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# SHELF AND SLOPE EXPERIMENTAL TAPHONOMY INITIATIVE (SSETI): BAHAMAS AND GULF OF MEXICO

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## ABSTRACT

The taphonomic signature on biogenic hardparts is an important aspect of all fossil assemblages. A rigorous long-term study was undertaken to better understand these signatures and to document specific signatures relative to given depositional environments. The Shelf and Slope Experimental Taphonomy Initiative (SSETI) seeks to establish taphonomic signatures, and rates of taphonomic alteration, for shell, wood, and other organism hardparts placed at various depths and bottom types along the continental shelf and slope in both the Gulf of Mexico and in the northern Bahamas. The Gulf of Mexico experiments were deployed primarily in siliciclastic sediments whereas the Bahamian experiments were deployed in carbonate sediments to compare the effects of sediment type on taphonomic signature. Experiments were retrieved at one and two year intervals between 1993 and 1995.

Results are compared for molluscs from two Bahamian sites after one year, one at 15 meters depth and one at 210 meters depth. Dissolution and epi/endobiont settlement are the most notable taphonomic features on the shells. Taphonomic signatures were found to vary with species within a site. For example, Mytilus edulis suffered far more alteration than Codakia orbicularis. Species differences in response to taphonomic processes point out the importance of shell composition and microstructure in controlling preservation and the final community attributes of the assemblage. Depth differences were also important. Both dissolution and epi/endobiont infestation were pervasive at the shallow site after only one year, whereas taphonomic alteration was proceeding at a much slower rate at the deeper site. The implications of such disparate taphonomic signatures at two closely juxtaposed sites after only one year of exposure are important for paleoecologic reconstruction and for modern ecologic studies.

#### INTRODUCTION

Reconstructing paleocommunities from fossil data requires a clear understanding of the variety of possible effects that post-mortem processes have on remains within their depositional skeletal environment. Taphonomy is the study of the processes that affect the post-mortem remains of organisms. Taphonomic changes include such physical processes as breakage, abrasion, dissolution, burial, and transport; and such biological processes as organic decomposition, epibiont overgrowth, boring and etching. Because of taphonomic alteration, the original community is rarely if ever fully preserved. Most studies of taphonomic processes have been observational in nature. In recent years, however, experimental taphonomy has shed new light on rates and modes of biological breakdown and preservation of skeletal and organic remains (Callender et al. 1990; Greenstein 1991; Kidwell and Baumiller 1990; Meyer and Meyer 1986; Walker and Carlton 1995).

The expanding interest in experimental taphonomy has been in part spurred by work on fossil assemblages and the development of the 'taphofacies' concept by Brett and Baird (1986). Most of the ensuing studies have concentrated on shallow water depositional environments and have been limited to periods of 1 to 2 years (Davies et al. 1989; Fürsich and Flessa 1987; Meldahl and Flessa 1990; Staff and Powell 1990). Many of these have used spatial and temporal sampling of the in situ assemblage to study the processes of decay and preservation. Sampling of the natural assemblage limits quantification of the rates of taphonomic processes and thus constrains the range of hypotheses that can be tested to explain observed variations in taphonomic signature. The research described here was designed to investigate taphonomic processes over longer time periods and in deeper-water shelf and slope settings where the bulk of fossil assemblages are preserved. The experimental protocol was designed to quantify rates of processes that produce natural shell accumulations rather than relying solely on observation of the natural assemblage which is already a product of years of taphonomic alteration.

## SSETI EXPERIMENTAL DESIGN

The SSETI program was designed as a controlled experiment to measure and compare rates of taphonomic processes over a wide range of continental shelf and slope environments of deposition (EODs). The program was designed to compare the range of common (aerially extensive) EODs typical of the shelves and slopes of the Gulf of Mexico and Caribbean Sea, as well as a series of unique (aerially restrictive) EODs of potential importance in the fossil record such as brine pools, collapsed basins, and carbonate-capped topographic highs. Because of the suspected slow rates of some important taphonomic processes in some EODs, each of the experiments was designed as a long-term deployment, some destined for a minimum of ten years on the sea floor. Of necessity, this program required the use of submersibles for experimental deployment and recovery. Accordingly, the experimental design was developed to permit dependable relocation of experimental sites, rapid deployment of experiments, and rapid and complete recovery of deployed experiments. In addition, the design encompassed the deployment of a wide variety of skeletal types in sufficient numbers to support rigorous quantitative analyses and statistical comparisons of EODs, skeletal types, and deployment periods.

