carbonate sediment which buffers acids and thus slows dissolution. Allison (1988) and Briggs and Kear (1994) conducted all of their studies in the lab, placing shrimp remains in jars with varying degrees of oxygenation; they both found that anoxic conditions did not significantly reduce the decomposition of the arthropods.

Schäfer (1972) describes a field study on the decomposition of crab remains in the North Sea immediately after death as follows: first, the carapace and the thorax separate, remaining connected only by the skin that covers the inside of the carapace. The abdomen begins to separate from the thorax as well, and the three body segments finally detach from each other, although each segment remains internally intact for a long time, and these intact segments are often found along beaches and on the sea floor. When the segments finally break apart, the heavier parts, claws and mandibles, separate out first. Schäfer further notes that the shell itself becomes weaker and more brittle after about four weeks; he attributes this not to decalcification, which simply makes the skeleton more elastic, but to disintegration of the connective tissue between the layers of the cuticle. However, actual breakage of the shell will not occur without a physical disturbance of some sort.

THE BIG PICTURE: The Shelf and Slope Experimental Taphonomy Initiative

In 1993, the Shelf and Slope Experimental Taphonomy Initiative (SSETI) was formed in order to investigate taphonomic processes in a variety of unique environments of deposition, and over long periods of time (Parsons-Hubbard et. al., 1997 and 1999). The SSETI employed a common technique of modern experimental taphonomy - the deployment of dead organisms on the sea floor, and then subsequent retrieval and analysis of decomposition after a specified period of time. While most modern taphonomic experiments encompass a time frame on the order of days to months, the SSETI samples were deployed for a minimum of one year. There are other significant distinctions to be made between previous studies and the SSETI experiment. Besides the difference in running time, the SSETI experiment covers a wide range of depths - from 15 to almost 700 meters deep, covering shelf, slope, and bathyal environments. The SSETI study was set up in the field, and specimens were placed directly on the sea floor in mesh bags, as opposed to the buried specimens in the Plotnick experiments; burial in the SSETI experiment takes place only as a result of natural sedimentation at the site.

The experiment was conducted at three separate sites: two in the Caribbean, on a carbonate platform, and one in the Gulf of Mexico, a terrigenous outer-shelf/slope environment. Sites covered a wide range of depths and substrates, encompassing hardground, sand channels, mud, a near-vertical wall, talus slopes, and dunes (Parsons-Hubbard et. al., 1999). In addition to regular

shelf, slope, and basin sites, some samples were deployed at more unusual sites such as brine seeps, petroleum seeps, and hardground environments (Parsons, et. al., 1997). Samples of freshly killed crabs and sea urchins, mollusc shells, and wood were enclosed in mesh bags (1 x 1.5-cm holes) that were tied to 1.2-m. long PVC poles. The urchins and crabs were both enclosed in smaller, finer (3 mm) mesh bags before being placed inside the larger bags. The poles were deployed by submersible in groups of four replicates, at depths ranging from 15 to 260 meters (50 to 875 feet) in the Bahamas and 75 to 267 meters (246 to 876 feet) in the Gulf of Mexico (see Figures 1-2). In addition to the poles, tethered shells and free shells were scattered at each site.

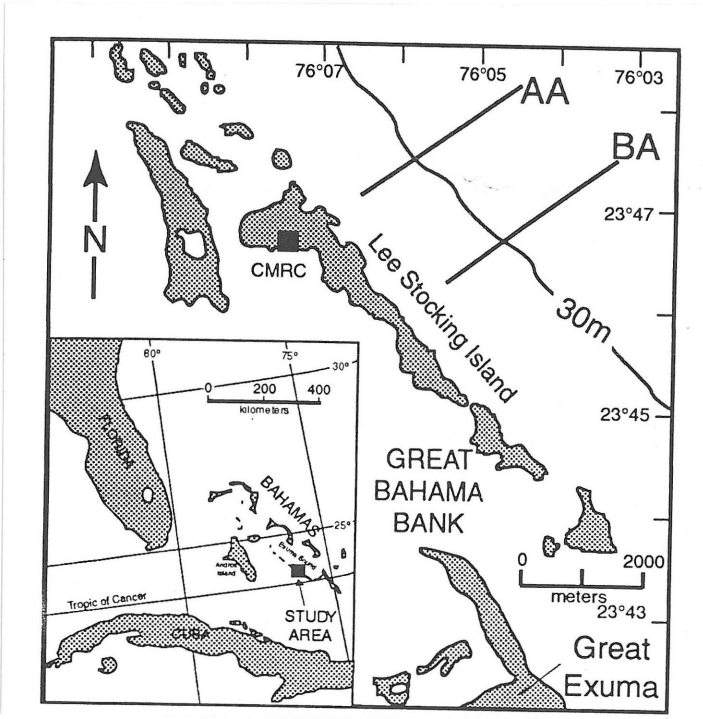


Figure 1: Location map of the Bahamas experiment sites (from Parsons-Hubbard, et. al., 1999). Location map of the Gulf of Mexico sites is omitted, as it is not dealt with in this study.

Specimens were retrieved in 1994, 1995, 1996, and 1999; another round of collection will be done in the summer of 2001. In addition to the retrieval of deployed specimens, temperature and salinity data were taken by the submersible at 5-10 meter depth increments, and extensive video footage was taken at every site.

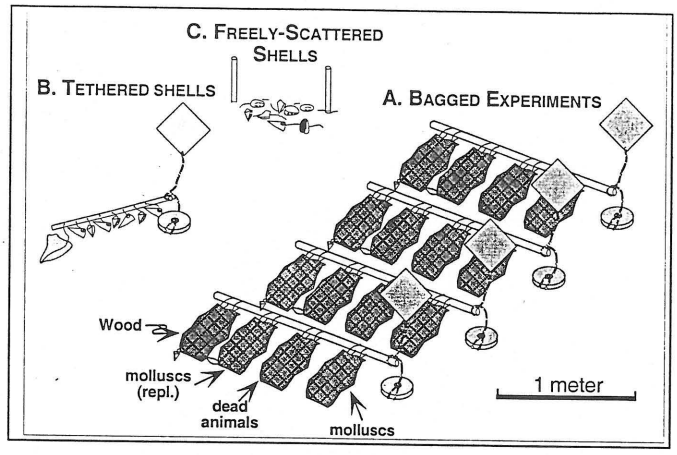


Figure 2: SSETI experimental set-up (from Parsons et. al., 1997)

My project focuses on the gross taphonomy (disarticulation and breakage) of the crab specimens (species *Callinectes sapidus*) from the two Bahamas transects, deployed in 1993 and 1994 and retrieved in 1994, 1995, 1996, and 1999. In addition, a preliminary study of the molecular-taphonomic processes that affect the crab cuticle using scanning electron microscopy will be presented.

Deployment sites

The crabs were deployed along two lines perpendicular to shore off of Lee Stocking Island in the Bahamas. The two lines, referred to as the AA transect and the BA transect, are approximately 2000 meters apart, and are parallel to each other (see Figure 1). The sites cover a wide range of environments and substrates, which are covered in Table 1.

TABLE 1-- Descriptions of experiment sites along the platform and steep slope into Exuma Sound off Lee Stocking Island, Bahamas. CSS= carbonate silt and sand, CCS=coarse carbonate sand, MCS=medium carbonate sand, FS=fine sand, HG=hardground. Modified, from Parsons-Hubbard, et. al., 1999.

Site name	Location	Site description	Bottom type	Depth (m)
PLATFORM TOP				
AA50RID	patch reefs	Low-relief hardground with a diverse Atlantic shallow reef community.	HG	15
BA50NO	sand channel	Open sand bottom with migrating ripples. Macrofauna include a diverse gorgonian assemblage.	CCS	15
BA50MUD	mudhill	A low-relief sand hill stabilized by gorgonians.	CCS	15
AA100NO AA100SO	sand channel	Sandy area between patch reefs. Bottom fauna dominated by *Halimeda* and gorgonian assemblage.	MCS	33
BA100NO	sand channel	Rippled sand between patch reefs. *Halimeda* is common.	MCS	33
BA100SO	sand channel	Replicate of BA100NO.		
NEAR-VERTICAL WALL				
AA240WA	wall	Narrow ledge on a near-vertical wall. Plate corals, sponges, gorgonians, and a diverse encrusting community.	HG	73
AA290WA	wall	Narrow ledge on the wall. Associated fauna include plate corals, sponges, and diverse encrusters.	HG	88
BA230WA	wall	Narrow ledge on the wall. Common associated fauna include plate corals, sponges, gorgonians, and encrusting algae.	HG	70
BA230WN	wall	Replicate of BA230WA.		70
TALUS SLOPE				
AA700CR	talus	Carbonate rock promontories on sloping bottom. Fauna includes stalked crinoids, arrow crabs, and sea whips.	FS	213
BA600CL	talus	Shingled rock and boulder strewn slope with stalked crinoids, crabs, and sea whips.	FS	183
BA640CL	talus	Replicate of BA600CL.		195
BA740BO	talus	Talus strewn slope with carbonate promontories on a fine sandy bottom. Stalked crinoids are present.	FS	226
BA705BO	talus	Replicate of BA740BO.		222
DUNES				
AA850CR	dune crest	Crest of relict dune aligned parallel to dip of slope. The area has sparse crabs, sea whips, many tracks & trails.	FS	264
BA830CU	crest	Crest of relict dune aligned parallel to dip of slope. The sparse macrofauna includes crabs, holothuroids, and sea whips. Tracks and trails are common.	FS	253
BA860DP	crest	Deeper on the same dune crest as BA830CU.	FS	262
AA875TR	trough	Trough of relict dune aligned parallel to dip of slope. The area has sparse crabs, sea whips. Bottom has patches of consolidated sand.	FS	267
BA850TN	trough	Trough of dune with sparse macrofauna including crabs, holothuroids, and sea whips. Tracks and trails common.	FS	259
BA860TR	trough	Replicate of BA850TN. Bottom sediments are somewhat consolidated.	FS	262

CALLINECTES SAPIDUS

The crab *Callinectes sapidus* belongs to the phylum Arthropoda, subphylum Crustacea, class Malacostraca, order Decapoda, infraorder Brachyura, family Portunidae, and was first described by Dr. Mary Rathbun in 1896. In Latin, the name *callinectes sapidus* means "savory beautiful swimmer," but the common name, Atlantic blue crab, suggests *Callinectes'* primary habitat and distinctive coloring. The blue crab is an important part of the estuarine/nearshore environment; it is one of the most abundant large invertebrates, and is a major link in the food chain, significant both as predator and as prey. It is a mainstay of the fishing industry on the Atlantic and Gulf coasts and is of tremendous economic importance to states like Delaware and Maryland, the latter of which went so far as to designate *Callinectes sapidus* the state crustacean in 1989.

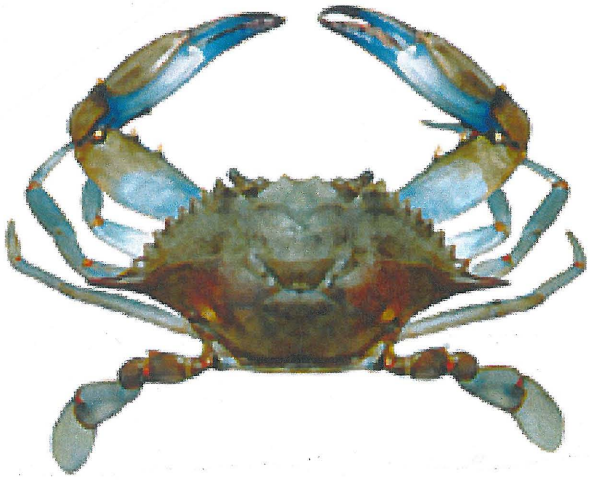


Figure 3: *Callinectes sapidus*, from Steve Zinski, Richmond University

Blue crabs prefer grassy estuarine or near-shore environments, and tolerate low salinities; they are often found in brackish estuarine waters. Their

primary range is along the eastern coast of the Americas, although they have been introduced to France, Holland, Denmark, and Israel, probably through transport in ships' ballast water. *Callinectes* can be found up to about 37 meters deep;[1] this is clearly not as deep as our studies go, and a pertinent question is whether or not our data are flawed if we are not dealing with species endemic to the study area. However, crabs persist even at bathyal depths, and the species particular to the study area are related closely enough to *Callinectes* that their decomposition is comparable.

Because of their popularity and abundance, blue crabs are well-studied, and were used for this study primarily because of their easy availability. Although the crabs don't make up the bulk of the deployed specimens in the SSETI experiment, they are the most taphonomically sensitive organism of the group due to their chitinous test; thus they undergo the most change over the sample intervals and may be accurate predictors of the later taphonomic trends of the other deployed organisms.

MORPHOLOGY

The decapod body consists of a fused cephalothorax, a segmented abdomen, which in crustaceans has become completely folded under the cephalothorax, and pairs of appendages - antennae, mandibles, maxillae, and

[1] Habitat information from the web pages of the Marine Biological Institute at Woods Hole and the National Aquarium in Baltimore:http://www.mbl.edu/html/KEYS/INVERTS/13/list.html and http://www.aqua.org/animals/species/bluecrab.html

legs - that are attached to each body segment. *Callinectes*, like all decapods, have five pairs of legs. The front pair of these legs is the chelipeds, or claws, which are used to catch and shell prey. The claws are made up of four main parts: the merus, the carpus, the manus, and the dactyls (see Figure 4). The dactyls are the most commonly preserved parts of our experiment crabs. The rear pair of legs is adapted into paddle-like appendages for swimming, in a modification peculiar to the species, and the central three pairs are simple walking legs.

