

RESEARCH ARTICLES

RAPID SEAFLOOR MAPPING OF THE NORTHERN GALAPAGOS ISLANDS, DARWIN AND WOLF

By: César Peñaherrera-Palma^{1,2}, Karen Harpp³ & Stuart Banks¹

¹Charles Darwin Foundation, Puerto Ayora, Galapagos, Ecuador

²correspondence: <cesar.penherrera@fcdarwin.org.ec>

³Geology Department, Colgate University, Hamilton, NY 13346, U.S.A.

SUMMARY

Darwin and Wolf are the most remote of the Galapagos islands and are famous for their remarkable pelagic and benthic marine species abundance and diversity. However, little is known about their surrounding bathymetry. Rapid surveys were carried out in 2008 and 2009 to collect geo-referenced depth soundings down to 100 m around both islands, as a step towards a better understanding of their habitat and species distribution. Five spatial interpolation methods were tested on the data, to find the most accurate. The Triangular Irregular Network (TIN) was the best interpolator for these data sets with the fewest interpolation errors, and was then used to create contour and three-dimensional maps of the seafloor topography of both islands. Darwin has a bigger insular platform with gentle submarine slopes whereas Wolf has very steep slopes with a smaller platform.

RESUMEN

Mapeo rápido del fondo submarino de las islas del norte de Galápagos, Darwin y Wolf. Darwin y Wolf son las islas más remotas del Archipiélago de Galápagos. Son famosas debido a la alta biodiversidad marina de especies pelágicas y bentónicas. Sin embargo, ningún estudio ha levantado información sobre su batimetría. Se realizó una serie de sondeos rápidos en 2008 y 2009 para coleccionar información geo-referenciada de hasta 100 m de profundidad alrededor de ambas islas, para mejorar el entendimiento de la distribución de especies y hábitats. Cinco métodos de interpolación espacial fueron probados sobre los datos para encontrar el más preciso. La Red de Triangulación Irregular (TIN, por sus siglas en inglés) fue el mejor, generando los valores de error más bajos, y fue el usado para generar mapas de contorno y de tres dimensiones de la topografía del fondo submarino de ambas islas. La plataforma insular de Darwin es mucho mayor y con pendientes más suaves que la de Wolf, que presenta pendientes muy fuertes y menor plataforma.

INTRODUCTION

Mapping the seafloor is a key step towards understanding the bio-geological dynamics of marine environments. Horizontal circulation of water interacting with geological features often results in complex marine current interactions (including upwellings) that shape the environmental conditions and thus the biodiversity and community distribution of pelagic and benthic ecosystems (Hamner & Hauri 1981, Witman & Smith 2001, Genin 2004). Nevertheless, producing seafloor maps is not straightforward since it typically requires the use of expensive specialized equipment, including side-scan and multi-beam sonar, which often involve costly ship time, sophisticated processing equipment and skilled operators. There have been few applications of such high technology in shallow waters.

In Galapagos, seafloor mapping was initiated in the 1940s by the U.S. Navy under the command of the U.S. Defense Mapping Agency (DMA 1944–85). They carried out many expeditions and produced the first charts for Galapagos. Since then, several attempts have been made to review and update the information available (INOCAR 1985–2000, Michaud et al. 2006, <<http://www.pmel.noaa.gov/vents/staff/chadwick/galapagos.html>> consulted July 2009). Even though the spatial scale achieved is moderately good and covers most of the archipelago, many areas remain either incorrectly characterized or entirely lack soundings.

This is the case for Darwin and Wolf Islands, the most northwesterly islands in the Galapagos Marine Reserve (GMR). Their bathymetry has not previously been mapped and is inaccurately represented on many of the digital nautical charts used today (e.g. 2008 MapSource

by Garmin® and 2009 Google Maps by Google®). The most accurate maps of their coastlines were based on satellite imagery and field data (The Nature Conservancy-CLIRSEN 2006), yet some errors still exist in island shapes, caused primarily by misrepresentation of shadows as land.

GPS-Sonar log data are often used for bathymetric mapping of lagoons and rivers, and are relatively cheap to collect and analyze. There are several statistical and non-statistical methods, called spatial interpolators, developed to interpolate between point data and predict unknown values from measured ones (Issaks & Srivastava 1989, Collins 1995). Spatial interpolators differ principally in their method: each is suitable for certain types of data and will produce different levels of accuracy in different situations (Johnston 2002, Sterling 2003). The present study compares the accuracy of five common spatial interpolators in order to produce bathymetric maps of both islands. In addition, several errors found in the coastlines of both islands are corrected, and estimations on depth area are provided as tools for future sub-tidal habitat coverage analysis.