The experiments consisted of three types of skeletal deployments: 1) bag arrays containing shells, wood, crab and urchin carcasses; 2) tethered shells; and 3) freely-scattered shells. In addition, grab samples were taken of the natural assemblage and, where possible, bottom-chemistry analyses were made in situ. Successful deployment and retrieval of all experimental arrays was conducted with some minor exceptions as noted below.

#### Experimental arrays

Shell material, wood, crab, and urchin carcasses were wrapped in net bags (1x1.5-cm mesh size). Bags were attached to a 1.2-m PVC rod so that all specimens in a single experiment could be deployed and recovered simultaneously by submersible. A  $25 \text{ cm} \times 25 \text{ cm}$  float made of sheet polyethylene was attached 1.5 meters above the array by polypropylene line. This float was easily seen by submersible and aided in re-locating the sites, particularly after burial of the rods (Fig. 1). This float and a 2.3 kg weight to counter its



Fig. 1: Diagram of experimental array site showing mesh bags containing shells, wood, and dead crabs and urchins; tethered shells; and freely scattered shells. The bag-array rods are weighted at one end with a commercial 4.5-kg weight.

buoyancy, were attached at one end of the rod. The wood bag had an additional small weight. Two bags of shells, 1 bag of wood, and 1 bag of urchins and crabs were attached to each rod by cable ties. Each bag contained multiple specimens with either 1, 2, or 5 individuals of each species per bag segregated within the bags by cable-tie partitions. The species and numbers of specimens are listed in Table 1.

To ensure equivalent taphonomic status among all shells, urchins, and crabs deployed, and to deploy them in the condition expected upon death of the living individual, skeletal hardparts from the natural assemblage at the experimental sites could not be used. Therefore species were obtained from wholesale vendors, from shellfish processors. and *Echinometra* and *Arbacia* were collected live in Florida. Mollusc bags were loaded with six species (5 individuals each) separated by cable-tie barriers. Molluscan types were chosen to cover a range of shapes and shell structures, however, these species were also chosen to be similar in size, shape, and shell structure to locally-occurring molluscs.

Wood species were chosen to maximize the variety of wood types (i.e., primitive woods, complex woods). The wood specimens were sawed into rectangular shapes to facilitate reconstruction of blocks after loss of surfaces. Blocks of wood were put in bags in known positions within sectors separated by mesh barriers.

Because of their potential to disarticulate into smaller fragments, the crabs and urchins were placed into fine-mesh (0.5-cm mesh) bags and then enclosed in the larger net bags. The two kinds of urchins were placed in separate small-mesh bags as well. The experimental bags with their delicate specimens were kept frozen until 5-15 minutes before emplacement on the submersible for deployment. Controls for the bagged experiments were kept in a laboratory freezer. These were complete sets in mesh bags for shells, crabs, urchins, and wood.

Gastropods were tethered to PVC pipe by nylon fishing line tied through a hole drilled through the body whorl just behind the aperture. These "hermit crab traps" contained 10 shells each; 2 Busycon canaliculatus, 4 Telescopium telescopium and 4 Strombus luhuanus. A polyethylene float and a 2.3-kg weight were attached at the end of the rod.

### Site arrangement

With a few exceptions, four deployment sites were established in each EOD. In some cases, EODs were relatively uniform in topography and sediment texture. Multiple sites allowed comparisons to be made between within-EOD and between-EOD rates of taphonomic processes. However, some EODs offered a complex array of habitats so that each single site represented some point in a complex gradient of topographies and sediment textures. Four bag arrays, one shell-scatter area marked by two vertical PVC marker poles, and one tethered shell array were deployed at each of the 4 sites (Fig. 1).

## Video surveys

All sites were surveyed annually by video to observe movement of the arrays, the burial rates of arrays, and movement/burial of shells freely scattered on the bottom. Computerized frame-capture techniques were used to assess burial and the distance and direction of transport.