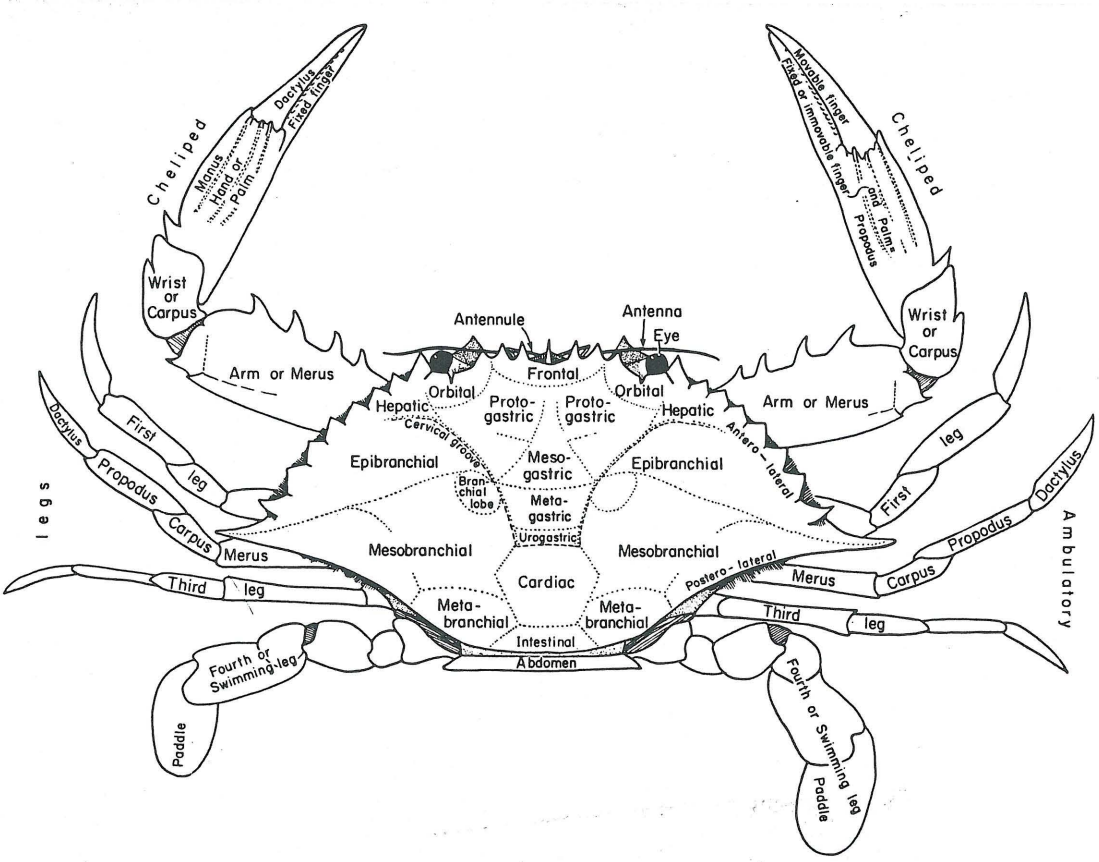


Figure 4: Crustacean morphology (from Schmitt, 1965, after Rathbun, 1935)

Skeleton: Macrostructure

The skeleton of *Callinectes* is centrally composed of a hard shell or carapace, which is protected at the edges by a row of small spines; the carapace extends out to two larger single points at the lateral edges (see Figure 4). Dorsally, the carapace is separated into a number of smaller regions divided by faint grooves that are probably sutured, since they originally demarked the separate body segments (Glaessner, 1969). I suspect that in our experiment, the carapace broke first along these grooves. *Callinectes* does have an internal skeleton that serves as an attachment structure for muscles (Dennell, 1960), but this skeleton is much less calcified than the external skeleton, and so degenerates quickly; it was never found in our samples, and is rarely found in fossilized specimens.

Like all arthropods, decapods molt several times during their life-span, but in contrast to other arthropods (most notably trilobites), they eat the discarded shell immediately after molting, in an effort to recycle the biomolecules that harden the carapace (Schmitt, 1965). Since this behavior is characteristic of all living decapods, it is fair to assume that fossil decapods practiced this as well, and as a result, crustacean molts usually aren't found in the fossil record. Thus, two problems, inflated population estimates and the difficulty in distinguishing between fossilized molts and bodies, common with

trilobites and other arthropods, do not arise in the study of fossilized crustaceans.

Cuticle: Microstructure

The crustacean shell, or cuticle, is made up of a protein-polysaccharide compound called chitin, which is hardened with $CaCO_3$ and other calcium salts; the more flexible shell material between body segments which allows the joints to move lacks these salts. The cuticle is divided into several distinct layers: the protective epicuticle and the endocuticle, which is composed of the pigmented layer, the calcified layer, and the uncalcified layer (see figure 5).

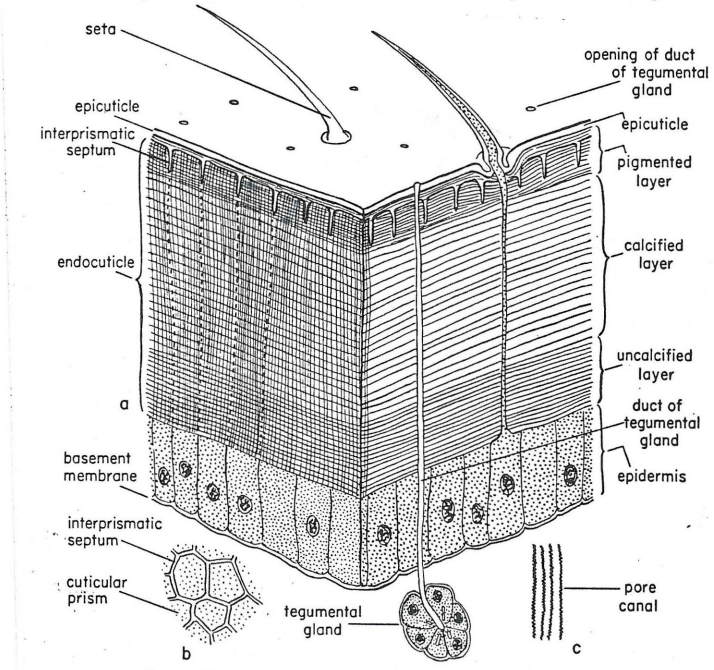


Figure 5: Structure of the crustacean cuticle (from Dennell, 1960)

All layers but the uncalcified layer predictably are calcified, and while the endocuticle is chitinous, the epicuticle is not. The epicuticle is a protective layer which contains lipid molecules, and is more impervious to the effects of acids than the inner layers are; this is also due to a thin binding membrane around the

epicuticle that is highly resistant to even strong acids (Dennell, 1960). Therefore once the epicuticle is gone, the cuticle is more likely to degenerate quickly in the presence of acids. The pigmented layer is heavily calcified, and contains granular deposits of a melanin-like substance (Dennell, 1960). Its structure, like the rest of the endocuticle, is laminated, and it is semi-porous. The calcified layer is the thickest of the layers, and is free of vacuoles and melanin-like substance. It does, however, carry a faint blue pigment that is spread throughout the layer. The uncalcified layer is relatively thin and simple, and is thought to be developmentally more primitive than the other layers; in contrast to the other layers, it does not appear until after each molt has occurred (Dennell, 1960). It is likely that, due to the very different natures of the layers of the cuticle, the rate of degeneration changes drastically as each layer is subsequently worn away.

CRUSTACEANS IN THE FOSSIL RECORD

Crustaceans begin to appear in the Triassic (Glaessner, 1969), and Plotnick (1986) counts 366 known fossil genera, 86 of which are Brachyurans. Fossil crab assemblages have been described by Rathbun (1935) and Bishop (1986), and unusual preservation in coal beds (e.g. Imaizumi, R., 1959), and in concretions (e.g. Park, 1991, and Benson, 1950) have been described as well. In most instances, only chelipeds are found.

Because they are soft-bodied, crustaceans are usually found in the fossil record only under conditions of exceptional preservation (Martin, 1999). In general, they are rare, and are often found simply as an assemblage of claw pieces, but occasionally, an entire carapace or even the entire crab will be preserved. The soft parts of the crabs are rarely preserved, and this is the rule for most fossil assemblages. But in the rare instances where the soft parts of organisms are preserved, such as the Burgess Shale, a great deal of information can be obtained.

Plotnick (1990) did a study of crab death assemblages in Texas, in a nice bridge between the study of the taphonomic processes themselves on one hand and their already-fossilized results on the other. Samples were taken by digging and coring in up to 15 cm of sediment in the nearshore environment. Crab parts were found at almost every site sampled, and at some sites carapaces and whole thoraxes were turned up. Many of the crab parts were small and difficult to identify without some knowledge of crab morphology, leading Plotnick to believe that crab remains are often overlooked in the fossil record for the same reasons.

Almost no work has been done on paleoecological reconstruction of crustacean assemblages based on the taphonomic state of the fossils, but this may be due more to a lack of knowledge of the taphonomic process than to any deficiencies in the fossils themselves or in the amount of information the taphonomic process has to offer. All in all, crabs may be a more important part of the fossil record than has previously been thought. We just need to look more

closely for crab parts in fossil assemblages in which they aren't immediately obvious, and at the same time we need to look harder at the state of the fossilized crabs we already have for a clue to their paleoenvironmental significance.

METHODS

DATA COLLECTION

Once the samples were collected, the crabs were removed from the mesh bag, labeled with the date and site name, frozen, and later transferred to ethanol. Sorting took place in the lab post-collection. The parts most often found were four dactyls, two mandibles (resembling molar-like teeth), the two large distal points on the carapace, and various small, calcified hard parts that I interpreted as mostly joint coverings and smaller spines from the carapace. All fragments that didn't fit into these four categories (mostly flat, uniform 'flakes') were categorized as carapace fragments (see Figure 6), although I suspect that some of these came originally from the manera (palms). Since the crab samples were deployed with two crabs in each bag, measurements were based on an initial assortment of four sets of claws, four teeth, and four carapace points.

After sorting, counting, and cataloguing, qualitative and quantitative data were taken on each specimen: all samples were measured and weighed, and a protocol for degree of disarticulation and breakage was applied.

Because of the important role that burial plays in preservation, sedimentation rates were estimated from video footage at each site (see section on Sediment Cover, under 'Results').

Figure 6: Body part groups: clockwise from top left: carapace, carapace points, mandibles, joint covers, claws (center)

MEASUREMENTS

Length

Length measurements were taken with electronic calipers (resolution to 0.01 mm), and reflect the longest dimension of the fragment in each category, for each specimen. The claw pieces were separated into propodi (the bottom, or 'fixed' fingers) and dactyli (the top, or 'free' fingers). The propodi were measured in two places: from the tip (sometimes broken off; in these cases, measurement was from the point of breakage) to the focus of the hinge (called "claw 1"), and from the tip to the longest reach of the side of the hinge (called

"claw 2"). (see Figure 7). The difference between the two lengths was studied in a preliminary way to investigate degree of breakage of fragile parts, as the side of the hinge is fairly unstable, and longer lengths in this area would perhaps indicate a better-preserved specimen. Indeed, the graphs of this difference showed similar trends to other measurements and assessments taken (see Figures 13 and 25). The 'claw 1' measurement and the longest measurement of the dactylus were used as standard lengths, the length of the carapace point was taken by measuring the longest specimen, and the length measurement for the carapace fragments was taken simply by finding the longest dimension in the sample. Mandibles were measured, but did not yield any strong trends, and joint covers were not measured.

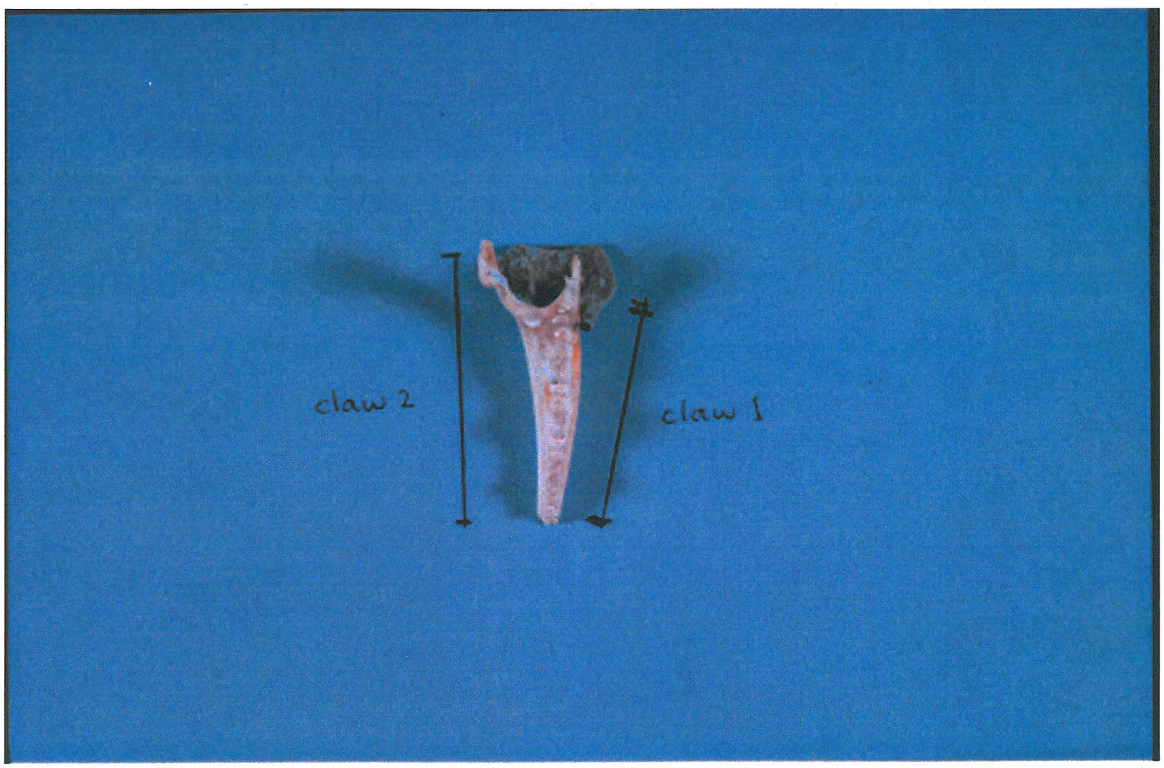


Figure 7: 'Claw 1' and ' Claw 2' measurements. The difference of the two measurements is used as a proxy for good preservation

Normalization of Length Measurements

A problem arises when considering the quantitative measurement data: no length or weight measurements were taken before the fresh crabs were deployed at the sites. This is not surprising, since the methods for quantifying subsequent degeneration were far from obvious when the experiment was planned. However, it makes it difficult now to assess whether differences in length and weight between samples is due to actual taphonomic processes, or to variation in the size of the original specimens. In an attempt to normalize the measurement data, I looked for a feature on the claw that is present in most specimens, and forms a consistent ratio with a full claw. The tip of the claw, where breakage very often occurs, is actually sutured; in most fresh specimens this can be seen in an abrupt change in color from dark blue at the tip to pinkish-orange on the claw. The total length of the bottom claw (propodus) from tip to hinge forms a consistent ratio in fresh crabs of 1.29 to the segment from suture to hinge. In the top claw (dactylus), this ratio is 1.17.[2]

With these ratios in mind, the measurement from suture to hinge was taken for the longest propodus and dactylus of each sample, when available. This measurement was then applied to the ratio, to obtain an estimate of the original length of the claw. The initial length measurement taken for the sample was then divided by this inferred original length to obtain a number that represents the percentage of the claw that remains after x years at a depth y.