METHODS

Study site

Darwin and Wolf Islands represent the northerly limits of the Galapagos Archipelago (Fig. 1). These oceanic islands are the eroded tops of two larger, extinct volcanoes that

rose from seafloor depths of more than 2000 m (McBirney & Williams 1969). Both islands are part of the Wolf–Darwin Lineament (WDL), a two million year-old bathymetric feature that includes several seamounts north and south of both islands (Harpp & Geist 2002). The WDL may have originated from the interaction between the 91°W transform fault along the Galapagos Spreading Centre and the horizontal migration of the Galapagos mantle plume (Harpp & Geist 2002).

Darwin, the northernmost island, is a semi-rectangular flat-topped edifice rising 170 m above sea level, at 1.673°N, 91.989°W. Wolf is a boomerang shaped island 255 m high, approximately 2.5 km long and 500 m wide, at 1.383°N, 91.822°W (McBirney & Williams 1969). Darwin presents two small reefs and two islets, the most extensive being Darwin's Arch on its southeast coast. Wolf has three small islets on its south and northern sides.

Data collection

Tracks were performed around Darwin and Wolf Islands on three field expeditions in July and November 2008 and March 2009. Depth and geographic coordinates were recorded using a Lowrance GPS-Sonar (model LMS-525 c-df) set in a fibreglass vessel 8.2 m long and 2.45 m wide, powered by two Mercury 75HP outboard engines. The vessel followed tracks perpendicular and parallel to the shoreline, only changing the planned course where strong swells were present (Fig. 2). Data were collected to a depth limit of 120–130 m at an average speed of 3 m.s⁻¹ with a sampling interval of 1 record per s.

Data preparation

Sonar log and GPS data were exported using the free software Sonar Viewer® (from Lowrance Co.). The depth data were stored in feet and then transformed to meters at 3.28 ft = 1 m. Because the GPS data were recorded in Mercator projection (datum WGS 84), a conversion was performed from the Mercator WGS 84 projection to the NAD83 Geographic coordinate system using the formulae in Schaefer *et al.* (2008), as follows:

$$\text{Latitude} = \text{RadtoDeg} \cdot (2 \cdot \arctan(\exp(Y/\text{SemiMinor}))) - \pi/2$$

$$\text{Longitude} = \frac{X \cdot \text{RadtoDeg}}{\text{SemiMinor}}$$

Where: the constants $\text{RadtoDeg} = 57.2957795132$ and $\text{SemiMinor} = 6356752.3142$; X is Lowrance position X in Mercator WGS84 and Y is Lowrance position Y in Mercator WGS 84. The resulting data were imported into ArcGIS® 9.3 software to display the depth data geo-spatially and to convert them into WGS 84.

Using field observations, aerial photography, using 2009 Google Earth® satellite imagery and LANDSAT 7 images (<<http://landsat.gsfc.nasa.gov/images/find.html>> consulted December 2008) and older maps (The Nature Conservancy-CLIRSEN 2006), new maps of the

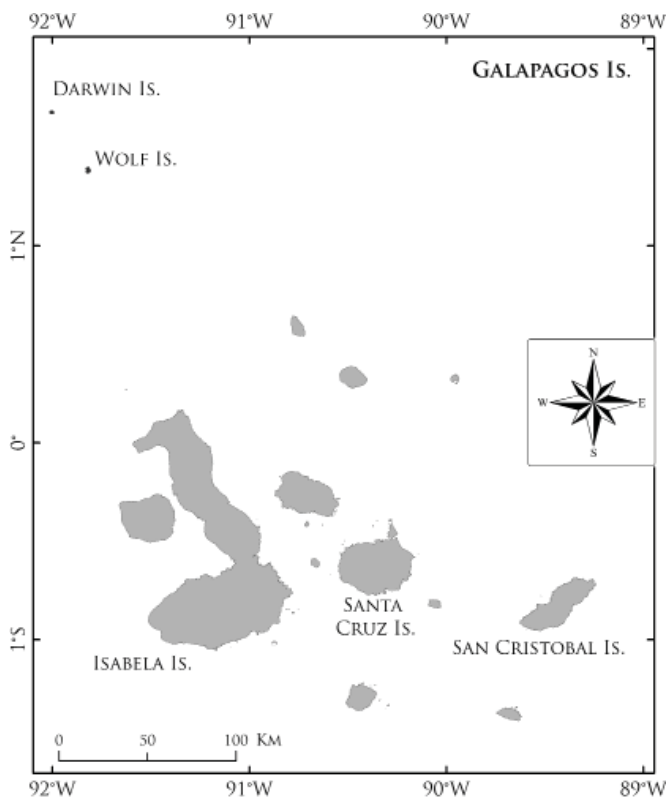


Figure 1. Location of Darwin and Wolf Islands in the Galapagos Archipelago.