#### Laboratory analyses

Taphonomic data were recorded using methods described in Davies et al. (1990). For animal taxa, the methods include measurement of size, wet weight, photography of each specimen, and evaluation of breakage, dissolution, abrasion, edge rounding, condition of periostracum (for mollusks), color, authigenic precipitation, and biologic alteration. For mollusks, each taphonomic characteristic was analyzed for each of 8 standard shell areas for bivalves (e.g., anterior margin, umbo) and 5 standard shell areas for gastropods (e.g., body whorl, spire). Taphonomic alteration of each shell area was graded either weight, density) quantitatively (e.g. or semiquantitatively (e.g., increasing levels of dissolution from chalkiness through pitting to complete loss of the surface shell layer). Biologic alteration was determined by estimating percent coverage of epi- and endobiontic species in each shell area. Definitions of the semi-quantitative scales used are given in Davies al. (1990). This approach is being utilized at least at a comparable level by a number of workers (Walker 1992; Kowalewski et al. 1994; and Parsons and Brett 1990) which allows these results to be compared with the other taphonomic studies mostly done in shallowwater settings. Crabs and urchins were analyzed with the same scheme as for mollusks, but using 4 and 12

Table 1: Contents of specimen bags attached to each experimental array. Occasional substitutions of the following species were necessary: \*or Arctica islandica, \*\*or Arbacia sp., tor Argopecten irradians, ttor Turitella terebra.

Wood Bags Species	No.	Mollusk bags (2 per rod) Species	No.	Crab/Urchin bags Species	No.
aged <i>Quercus</i> (oak)	1	Bivalves	-	Callinectes sapidus	1 or 2
new <i>Quercus</i> (oak)	1	Mytilus edulis (muscle)	5	"blue crab"	
Pinus (pine)	1	Mercenaria mercenaria* (Quahog)	5		
Magnolia (magnolia)	1	Codakia orbicularis (lucinid)	5	Echinometra lucunter**	2 or 3
Araucaria (parana pine)	1	Glycymeris undata†	5	"thin-spined urchin"	2 02 0
Sequoia (cedar/red wood)	1	Gastropods			
(Pinus) pine cones	0-2	Strombus luhuanus	5	Eucidaris tribuloides	1
Juglans (walnuts)	2	Telescopium telescopium††	5	"pencil urchin"	1
		(Philippine mud snail)			



Fig. 2: Location map for the Gulf of Mexico continental shelf and slope experimental sites. STS -South Texas Shelf, 200m; MS - Mid-Continental Shelf, 75m; IMS - Intermediate Shelf, 125m; OCS - Outer Continental Shelf, 190m; CS - Continental Slope, 363m; EFG - East Flower Garden (3 sites, 65-100m); GC -Green Canyon, 548-734m; GB - Garden Banks Petroleum Seeps, 570m; PB - Parker Bank, 120m.

test positions respectively (e.g., claws, carapace for crabs; 5 aboral and 5 oral test positions for urchins). Each specimen was weighed, measured and then frozen for future analyses of amino acid, protein, lipid, and carbohydrate content of soft parts.

Each specimen of wood was photographed, measured, assessed for patterns of loss of material (e.g., ragged edges, raised grain), percent of surface bored and encrusted, and color. Specimens were divided in half. One half was frozen for detailed chemical analyses and for calculation of density (dry weight to volume). The other half was preserved in a formalynbased fixative (FAA), embedded in epoxy and thinsectioned for microscopic examination.

#### Grab samples

Samples of natural shell assemblages were collected by grab sampler. These shells are being subjected to the same taphonomic examination as the experimental shells for comparison.

#### In situ chemical tests

Important taphonomic processes such as dissolution should be related to sediment chemistry. Therefore, a "benthic lander" (Rowe et al. 1994) was deployed at most locations to measure sediment-oxygen demand and nutrient fluxes. At shallower sites, paired clear and opaque chambers were used to measure heterotrophy and photosynthesis simultaneously; photosynthesis was not important at the deeper stations. Samples for water and interstitial water chemistry were also taken at each lander site.