[2] These numbers represent the mean measurements taken on four sets of fresh crab claws.

Due to breakage, fourteen of the seventy-four samples weren't measurable, so the normalized data set is not complete, but is more accurate than the complete set of non-normalized length measurements taken previously. Another problem to take into account is the fact that many crustaceans have unevenly sized claws - a large, dull one for grasping and a small, sharp one for cutting. Normalized measurements based on the small claw would give a false impression of being more degenerated when compared to measurements based on the large claw. However, the grasping and cutting claws of the fresh crabs were highly comparable in size, and this problem seems only to have arisen with one specimen.

Weight

All specimens were weighed on an analytic balance (resolution to 0.001g). Weights were taken for each body part category, but since the only categories that showed any real variability from specimen to specimen were the claws and the carapace fragments, the data were organized into categories titled 'claw weight', 'carapace weight', and 'total body weight.' The latter represented the sum of the weights of each body part group. In the graphs and in further discussion, weight data are referred to with these category names.

BREAKAGE AND DISARTICULATION PROTOCOL

In an effort to quantify degeneration, I set up a protocol to measure the amount of breakage, on a scale from one to five, of the claws, carapace points,

and mandibles of each sample; the other body parts didn't lend themselves well to this type of evaluation. This results in a semi-quantitative system for ranking levels of degeneration. The protocol was set up to take both degree of breakage and missing parts into account. Even though the mesh size of the bags was fine, body parts were often missing, probably due to a combination of dissolution, breakage, and other environmental factors. However, since the loss of body parts is less informative taphonomically than the degeneration of the parts we have, breakage has a greater weight in the protocol than presence or absence of parts does.

For the claws, the protocol is as follows (see Figure 8):

1 - whole and articulated

2 - whole tip to joint

3 - missing the tips

4 - fragmented above joint, but whole in cross-section

5 - fully fragmented

The number assigned to each specimen was based on the highest level of degeneration found in the specimen; for example, the protocol value for a claw sample where some of the claws are whole and some of the claws have missing tips is three.

For the carapace points and the mandibles, the protocol is slightly different (see Figure 9):

1 - all four whole and present

2 - all whole, one to three missing

3 - fragmented, all present

4 - fragmented, one to three missing

5 - all missing

Although the values obtained for each body part do stand on their own, the three values were also averaged to obtain an overall picture of the taphonomic effects of the environment over the entire crab; this average is discussed in the Results section.

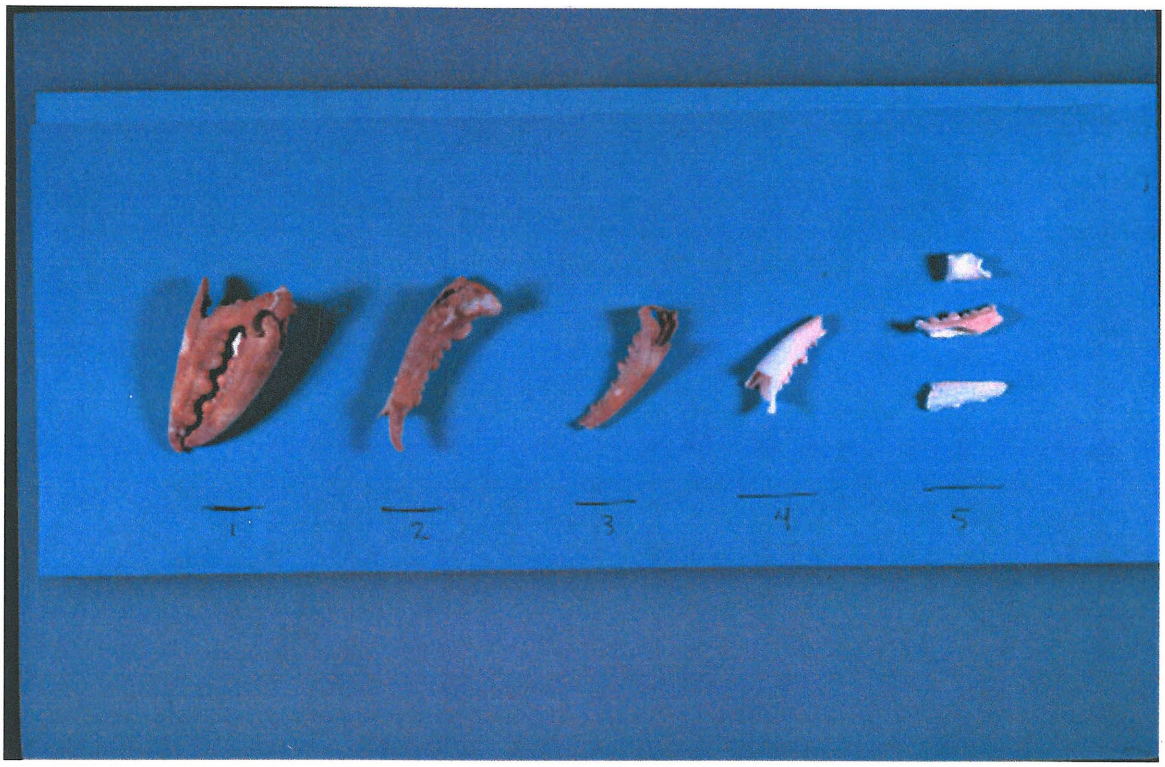


Figure 8: Values for the claw breakage protocol: 1=whole and articulated; 2=whole tip to joint; 3=missing the tips; 4=fragmented above joint, but whole in cross-section; 5=-fully fragmented.

Microscope Analysis

Samples were examined first with a light microscope for general surface trends like loss of pigmentation and large-scale pitting. Several samples from the BA transect were then examined using the scanning electron microscope for more specific instances of dissolution. Claw fragments were mounted on

aluminum stubs with conductive carbon cement, sputter-coated with gold, and examined, using a beam amplitude of 14 kilovolts, at up to approximately 540 times magnitude.

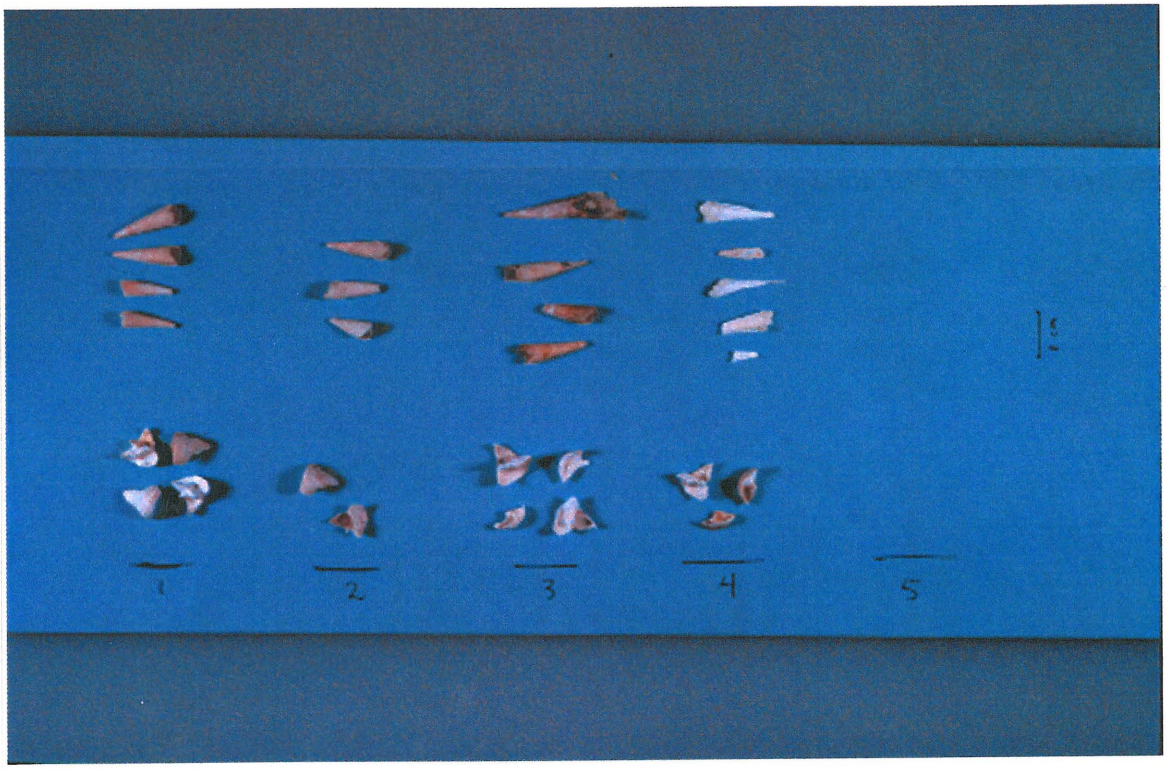


Figure 9: Values for the mandible/carapace point breakage protocol: 1=all four whole and present; 2=all whole, 1-3 missing; 3=fragmented, all present; 4=fragmented, 1-3 missing; 5=all missing.

SEDIMENTATION

Sedimentation rates were determined through careful assessment of the Bahamas video footage. Visual estimates of sediment depth on the bags were made for every site. The minimum amount of sedimentation seen was a 'dusting', which was given a value of 0.1 centimeters. The maximum sedimentation found was approximately 5 cm., which was sufficient to cover the mesh bags.

METHODS OF DATA ANALYSIS

Since only one crab sample was taken each year and at each depth, our sample sizes are fairly small, and this makes data analysis difficult. In order to conduct a t-test or an Analysis of Variance test, the mean of a group of data for each depth and year are needed, whereas we have only one number. Therefore the data can not be supported by statistical verification, but can be considered a summary of the taphonomic information based on the available data. I looked for the best and worst preservation across a depth gradient by identifying the peak or peaks in each graph which represent the highest level of preservation, and the valleys or low points, which represent the lowest level of preservation. In some of the graphs, more than one peak or valley appears, or the point that represents a suspected high or low is very close in value to another point on the graph. In these cases, I have somewhat arbitrarily established a 10% threshold for significance: if a point is within 10% of another point on the graph, the two are considered equivalent and their difference is considered to be unimportant. If the two high or low points on the graph are more than 10% apart, the peak or valley is considered to represent a real difference in preservation quality.

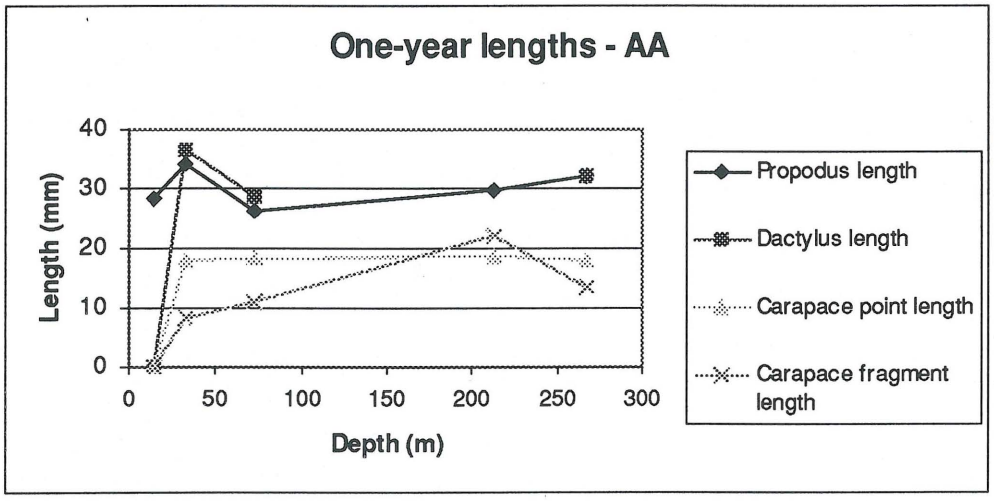
RESULTS

THE AA TRANSECT CRABS

In general, the best preservation along the AA transect occurs in the 70 meter to 88 meter depth range; although the deepest depths also show good preservation in a number of instances, these data are more variable. However, it seems that the nature of the crab shell is that different parts of the shell react differently to taphonomic processes. This makes overall trends difficult to pick out.

Length

One-year samples



The crabs on the AA (northern) transect were deployed in 1993; a year later, specimens at 15 meters, 33 meters, 73 meters, 213 meters, and 267 meters were collected. Figure 10 shows the variation in non-normalized length of the dactylus, propodus, carapace point, and carapace fragment over the range of depths. The dactylus length peaked at 33 m; the propodus was longest at 33 m too, but was only 6% longer than 267 m site. The carapace fragment peaked at the 213 m site, and the lengths of the carapace points at the various depths were so close that, while the 213 m specimen was marginally longer, no significant trend appears.