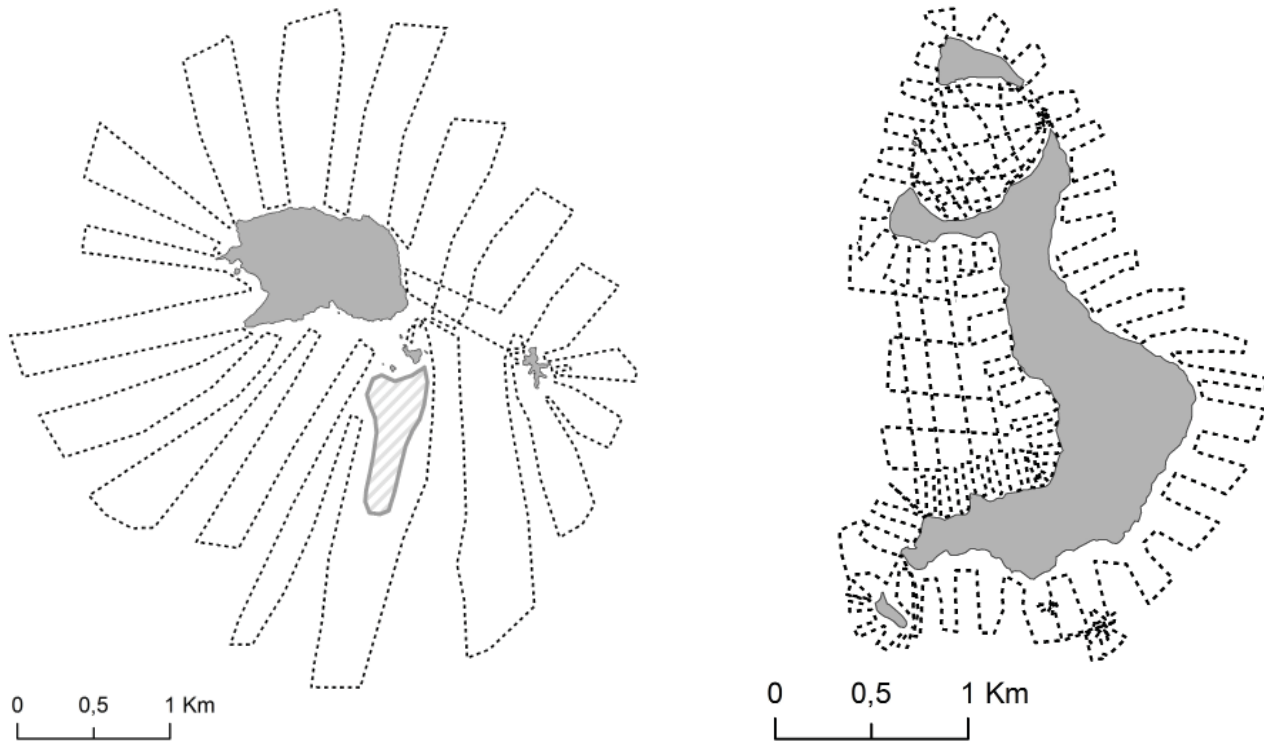


Figure 2. Data collection tracks for depth sounding around Darwin Island (left) and Wolf Island (right). Grey striped area on the map of Darwin represents the unsampled area.

Darwin and Wolf coastlines were developed in order to correct errors detected in the old maps. The new coastline developed for Darwin differs primarily in the position and size of Darwin's Arch and the south reef. Both features were considerably under-sized and slightly misplaced in earlier maps (Fig. 3). Similarly, at Wolf Island, shadow effects misrepresented some coastline features on Wolf itself and on Banana and Elephant islets (Fig. 4).

Finally, using these new coastlines, boundary files were created and merged with the depth data to prevent erroneous interpolations.

Spatial analysis

Five interpolation methods were tested to produce contour interval maps. Interpolators used were: 1) triangular



Figure 3. Comparison between the previous mapped coastline (black dashed lines: The Nature Conservancy-CLIRSEN 2006) and the revised coastline determined here (grey areas) of Darwin Island.



Figure 4. Comparison between the previous mapped coastline (black dashed lines: The Nature Conservancy-CLIRSEN 2006) and the revised coastline determined here (grey areas) of Wolf Island.

irregular network (TIN); 2) inverse distance weighting (IDW); 3) spline; 4) ordinary kriging; and 5) universal kriging.