#### SSETI DEPLOYMENT SITES

Experiments were deployed in 1993, 1994, and 1995 to directly measure the rates of taphonomic and burial processes in selected environments of deposition. The Johnson-Sea-Link was used in the Gulf of Mexico and the Nekton Gamma in the Caribbean. One-year samples have been collected from all 1994 sites in the Bahamas. In addition, two-year samples have been collected from all 1993 sites in both the Gulf of Mexico and the Bahamas. Preliminary shallow-shelf and deeper slope data from a one-year (1993) deployment in the Bahamas are reported here. Rigorous analyses of the data are underway for one and two-year samplings; only general trends are discussed.

#### Gulf of Mexico

Experimental arrays were deployed at 14 locations that encompassed a variety of terrigenous and carbonate settings on the Texas-Louisiana continental shelf and slope (Fig. 2). The open shelf and slope sites, predominantly floored with terrigenous gray to black



Fig. 3: Southern Bahama island chain showing location of transects AA and BA at the shelf edge northeast of Lee Stocking Island. The two sites on transect AA discussed in the text (15 m and 210 m) are marked. CMRC (Caribbean Marine Research Center).

mud, ranged in depth from 75 - 190 meters on the shelf to 363 meters on the slope (Hay and Southam 1977; Milliman 1974). Sample arrays were also set out at atypical locations such as brine seeps, petroleum seeps, hardgrounds, a collapsed carbonate bank, carbonate sands, and deep-water reefs (Fig. 2). The deepest sites, at petroleum seeps, exceeded 600 m.

#### Bahamas

Experiments were deployed in four different depositional environments along the Atlantic side of Lee Stocking Island, Bahamas (Fig. 3, 4): 1) shallow coral reef (15 to 33 m), 2) near-vertical wall (73 m), (210 m), and 4) deep-water carbonate slope 3) carbonate dune field (292 m). The reef sites included both sand and hard bottom areas of a larger reef and patch-reef complex. The wall drops off from a depth of 33 m at a slope exceeding 60°, to depths greater than 200 m. Wall sites are characterized by hard-bottom substrates affected by moderate current velocities and populated by a variety of attached biota. Experiments were deployed along narrow ledges projecting from the wall. Below the wall, the slope begins to moderate at about 220 m. Carbonate sands with occasional outcroppings of carbonate rock dominate the bottom in this area. The sparse macro-biota include stalked crinoids, basket stars, and crustaceans. Further downslope, the deep-water dune field (300 m) consists of carbonate mud with a sparse macrofaunal assemblage. Samples were deployed along two permanent transects established by NURP (National Undersea Research Program), AA and BA, that cross the above environments (Fig. 3). A slightly higher-energy regime was observed along transect AA (Table 2). Along transect BA sediment cover was somewhat greater and higher burial rates of the experiments were observed. The two sites compared in this brief analysis are from the Bahamas transect AA. The shallow site (15 m) lies about 1 km landward of the shelf break. The experimental arrays were deployed in a low carbonate ridge. The deeper site (210 m) was located near the base of the wall. The bottom consisted of muddy carbonate sand with outcroppings of carbonate rock and rubble.

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### RESULTS

Analyses are ongoing for the 1- and 2-year Bahamian samples. Only general observations and conclusions can be offered for 2-year samplings. Two sites, one on the shelf and one on the slope, are compared here. At the 15-m site, over the period of one year, arrays were not transported, but were intermittently buried, often completely, by shifting sands. The deep, 210-m site showed little evidence of movement or transport and no burial of the arrays was noted after one year.

Taphonomic changes that occurred between deployment of the arrays in July 1993 until collection in August 1994 were considerable, especially at shallower sites. Shells that were deployed at 15 m showed considerable breakage. In contrast, shells at the deeper site showed no breakage. Shells were deployed whole, but disarticulated with the exception of Mytilus which were deployed paired and articulated. After one year, all Mytilus valves were disarticulated at both depths, and 70% of the valves were broken at 15 m. No breakage occurred in Mytilus valves at 210 m despite their fragile character. Ten percent of Strombus shells were broken at the shallow site, and all of the Telescopium and Codakia remained entire after one year (Table 3a and b).