Two-year samples

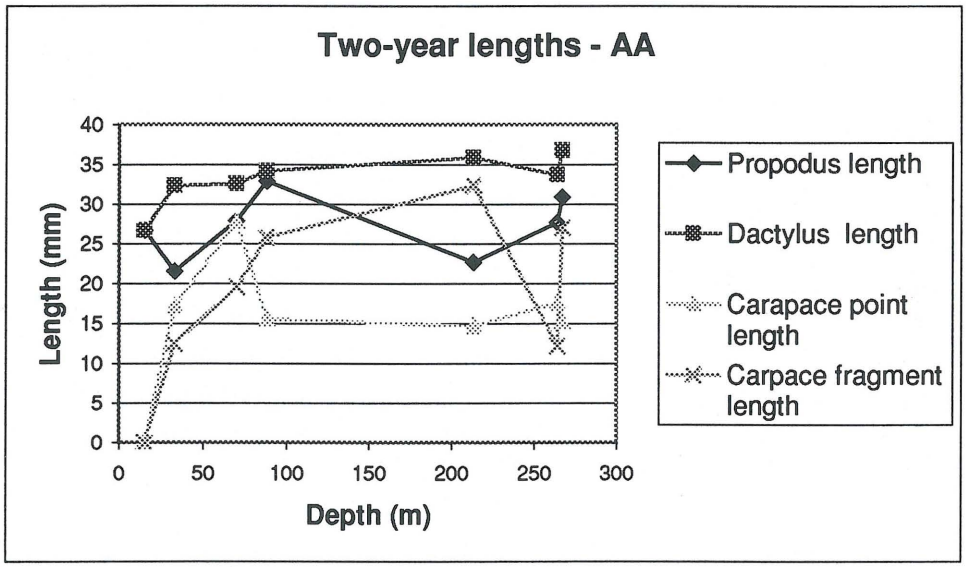


Figure 11: Length after two years (AA)

After two years, specimens were picked up at 15 meters, 33 meters, 73 meters, 88 meters, 213 meters, 264 meters, and 267 meters. The length data were more scattered for this round of specimens, with fewer evident trends (see figure 11). Dactylus length peaks at 267 m, but is within 8% of the 88 m, 213 m, and 264

m specimens. Propodus length peaks at 213 m, but is only 6% longer than the 267 m specimen. Carapace point length peaks at 70 m, and carapace fragment length peaks again at 213 m.

Six-year samples

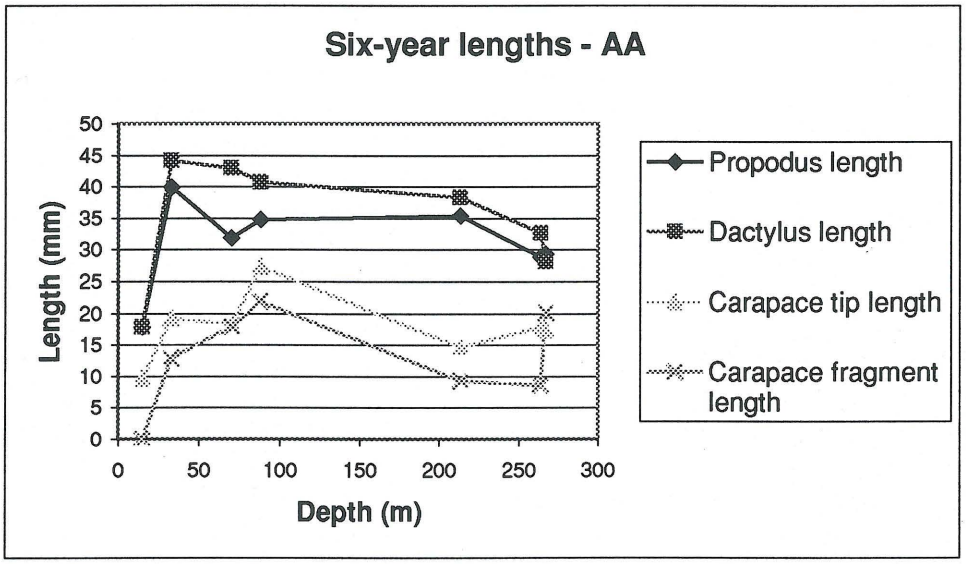


Figure 12: Length after six years (AA)

After six years, specimens were retrieved at 15 m, 33 m (one from each of the two 33 m sites, S1 and S2), 70 m, 88 m, 213 m, 264 m, and 267 m Measurements from the two 33 m sites were averaged, and the result was a graph with a much more obvious trend: most body parts are longest in the middle depths (33 m - 213 m) and tail off at either end. Dactylus length peaks at 33 m, 8% longer than the 70 m and 88 m sites. The propodus was longest at the 33 m site, the carapace point was longest at the 88 m site, and the carapace fragment was longest at the 88 m site, although it was within 8% of the 267 m site.

Hinge length

As was previously noted, this length (see Figure 7) may be a good proxy for preservation, as it is fragile, and is therefore more sensitive to destructive taphonomic processes. The difference in the 'claw1' and 'claw2' measurements showed trends similar to the length data: in the AA crabs, the largest differences in the two measurements occurred at 33 m after one year, at 88 m and 264 m after two years, and at 70 m and 267 m after six years (see Figure 13). This shows that short term response differs from the longer term, and reinforces the trends established in the length and weight measurements.

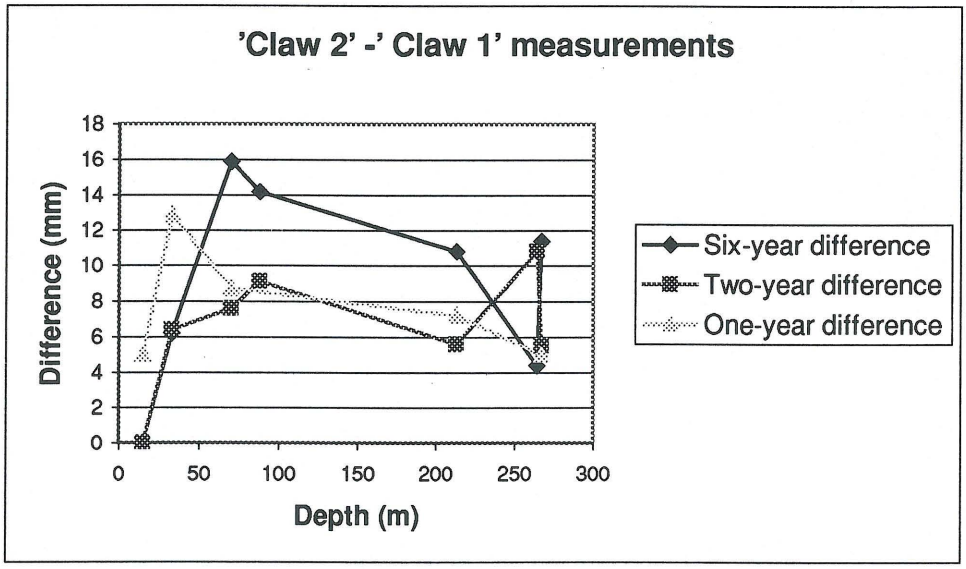


Figure 13: AA 'Claw 2' - 'Claw 1' measurements

Normalized lengths

One-year samples

The normalized length data for the dactylus and propodus after one year is difficult to report. In this group, more than in any other, the normalizing

length was not complete in many of the specimens. All of the propodi measurements are present, however, and the graph of their length has a very sharp peak at 33 m. The ratio at this depth of the specimen's original measured length to the normalizing length is about 12% higher than the ratio at the 15 m site, the nearest data point (see Figure 14).

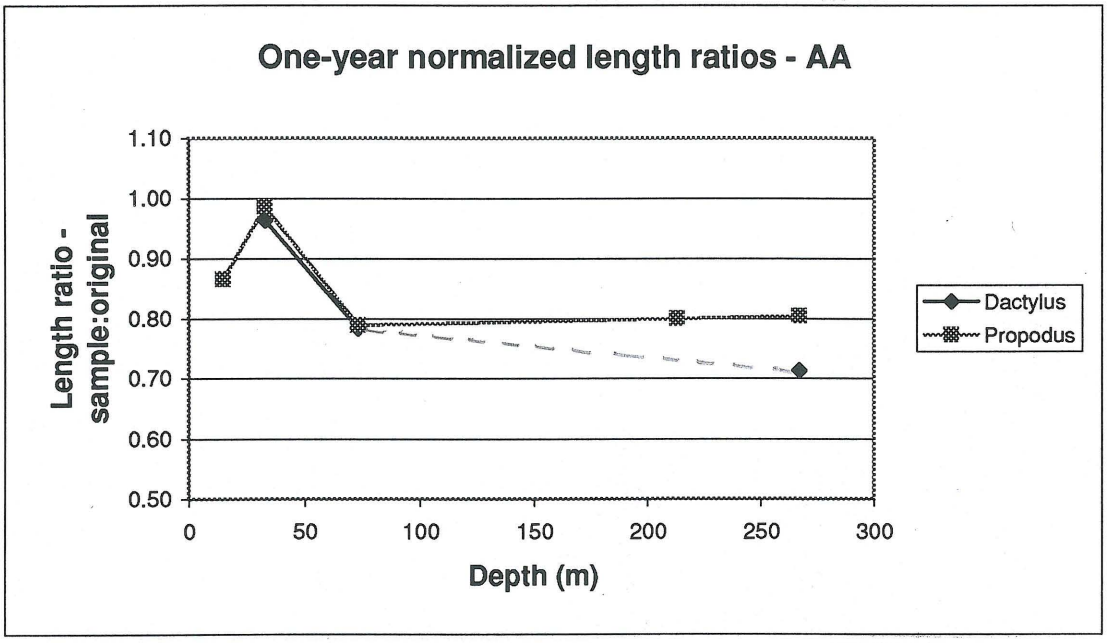


Figure 14: Normalized length ratios after one year (AA)

Two-year samples

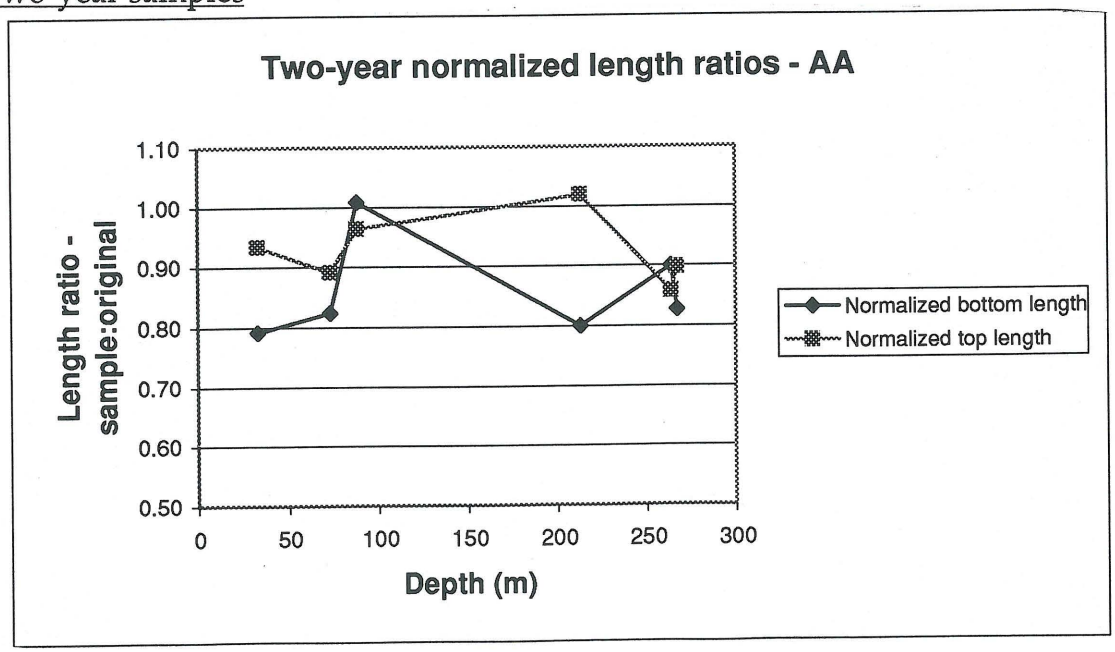


Figure 15: Normalized length ratios after two years (AA)

After two years, the normalized claw length data shows the now-familiar peak of preservation in the middle depths, tailing off to shorter fragments at both the shallow and the deep ends of the graph (see Figure 15). In this case, however, the propodus ratio peaks at 88 m and varies greatly, whereas the dactylus ratio peaks at 213 m, but is more uniform: the 88 m ratio is only 6% lower.

Six-year samples

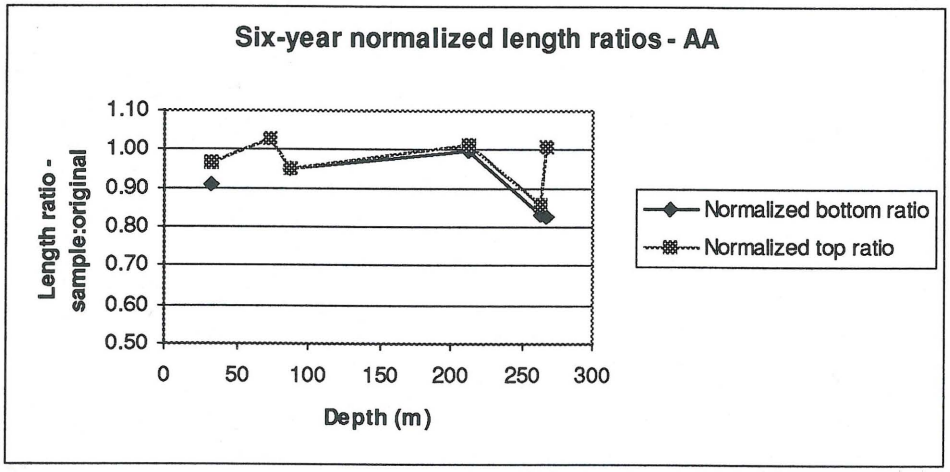


Figure 16: Normalized length ratios after six years (AA)

The six-year normalized length data is also somewhat inconclusive. Both dactylus and propodus trends are fairly uniform, and both maxima are within 5% of the next highest value (see Figure 16). In this sample the dactylus data peaks at 73 m, and all sites except for the 264 m site are within 8%, giving us very little information. The propodus data peaks at 213 m, and is within 9% of the 88 m and 33 m sites.

Weight

One-year samples

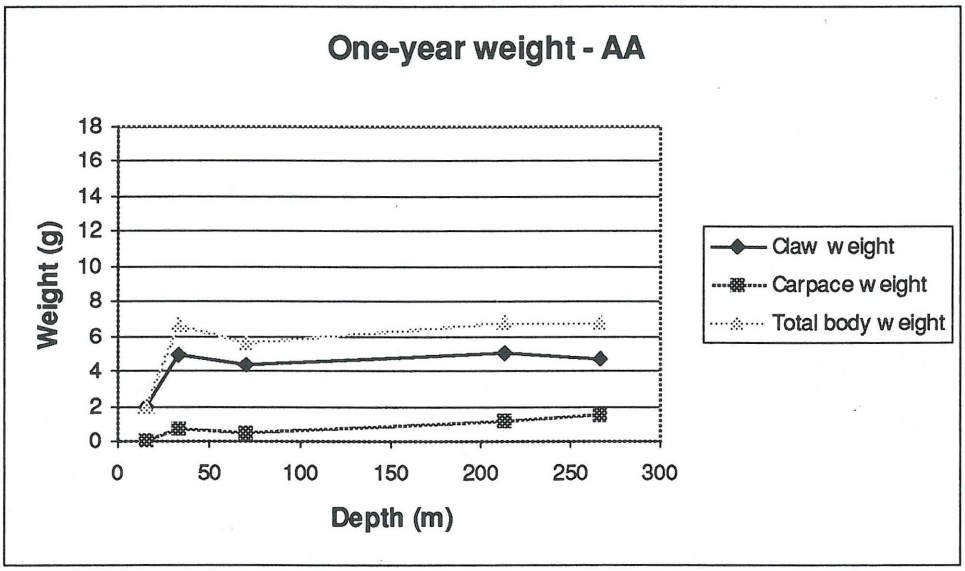


Figure 17: Weight after one year (AA)

Weights of crabs that had been deployed for one year were surprisingly uniform (no two measurements are more than 4.92 grams apart), and also surprisingly low compared to later years (see the time trend section below). The claw weight is highest at the 33 m site, but is within 6% of the 213 m site and the 267 m site. The carapace weight is highest at the 267 m site, and the total body weight is highest at the 33 m site, but is within a mere 2% of the 213 m site and the 267 m site, and is likely not significant (see Figure 17).

Two-year samples

The weight data for the two-year group of samples looks similar to the six-year length data (see Figure 18). Carapace weight and total body weight are both highest at the 88 m site. Claw weight is highest at the 267 m site, but this

weight is only 2% higher than the weight of the 70 m specimen, and so not considered different. Variation between depths over the whole graph, however, particularly in the total body weight category, is substantial. Again, the trend of these data show a distinct high at middle depths.

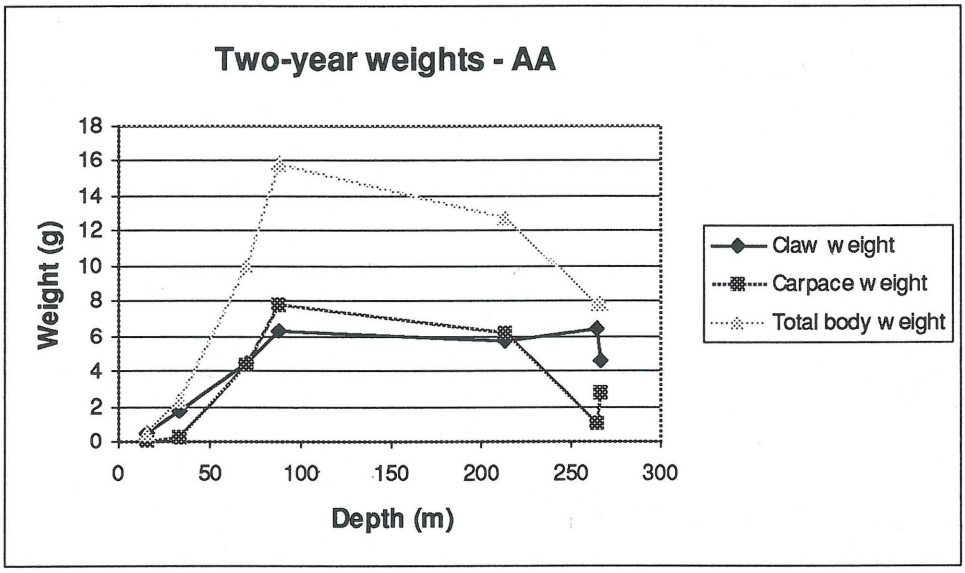


Figure 18: Weight after two years (AA)

Six-year samples

The six-year weight trends again show a peak in preservation around the 70 m- to 88 m range (see Figure 19): The claw weight is highest at the 73 m site, exactly 10% higher than at the 213-m site. Carapace weight is highest at the 88 m site, but only 6% higher than the 267-m weight. Total body weight, however, is conclusively highest at the 73 m site. Variation in weight is high across the depth gradient. In this graph, however, it is also significant to note that the carapace weight and claw weight trends mirror each other in a marked way. When one is increasing, the other is decreasing, and vice versa. This is also true,

although over a smaller depth range, for the 2-year data. This seems to suggest that processes that preserve the carapace are degenerative when applied to the claws, and vice versa.

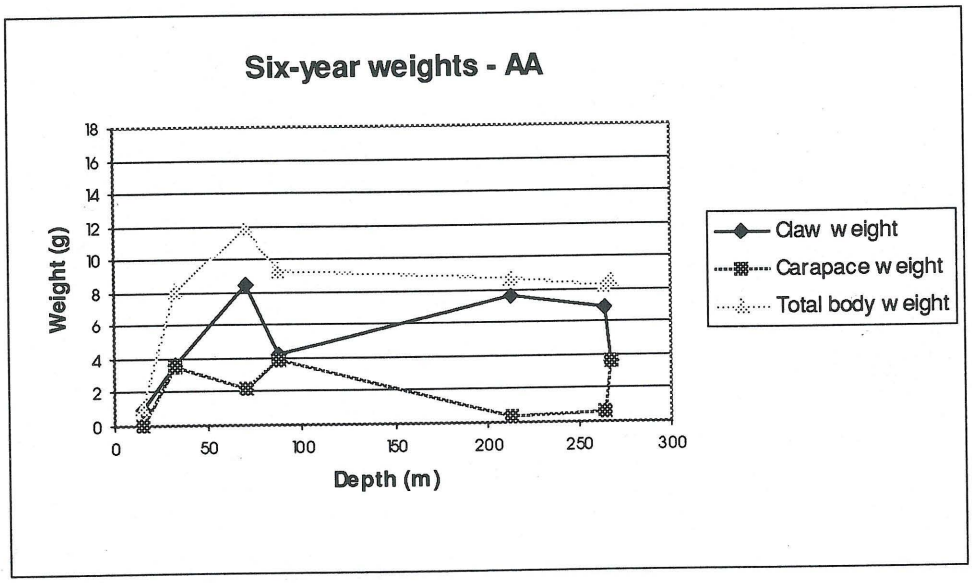


Figure 19: Weight after six years (AA)

Disarticulation and Breakage

One-year samples

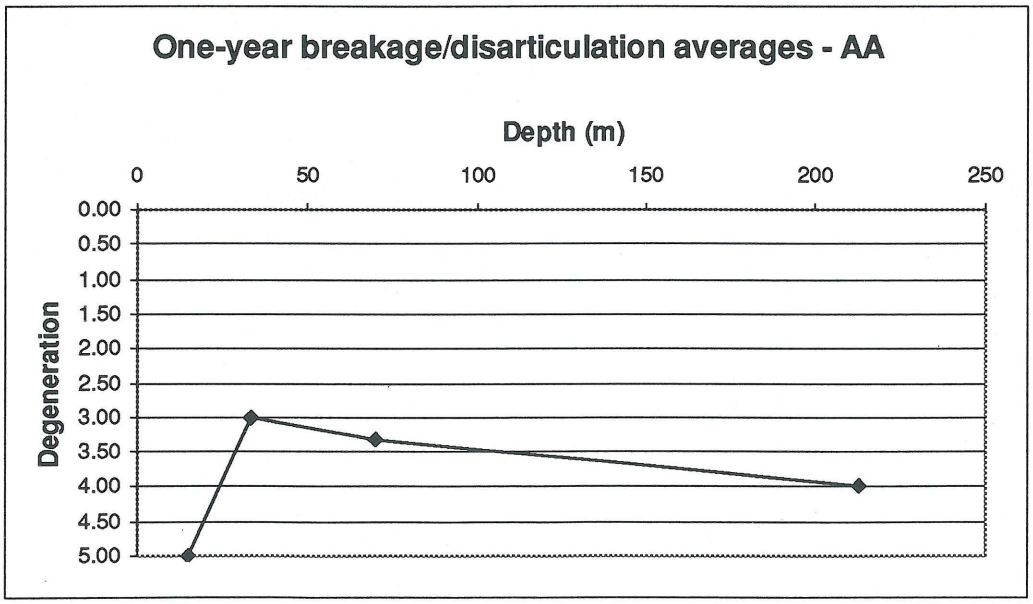


Figure 20: Disarticulation/breakage averages after one year (see Figures 8-9) (AA)

The disarticulation/breakage protocol values (taken as the average of the protocol numbers for the claws, mandibles, carapace points to represent degeneration over the entire body) show little variation, due to the somewhat narrow numerical scale, but the peak in preservation (in these cases the lowest number) for the one-year samples occurs at the 33 m site. The 267 m site is a close second, but is outside the 10% window, and the rest of the samples are ranged in greater states of degeneration (see Figure 20).

Two-year samples

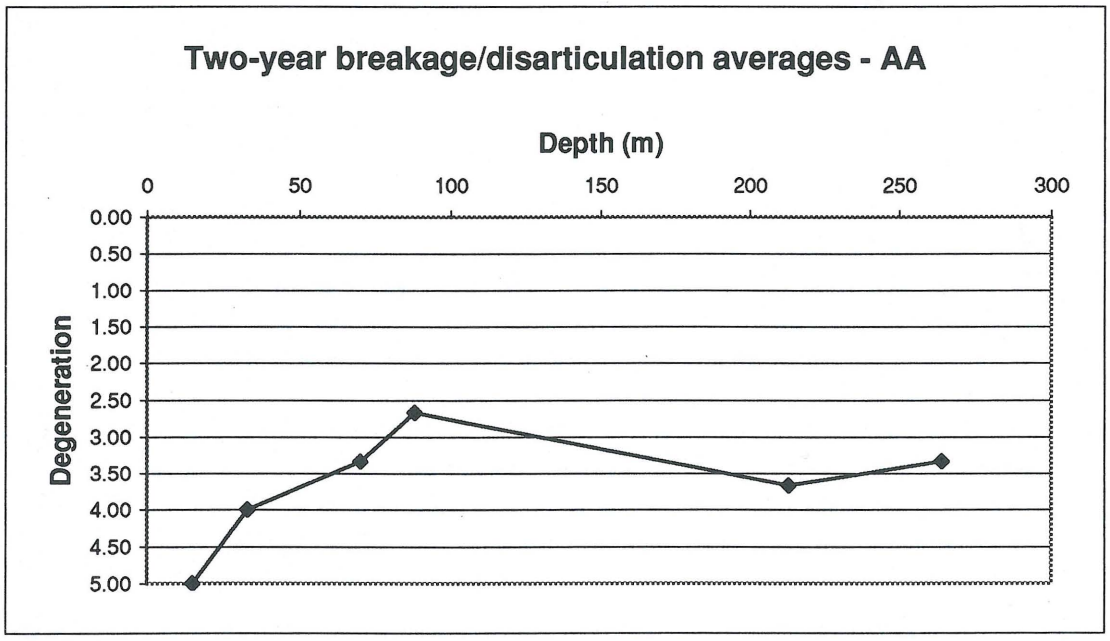


Figure 21: Disarticulation/breakage averages after two years (see Figures 8-9) (AA)

After two years, the variation in degeneration has increased. The peak for this group of specimens is at the 88 m site, and the difference between this protocol value and the next-highest value is two-thirds of a protocol point, which amounts to 13% more degenerated (see Figure 21).

Six-year samples

The six-year data show the widest variation of all the protocol data. The best preserved of these specimens occurs at 267 m deep; the 88 m site is 12% lower (more degenerated), but this value is only 2/3 of a protocol point (see Figure 22).