The proteinaceous periostracum and ligament serve to protect many molluscs from predation, biont settlement, and destructive chemical action. Upon death, this coating may be rapidly broken down by bacterial attack. Mytilus and Arctica shells were deployed with periostracum either partial or complete. Ligament was present on all Mytilus valves; 90% had complete periostracum and 10% partial. After one year however, periostracum and/or ligament was completely gone in 40-50% of Mytilus shells and only partial periostracum remained on the other 50-60% of shells. In contrast, no changes were noted in Arctica shells at either depth (Table 4). Codakia, Strombus, and Telescopium shells did not have readily observable periostracum. Dissolution was a significant factor on shells deployed for one year (Fig. 5). Codakia valves showed a significant increase in the amount of dissolution in shallow water, with from 60% of the shells exhibiting no dissolution to 100% showing at least minor dissolution. In deeper water, however, Codakia was less affected by dissolution. On the other hand, dissolution increased with depth for Arctica. Arctica controls showed evidence of minor and major dissolution, whereas 70% of shells collected from 15 m



Fig. 4: Generalized slope profile of the AA transect in Exuma Sound, north of Lee Stocking Island, Bahamas. The general character of the bottom is described along the slope. Experiments are deployed at each of the markers shown on the diagram.

registered extreme dissolution after a year on the sea floor and, at 210 m, all shells showed extreme dissolution. Extreme dissolution refers to shells which have lost all surface sculpture and are deeply eroded and pitted, minor dissolution would include shells with a slightly "chalky" appearance. Gastropods exhibited patterns similar to *Codakia*, with the shallow shells affected more than the deep shells.

The incidence of dissolution in *Mytilus* appeared to decrease at 15 m relative to controls, however biont coverage at 15 m made minor dissolution difficult to discern. Dissolution increased at 210 m, where biont coverage was much lower. No authigenic precipitation was recorded.

Increases in epibiont colonization were significant at 15-meters depth over the one-year period. The average percent area colonized by skeletonized epibionts in one year ranged from 11% cover on Arctica islandica to 37% cover on Mytilus edulis, with some individual shells having their surfaces completely covered.

Table 2: Descriptions of experiment sites along the shelf and slope on transect AA north of Lee Stocking Island, Bahamas. Descriptions are generalized for the area.

Transect	depth (m)	name	bottom type	site description	associated benthic fauna
AA	15	"ridge"	hardground	on hardground of a low- relief reef on sand	diverse Atlantic shallow reef community
AA	30	" NW "	medium to coarse carbonate sand	in sand channel among patch reefs	diverse Atlantic reef community
AA	73	"wall"	hardground	rock ledge on near- vertical ledge	plate corals, sponges, gorgonians, diverse encrusting community
AA	88	"wall"	hardground	rock ledge on near- vertical ledge	plate corals, sponges, gorgonians, diverse encrusting community
AA	210	"crinoid"	fine carbonate sand and rock ledges	carbonate rock promon- tories and fine sand many stalked crinoids	sparse. stalked crinoids, spider crabs, and sea whips
AA	264	"crest"	fine carbonate sand	crest of sand dune aligned perp. to slope	sparse macrofauna, crabs, and sea whips
AA	267	"trough"	fine carbonate sand	trough of sand dune aligned perp. to slope	sparse. crabs, and sea whips



Fig. 5: Dissolution in molluscs deployed for one year at 15 m and at 210 m in the Bahamas. Controls were kept in a laboratory freezer. Significant differences from control shells are given above the bars.

Table 4: Presence of periostracum and/or ligament in Mytilus and Arctica. Codakiids and gastropods do not have a readily-preservable periostracum and none of the Codakia shells were deployed with ligament. Changes in Mytilus were significant (n=10, p<0.01).

		Mytilu	s eduli	Arctica islandica			
		ontrol		210 m	Control	15 m	210 m
Present	1000	90%					
Partial,	or	10%	60%	50%	100%	100%	100%
ligament	on	lу					
None			40%	50%			

Mytilus and Arctica shells were colonized primarily by polychaete tube worms and had lesser amounts of coralline and green algae (Fig. 6a,b). Average cover on Codakia orbicularis (Fig. 6c) was 29% of the total surface area. Some of this total was non-preservable green algae, and a large portion of the skeletonized epibiont community was coralline algae. Cover on Strombus luhuanus was dominated by coralline algae, polychaete worm tubes, and soft green algae. The total epibiont coverage on Strombus was 45%, and 37% of the total was preservable (Fig. 6d). Total coverage on Telescopium was 31% with the majority of the bionts being polychaetes, green algae, and coralline algae. Telescopium had the most diverse coverage including bryozoans, tunicates, forams, and sponges (Fig. 6e).