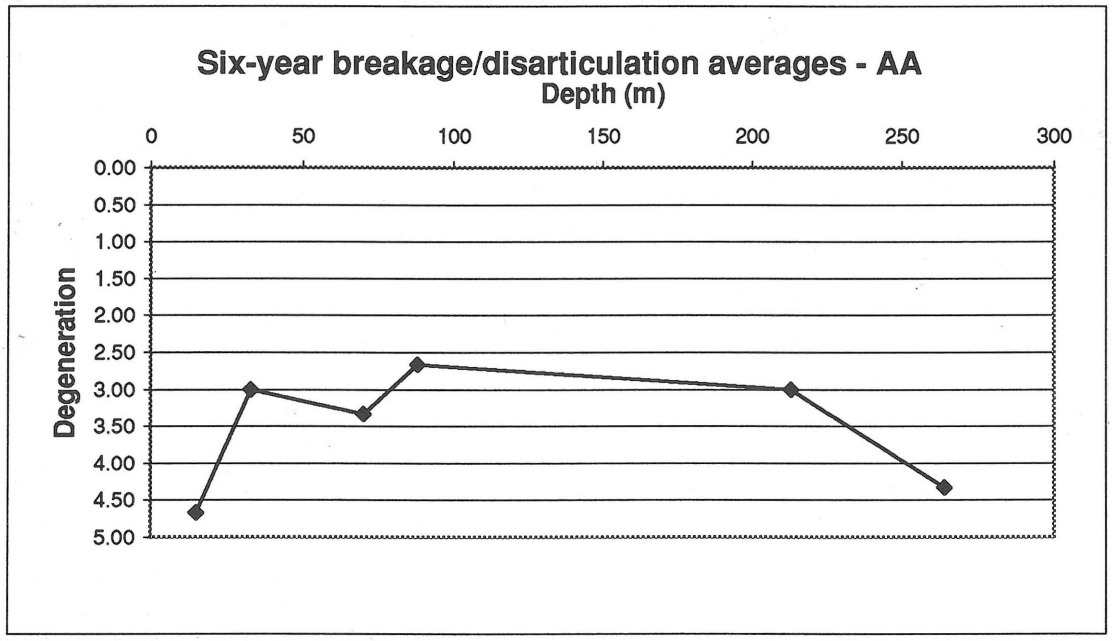


Figure 22: Disarticulation/breakage averages after six years (see Figures 8-9) (AA)

THE BA TRANSECT CRABS

In general, the BA (southern) transect data showed fewer strong trends than the AA data. Highs in preservation occurred most often at the deeper sites: at 183 meters, 253 meters, and 262 meters. The lack of strong trend may be due to the fact that the BA transect is further than the AA transect from a tidal channel between islands (Parsons-Hubbard, et. al., 1999, p. 341), and may therefore be slightly more protected from reversing tidal currents, increasing the time it takes for specimens to degenerate. In addition, six-year samples have yet to be collected from the BA sites.

Length

One-year samples

Specimens were deployed in 1994, and gathered from one of the 15 m sites, one of the 70 m sites, the 183 m site, the 195 m site, the 226 m site, the 253 m site, and the 262 m site. The one-year length data are somewhat confusing, with no general trends among the four body part groups (see Figure 23). Again, we see the same opposite trend between the claw length and the carapace length that showed up in the six-year AA crab weights. The carapace length peaks at 183 m, 10% higher than the length of the 195 m sample, and is lowest at 226 m, while the dactylus has its lowest value at 183 m, and its highest at 253 m. The propodus lengths and the carapace point lengths have less definite trends: the propodus line has peaks at 183 m and 253 m within 8% of each other, and the carapace point trend has peaks at 70 m, 183 m, and 253 m, all within 4% of each other. Clearly, in this case it is hard to tell the signal from the noise.

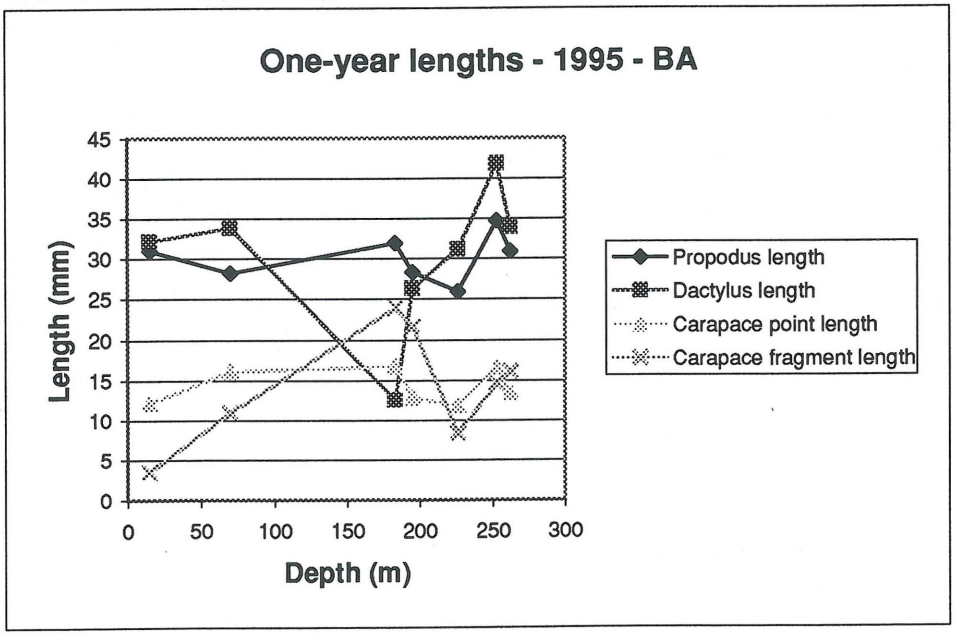


Figure 23: Length after one year (BA)

Two-year samples

Specimens were picked up after two years at two 15 m sites, two 33 m sites, two 70 m sites, the 183 m site, the 226 m site, the 253 m site, and the 262 m site. Data from depths where there are two sites (15 m, 33 m, and 70 m) have been averaged to give more accessible information. The graph of the lengths again shows little trend (see Figure 24). The only definite high occurs for the carapace point at 253 m. Inconclusive highs occur for the propodus at 262 m and 253 m (10% apart); for the dactylus at 33 m (7% larger than the 70 m, 226 m, and 262 m values); and for the carapace fragment at 253 m and 262 m (4% apart).

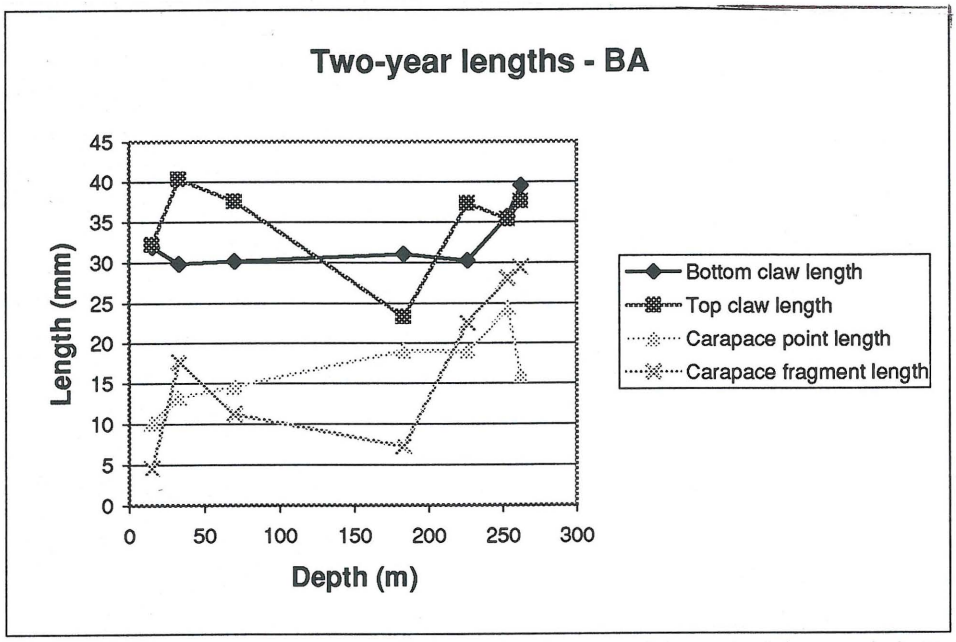


Figure 24: Length after two years (BA)

Hinge length

In the BA crabs, the difference between the 'claw1' and the 'claw2' measurements (Figure 25) were again similar to length and weight data. The largest differences were found at 183 m and 262 m after one year, and at 70 m and 253 m after two years.

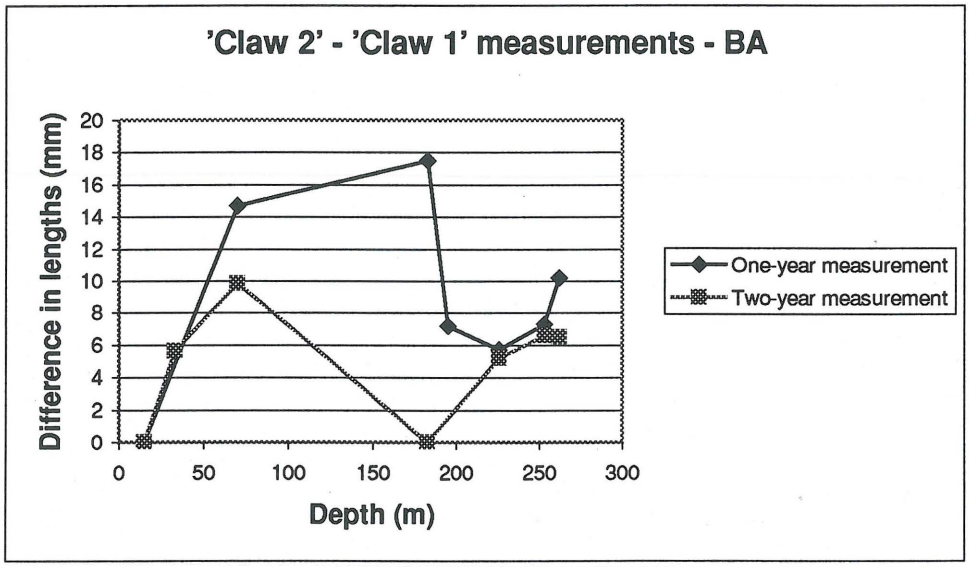


Figure 25: BA 'Claw 2' - 'Claw 1' measurements

Normalized lengths

One-year samples

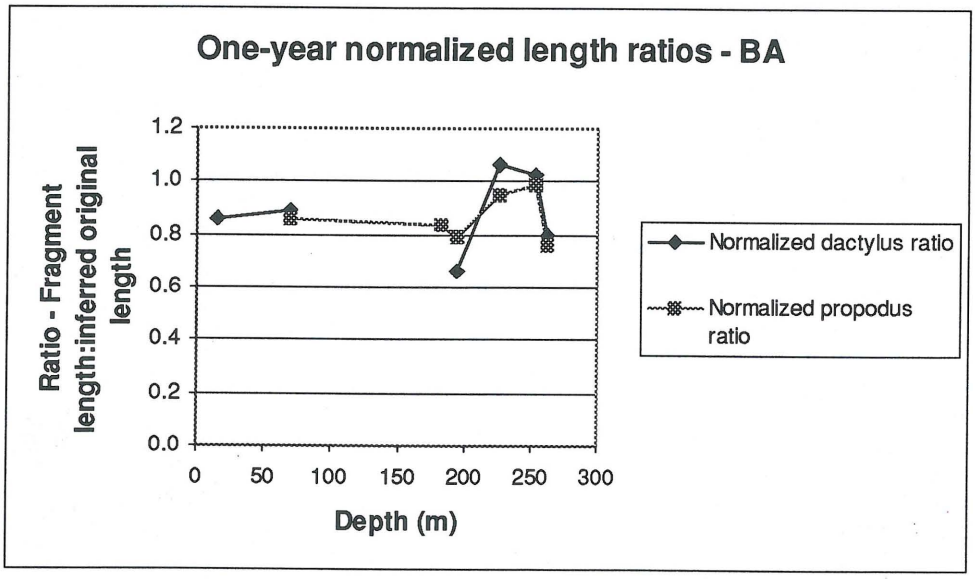


Figure 26: Normalized length ratios after one year (BA)

Data for the normalized length data after one year is markedly different from the uncorrected length data, which shows a large dip in preservation at the

middle depths. This graph (Figure 26), although incomplete, shows a more stable, straight trend with a swing upwards at the deep end. The dactylus peaks at 226 m, but is only 2% greater than the 253 m site, and the propodus peaks at 253 m, but is only 5% higher than the 226 m site.

Two-year samples

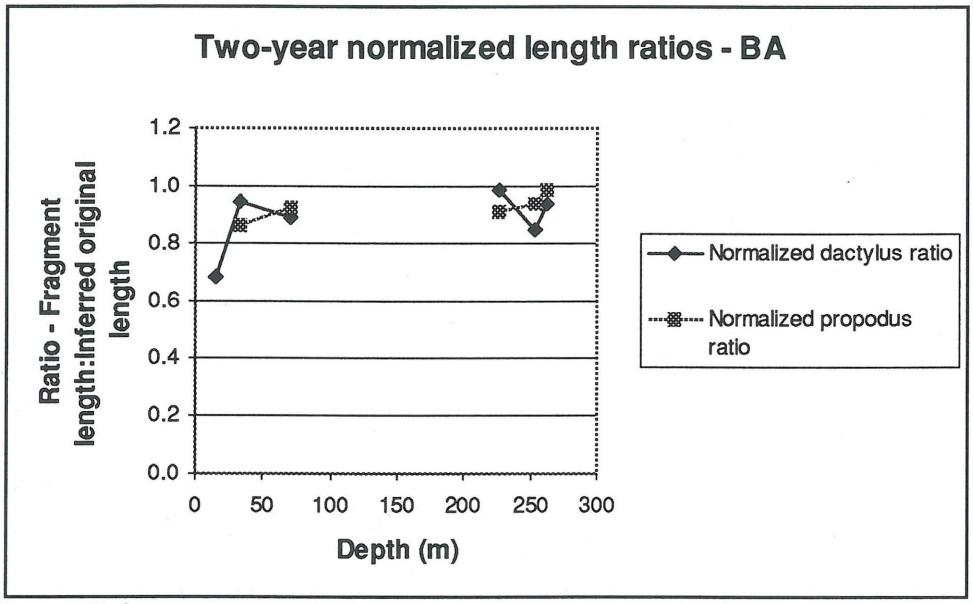


Figure 27: Normalized length ratios after two years (BA)

The normalized two-year length data is lacking the crucial middle-depth measurement, leaving two clusters of data, and no real trend (see Figure 27). Peaks occur at 226 m for the dactylus, and at 262 m for the propodus, but both of those values are within at 10% of one or two other sites. Normalizing this data didn't shed a lot of light on the original measurements taken on the two-year samples.

Weight

One-year samples

The graph of the weights of the samples by depth after one year show a somewhat striking lack of variation (see Figure 28); the difference between the lowest and highest total body weight, for instance, is only slightly more than two grams. The best preservation is deeper than on the AA transect, though; highs occur at 253 m for the claw weight (16% higher than the 70 m site) and the total body weight (16% higher than the 195 m site). The high for carapace weight occurs at 195 m, only 6% higher than the nearest peak, at the 183 m site. Again, it is interesting to note that the carapace weight trend and the claw weight trend are reverse images of each other.

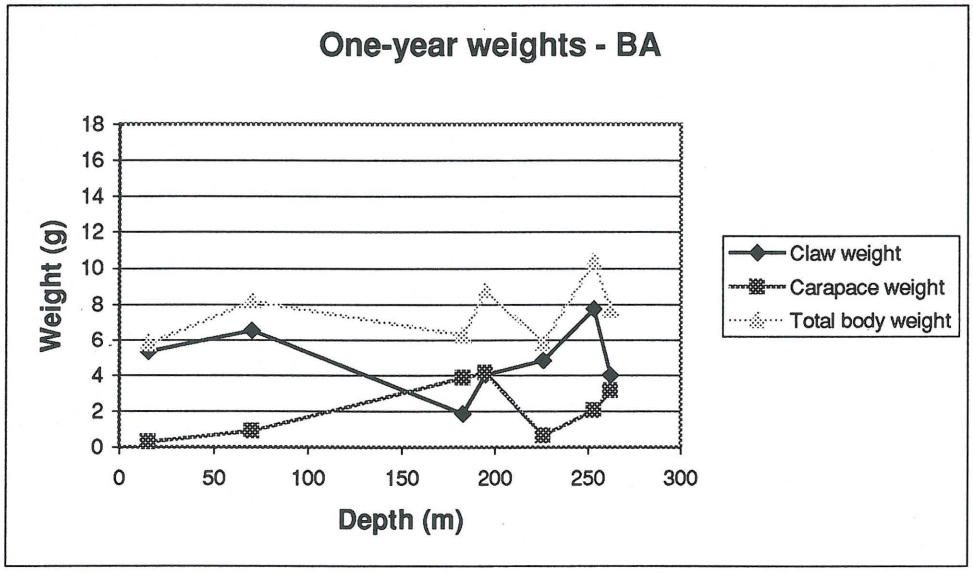


Figure 28: Weight after one year (BA)

Two-year samples

The graph of sample weights after two years shows an unexpected low in preservation at 183 m, and the amount of variation, especially when compared to

the one-year data, is large. All three categories have their lowest point at 183 m, by margins of 50% or more. All three also have their highest point at the 262 m site, by at least 13% (see Figure 29).

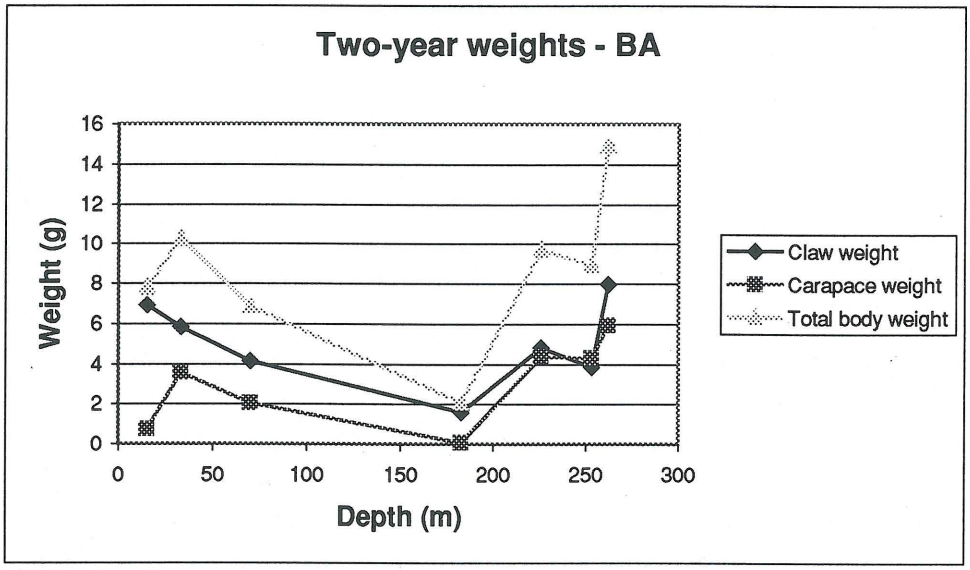
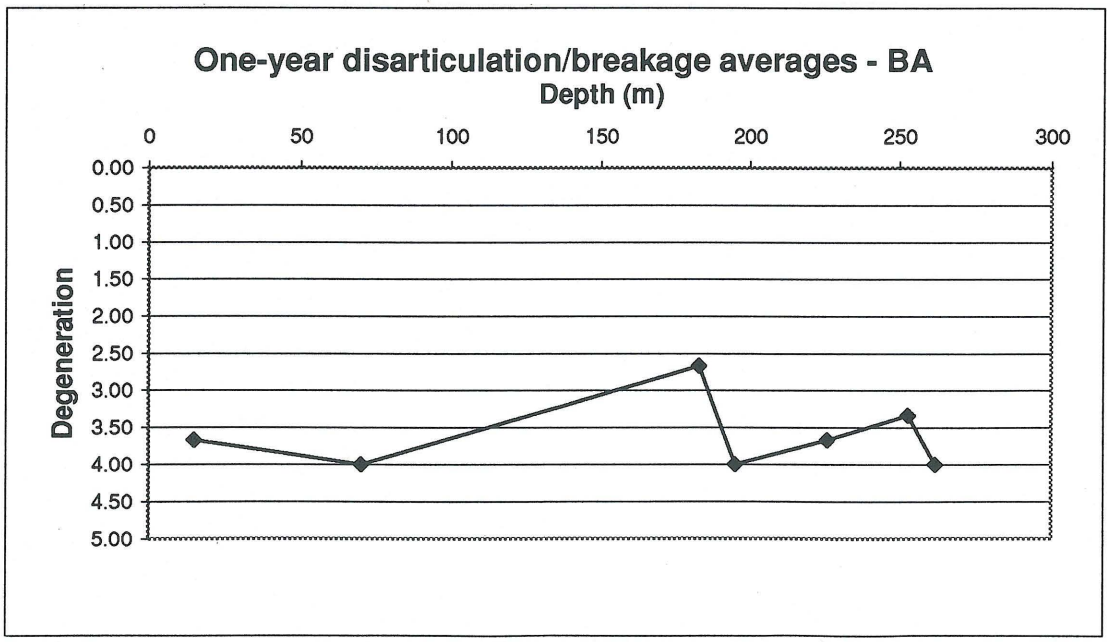


Figure 29: Weight after two years (BA)

Disarticulation and Breakage

One-year samples



The one-year disarticulation protocol data has a peak in preservation (represented in this case by the lower numbers) at 183 m, 20% better than the next smallest value, and tailing off to both sides of the trend (see Figure 30). Variation is fairly high.

Two-year samples

After two years, the peak in preservation has moved a little deeper, to 226 m, which is 11% better preserved than its nearest neighbor (see Figure 31). The variation of the protocol values is similar to that of the one-year data.

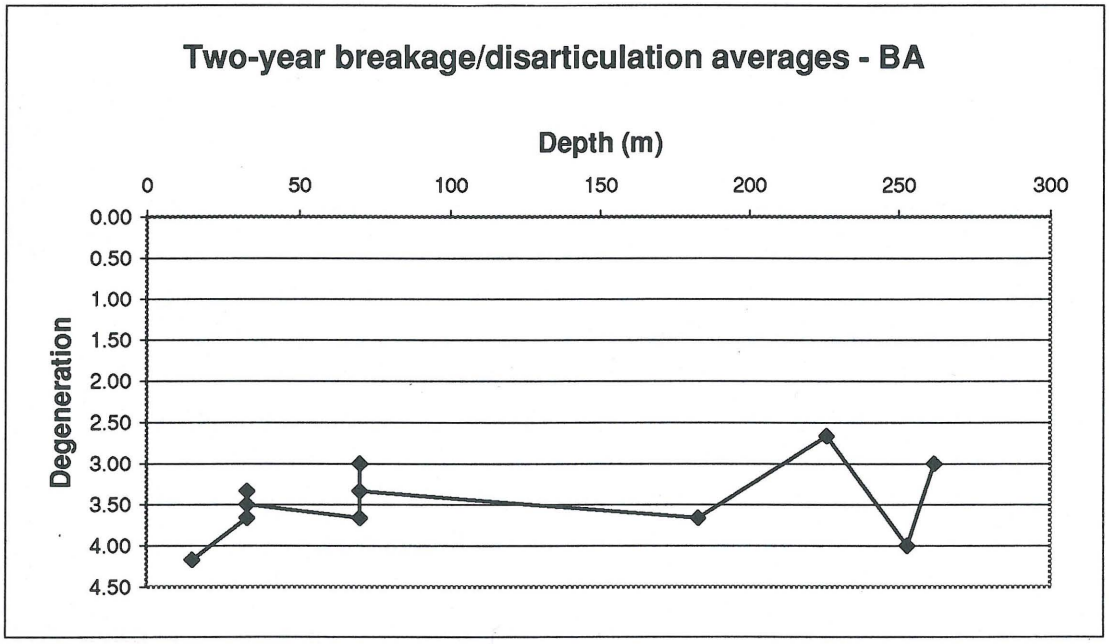


Figure 31: Disarticulation/breakage averages after two years (see Figures 8-9) (BA)

SURFACE CONDITIONS

Examination of the surfaces of the crab samples showed that the epicuticle, which gives fresh crab shells their slightly shiny appearance, was gone in all of the specimens, which had uniformly chalky surfaces. In most of

the samples, the pigmented layer of the endocuticle was gone as well, leaving the crab remains with a dull tan to white color. Pitting and cracking were evident, as was the layered structure of the cuticle; many samples showed breakage along these layers.

The scanning electron microscope images were somewhat difficult to interpret, but nevertheless showed a general trend of worse preservation and greater evidence of dissolution with increased depth. The control crab and the 15 m sample exhibit almost no pitting; the surface of the shell is fairly smooth except for extensive stringy features in the 15 m crab specimen, which I take to be the epicuticle or the pigmented layer degenerating (see Figures 32-33).

Figure 32: SEM image of fresh control crab shell

Figure 33: SEM image of claw dissolution at the 15 m site

The 33 m specimen and the 183 m specimen are almost identical, with a minimum of pitting and a fairly even surface (see Figures 34-35). Surface conditions at the 253 m site are much worse, with larger, more abundant individual pits and a more uneven surface, indicating more dissolution (see Figure 36). Given more time, it would be worthwhile and interesting to examine specimens from more of the AA sites as well as the BA sites. It has been shown, too, that the different parts of the crab shell dissolve at different rates (Plotnick, personal correspondence); since all the microscope samples were taken from

claw pieces, it is possible that analyzing a different body part, perhaps pieces of the carapace, would yield more information.

Figure 34: SEM image of claw dissolution at the 33 m site

Figure 35: SEM image of claw dissolution at the 183 m site

Figure 36: SEM image of claw dissolution at the 253 m site

TIME TRENDS

Surprisingly, time of residence on the sea floor does not seem to play much of a part in the comparative preservation of specimens along either transect. More often than not, sample measurements either remain constant or are slightly better preserved with longer deployment times, suggesting that the major portion of the degeneration occurs within the first year, after which more time on the sea floor doesn't affect the preservation of the samples too much.

SEDIMENT COVER

AA Transect

After one year, barely any sedimentation along the AA transect had taken place. Sedimentation was highest at the 33 m site and several of the deep sites, and bags were most exposed at the 15 m site and in the middle depths. Unlike preservation data, the sedimentation trends show a very steady increase with time (see Figure 37).

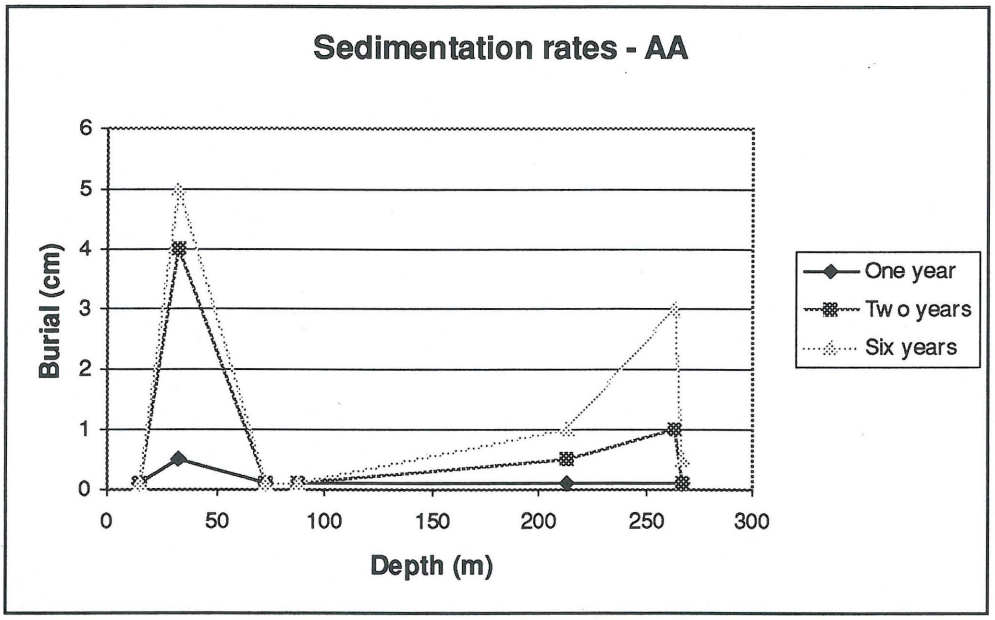
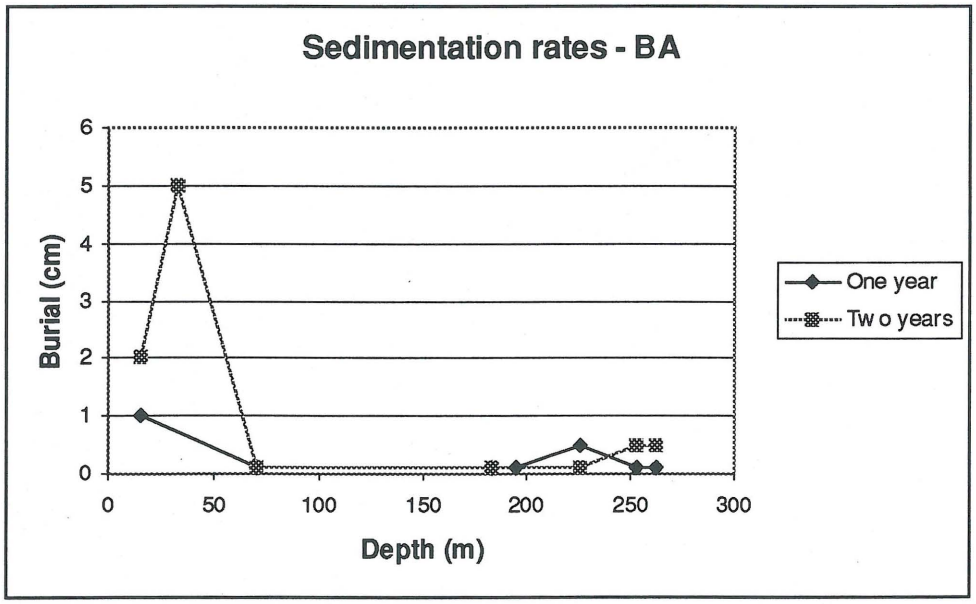


Figure 37: Sedimentation trends (AA)

BA Transect



The BA transect shows a pattern of sedimentation similar to the AA data—highest after two years at the 33 m site, a smaller peak at the deepest sites, and relatively little sedimentation in the middle depths (see Figure 38). Again, there is a marked increase in sedimentation over time.