Epibiont coverage was low on shells deployed in deeper water. Algae was virtually absent due to low light levels. The majority of epibiont species were tubeforming polychaetes, but foraminifers and fungi were also present in very low abundance.

#### DISCUSSION

A taphonomic signature significantly different from controls developed within one year of post-mortem history in shells deployed at both shallow and deepwater sites. Shells were more affected by physical factors at the shallow site as most fragmentation occurred at these sites rather than at deep sites. Disarticulation of Mytilus valves occurred at all sites. However, disarticulation could be caused by decay of the ligament and/or jostling during deployment or collection, rather than natural physical processes, so articulation must be considered with caution. Three of five molluscan species underwent more dissolution at the shallower site than at the deeper site. Arctica and Mytilus showed the opposite trend with increasing depth. Although the two species differ considerably in shell structure (e.g. Mytilus is very thin-shelled, Arctica is thick and heavy-shelled), these two species had partial periostracum. Possibly, degradation of the periostracum catalyzed a more rapid rate of carbonate dissolution. Overall, mussel shells were degraded by taphonomic processes more than other species. Codakia (lucinid) shells were degraded less. This same relationship was noted at petroleum seeps in the Gulf of Mexicc at depths of about 600 m by Callender et al. (1994).

Epibiont coverage was very high after only one year at 15 m. A large proportion of these bionts were algal, despite intermittent sand coverage. At 210 m, where algal bionts were rare, total epibiont coverage was also low. At depth, the most common bionts are polychaetes and forams which colonize more slowly and less densely. This demonstrates the importance of algal bionts in shallow water settings, particularly with respect to their speed of colonization - some individual shells had nearly 100% of their surfaces covered by algal bionts.

Overall, the taphonomic signature of shallow carbonate shelf molluscs after one year of exposure included fragmented shells with some evidence of dissolution and 30-40% coverage by epibiont growth. In contrast, shells from deeper water exhibited little breakage, sparse epibiont coverage (with no algal bionts) and species-specific trends in dissolution intensity.

Although samples collected in year 2 have not yet been fully analyzed, visual inspection indicates that the trends we observed after one year continued into the second year. It is possible that, at the shallower depths, very little shell material will remain in some species in samples collected in 2003, the tenth year of deployment. In particular, degradation rates of Mytilus suggest that Callender et al.'s (1994) calculation of a 10-yr. half-life at petroleum seeps. might be easily duplicated at the shallow Bahamian sites. On the other hand, samples at deeper sites may remain relatively pristine because, after two years, with the important exception of Mytilus, they show little more alteration in both the Gulf of Mexico sites and the Bahamian sites below 210 meters than was noted at the 210-m site after 1 year.



Fig. 6: Epibiont coverage on shells after one year. Controls for all species had no biont cover. \* = significant difference from the control. In the key, "skel. bionts" indicates preservable (skeletonized) bionts.

### CONCLUSIONS

Tremendous differences in taphonomic signatures were found between the 15-m and 210-m sites in only one year. Considering that these two sites are separated by little more than one kilometer laterally, potential for downslope transport of shallow-water remains into deeper-water depositional environments is high. Therefore, time-averaged fossil assemblages containing several grades of taphonomic alteration may contain shells from substantially different habitats. Davies et al. (1989) and others have addressed the potential of taphonomic signature for recording variations within some environments. Our observations after two years (data in prep), indicate that even nearby habitats differ substantially in taphonomic signature.

Callender et al. (1994) deployed Mytilus and Codakia shells at a petroleum seep in the Gulf of Mexico for 3 years. The species-specific trends observed by them were also observed by us in two additional, substantially different, habitats. They found that Mytilus valves were quickly altered, whereas Codakia remained nearly unaltered after 3 years of exposure at 600m. We have found the same trend. These observations emphasize the possibility that these biases may be conservative within a wide range of habitat types.

The scope of the SSETI program will enable us to address the variability and consistency of various taphonomic signatures in a wide range of habitatsMoreover, the SSETI program will establish the rates at which taphonomic processes progress and how these rates differ with both environment and organism type. Together, these findings are critical to our understanding of ancient communities. We gratefully acknowledge NOAA/NURP funding for this project.

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