TEMPERATURE AND SALINITY

Seawater salinity and temperature measurements were taken on several dives during the 1995 collection period, and the trends have a fairly consistent shape between the two transects (see Figure 39, but note the different scales on the AA and BA graphs). In general, these data are probably consistent through time and in the region of both transects; an unusually large increase in temperature or salinity would be required to affect any regional oceanic change.

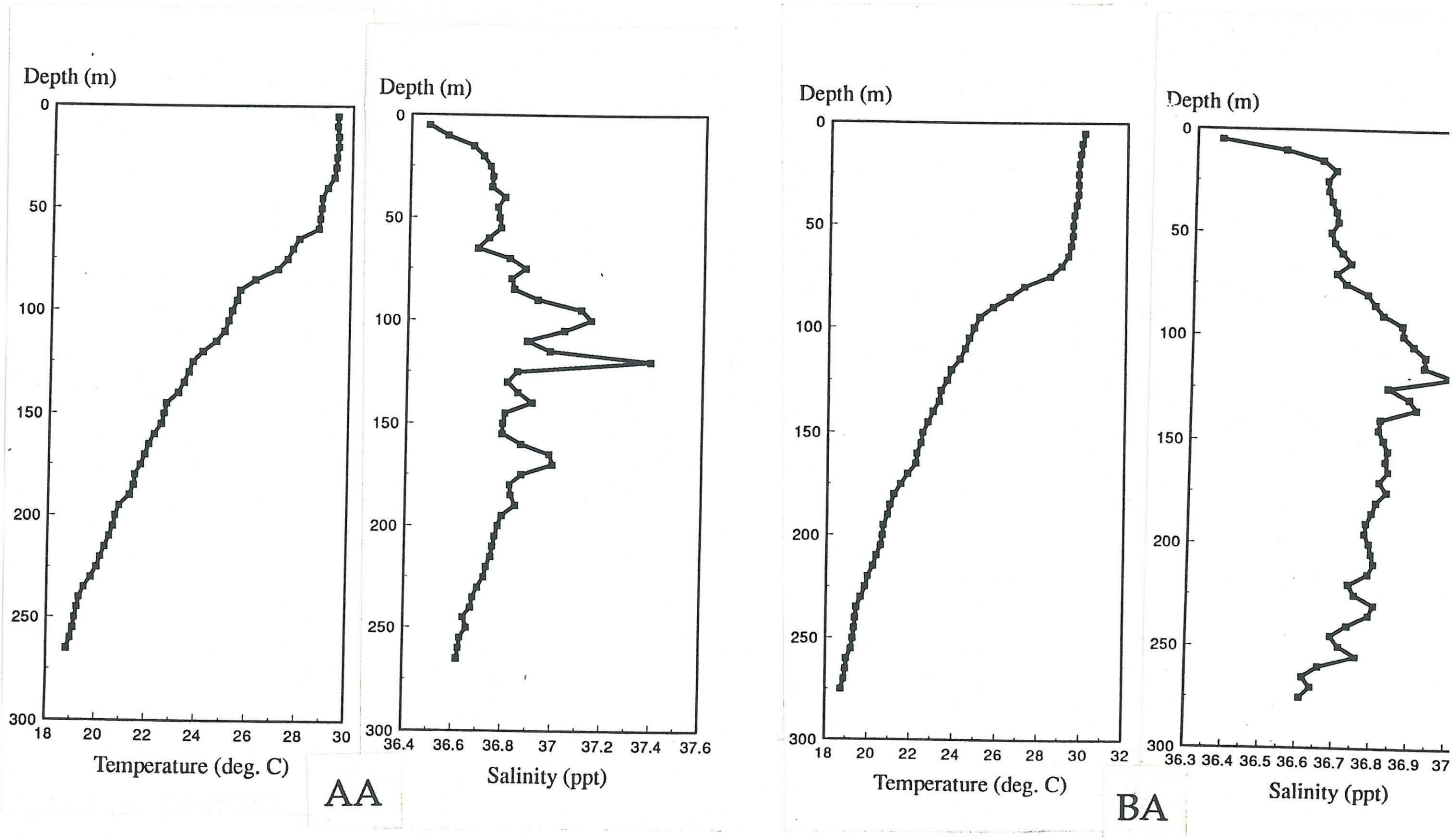


Figure 39: Temperature and salinity trends from two 1995 dives (courtesy Parsons-Hubbard)

Temperature

Temperature decreases from about 30.5° C (87° F) at the shallowest depth, around 5 meters, to about 18.5° C (65° F) at the deepest sites, between 260 and 275 meters. Temperature is fairly constant up to a depth of between 60 and 75 meters (close to the bottom of the photic zone), at which point it starts to decrease rapidly between 75 and 90 meters, and then at a somewhat slower constant rate down to the deepest sites.

Salinity

On average, seawater contains salts at a concentration of approximately 35 parts per million, although in tropical areas like the Bahamas this value is slightly larger due to evaporation. Along the two study transects, salinity ranges from approximately 36.3 parts per million at the shallowest depth (5 m) to a high of about 37 ppm at 120 m. Seawater salinity decreases from there, and at the deepest site (around 260 to 275 m), salinity is 36.6 ppm. It is interesting to note that the beginning of this spike in salinity coincides with the best-preserved specimens on the AA transect, at 73 and 88 meters. The spike ends between 150 and 175 meters, so these sites are the only ones that fall within this range of unusually high salinities.

DISCUSSION

Over the course of this study, these crabs have undergone an impressive amount of change. After only a year at even the most taphonomically inviting

depths, our crabs were transformed from whole animals into small piles of dust and debris. Only a few samples actually contained a still-articulated claw (the six-year 73 m AA site and the six-year 267 m site), and these samples had already begun to disarticulate themselves after retrieval. Retracing this path of degeneration has been interesting and at times surprising; trends I expected were nonexistent, and other trends that I would have deemed unlikely emerged instead. In the literal sense of the word, this research is groundbreaking in the field of modern taphonomy, so every result that emerges is of interest.

The breadth of this study is also one of its weaknesses, however. In an experiment of this magnitude, reconciling the large amount of data collected with the near-unlimited number of destructive and preservative factors that can be at work in the open ocean is a daunting task. However, trends do appear in the data, and some factors are more likely than others to strongly affect the deployed specimens; while I can't say conclusively that the data are directly caused by a specific environmental factor, I think I can present a few reasonable explanations for the trends in preservation observed.

Preservation is poorest at the shallow depths in all cases, but in many cases it is poor at deeper depths as well, and best in the middle depths. This is hard to explain with a single cause, but if there were one explanation for poor preservation at shallow depths and a different explanation for poor preservation at deep depths, then their interference would leave a space in the middle depths where good preservation is possible (see Figure 40).

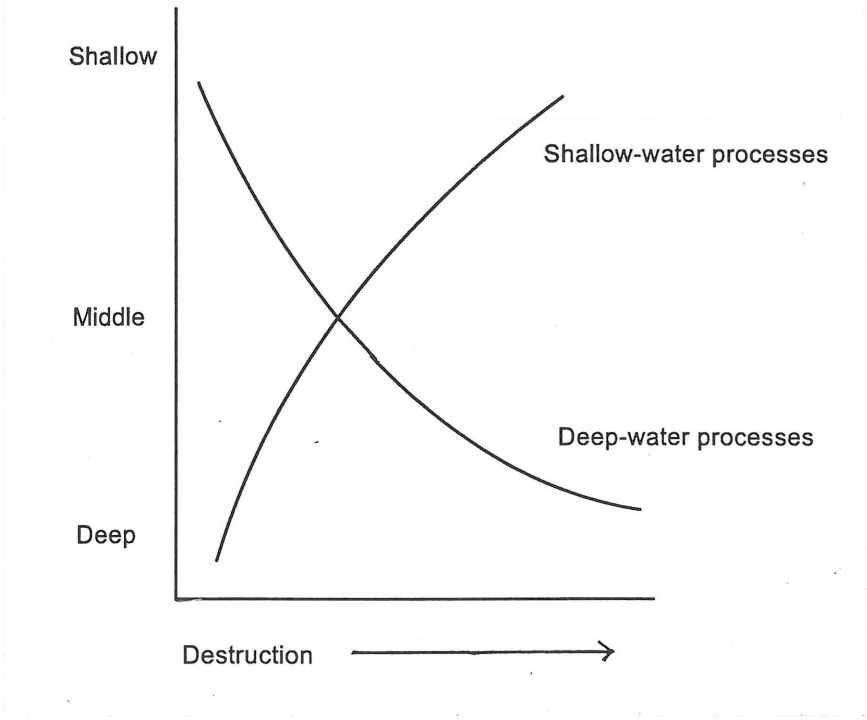


Figure 40: The interaction of shallow and deep water degenerative processes

In shallow waters, wave energy, predators, and microbial and bacterial decomposition play a huge part in the destruction of the crab remains, but these factors are much less important at depths below wave base and the photic zone (approximately 100 m). In the deeper depths, dissolution may play a larger part, since calcium carbonate solubility increases as temperature decreases and pressure increases (Linke, p. 270). Thus deeper, colder waters have the potential to retain more $CaCO_3$, and in the reaction $CaCO_3 \Leftrightarrow Ca^{2+} + CO_3^{2-}$, whereby the calcite crab shell is dissolved into the surrounding water, equilibrium is shifted to the right, in favor of dissolution, and subsequent decalcification of the chitin shell. Carbonate undersaturation is also the result of the CO_2 buildup from oxidation of organic matter (Canfield and Raiswell, 1991), a common occurrence

in deep, oxygen-rich waters. These mechanisms for deep-water degeneration are also supported by the scanning electron microscope images, which show greater dissolution at greater depths.

Several other factors may contribute to the unusual level of preservation found at the middle-depth sites: degree of burial, and salinity of surrounding water. Burial is thought to be a key to taphonomic preservation, but in this instance, sites with more burial did not necessarily coincide with better-preserved sites. It has been pointed out that predation is a major factor in taphonomic degeneration (Plotnick, 1986), and it is likely that burial prevents predation at least by macro-organisms. It may be that in this case, the fine mesh of the bags containing the specimens has served the same protective function that sediment burial does under normal circumstances, and so the protective effects that sedimentation have are masked by the protective effects of the mesh bags.

Another factor that may play a part in the selective preservation of the crab parts is seawater salinity. A spike in the salinity graph occurs at about 75 meters (see Figure 39), coincident with some of the sites of best preservation on both transects. A quick explanation for this is not as easy to come up with, but it is possible that the slight increase in salinity changes the environment enough to alter its biotic makeup, modifying or eliminating the degeneration that is the result of micro- and macro-predation and scavenging. Since the holes in the mesh are small enough to exclude larger predators and scavengers, micro-organisms are likely to play a part. Canfield and Raiswell (1991) discuss boring

micro-organisms; boring algae are active only in the photic zone and can be quite destructive, while boring fungi are found at depths up to 800 meters. It may be that the patterns left by the two are different enough that they create different types of degeneration in shallow and deep water. In any case, we may need to wait for more data before we are sure; the conclusive answers to the questions raised in this research project may come with the collection of another round of samples in the summer of 2001.

CONCLUSIONS

Although the body of data in this study was somewhat small, I feel that a significant trend of good preservation of crab parts in the middle depth ranges of a Bahamian carbonate platform was documented. When considered along with chemical and biological principles, as well as the work of other researchers in this field, this trend is well-justified, and may prove to be applicable to other marine environments.

Another round of specimens is due to be collected in the Bahamas in the summer of 2001, and this data will certainly add an important component to the conclusions I've arrived at in the course of this project. It will be interesting to see whether the data support these original findings, refute them, or a little of both. In any case, the taphonomic data that has been gathered on the crabs may be extremely useful in predicting the future taphonomic behavior of the molluscs and urchins in the larger SSETI study.

Once we begin to understand the ways in which environment affects alteration and preservation of organisms in modern oceans, we can finally begin to reconstruct a complete picture of the paleoenvironments in which fossil organisms lived and died.

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