TIN is a vector-based geometrical interpolation technique that constructs by triangulation a set of vertices (points). Each vertex is connected with a series of edges to form a network of triangles. There are different methods of interpolation to form these triangles, but the most commonly applied is the Delaunay triangulation method, which produces triangles that are as close to equilateral as possible (Issaks & Srivastava 1989).

IDW is an interpolation method in which values at unsampled areas are calculated from known points using a weight function in a search neighbourhood. Points closer to the interpolated area have more influence than points further away (Johnston 2002). IDW is one of the simpler interpolation techniques in that it does not require pre-modelling (Tomczak 1998).

The Spline method attempts to fit a surface through each observation of a dataset while also minimizing the total curvature of a surface (Davis 1986, Cressi 1993). Splines are well suited for calculating surfaces from a large set of points on gently sloping surfaces (Sterling 2003).

Kriging is a geostatistical interpolation technique which quantifies the spatial autocorrelation among measured points to generate surfaces that incorporate the statistical properties of the measured data and that include the error or uncertainty, as an indicator of how good the final predictions are (Issaks & Srivastava, 1989). Kriging builds these estimates using a semivariogram, which measures the spatial correlation between two points (Lam 1983). Weights are then given to points that have similar directional influence and distance. Kriging is typically applied when dependence between sample values decreases as the distance between observations increases. This is called ordinary kriging. However, if there is a general trend in data values, kriging can be adapted to accommodate such a trend. This routine is called universal kriging (Issaks & Srivastava 1989).

Performance of these spatial interpolators was tested using the Root Mean Square Error (RMSE) and Median Absolute Deviation (MAD) analysis. According to the Federal Geographic Data Committee (<www.fgdc.gov/standards/projects/FGDC-standardsprojects/accuracy/part3/chapter3> consulted 5 July 2008) the RMSE is the most accepted test for quantifying interpolation accuracy. It quantifies the validity of a predictive model by calculating the differences between observed and estimated data from the contour plot as follows:

$$RMSE = \sqrt{\sum \frac{(Z_i - Z_t)^2}{n}}$$

where Z_i is the interpolated depth of a test point, Z_t is its true depth and n is the number of test points (<<http://erg.usgs.gov/isb/pubs/factsheets/fs04000.html>> consulted 22 May 2007).

MAD is a robust statistical parameter used to cross-validate the performance of an interpolation method by assessing the absolute variance of the interpolated surface (Golden Software 2009). It is calculated by computing the data's median value, subtracting the median value from each point value, taking the absolute value of the difference and calculating their median. RMSE and MAD calculations were made using Surfer 9® (Demo Version) software.

Contours, area and volume

Contour maps were created based on the best interpolator method. In addition, digital elevation models (DEM) were generated for calculating the insular platform volume for Darwin and Wolf. Insular platform is defined as the sampled area between 0 and 100 m depth around each island. Area estimations were also calculated for the total and for the planar depth interval planar area (every 10 m). Planar area is defined as the area of a three-dimensional feature projected in a two-dimensional plane). These two estimations were then used for estimating an approximated volume of the water mass over the insular platform of both islands. Area and volume calculations were done using ArcGIS 9.3® software and cross-validated with an additional routine available in Surfer 9® (Demo Version) software.

RESULTS

Spatial analysis

Calculations of the RMSE showed TIN, IDW and Spline interpolations to perform better than kriging, contrary to our expectation (Table 1). TIN was most consistent in its accuracy for both islands, showing lower RMSE (1.86 m for Darwin; 0.9 m for Wolf) and the lowest MAD values (0.09 for Darwin; 0.14 Wolf). IDW error value was the lowest for the Darwin dataset (RMSE = 1.64) but its variance was higher in comparison to TIN (0.16). Spline had equal lowest RMSE values for one dataset (Wolf), but not lower than TIN.

Bathymetric models

The resulting bathymetric maps for both islands reveal different seafloor shapes at 100 m (Fig. 5). Darwin's platform reveals a large shield volcano underlying the island and surrounding reefs, extending over 1 km from

Table 1. RMSE and MAD calculations for five interpolation methods. All values are in meters.

Method	Darwin		Wolf	
	RMSE	MAD	RMSE	MAD
IDW	1.65	0.16	3.15	0.32
TIN	1.86	0.09	0.92	0.14
Spline	3.66	0.12	1.38	0.26
Ordinary Kriging	3.17	0.33	5.55	0.35
Universal Kriging	3.05	0.28	3.10	0.33

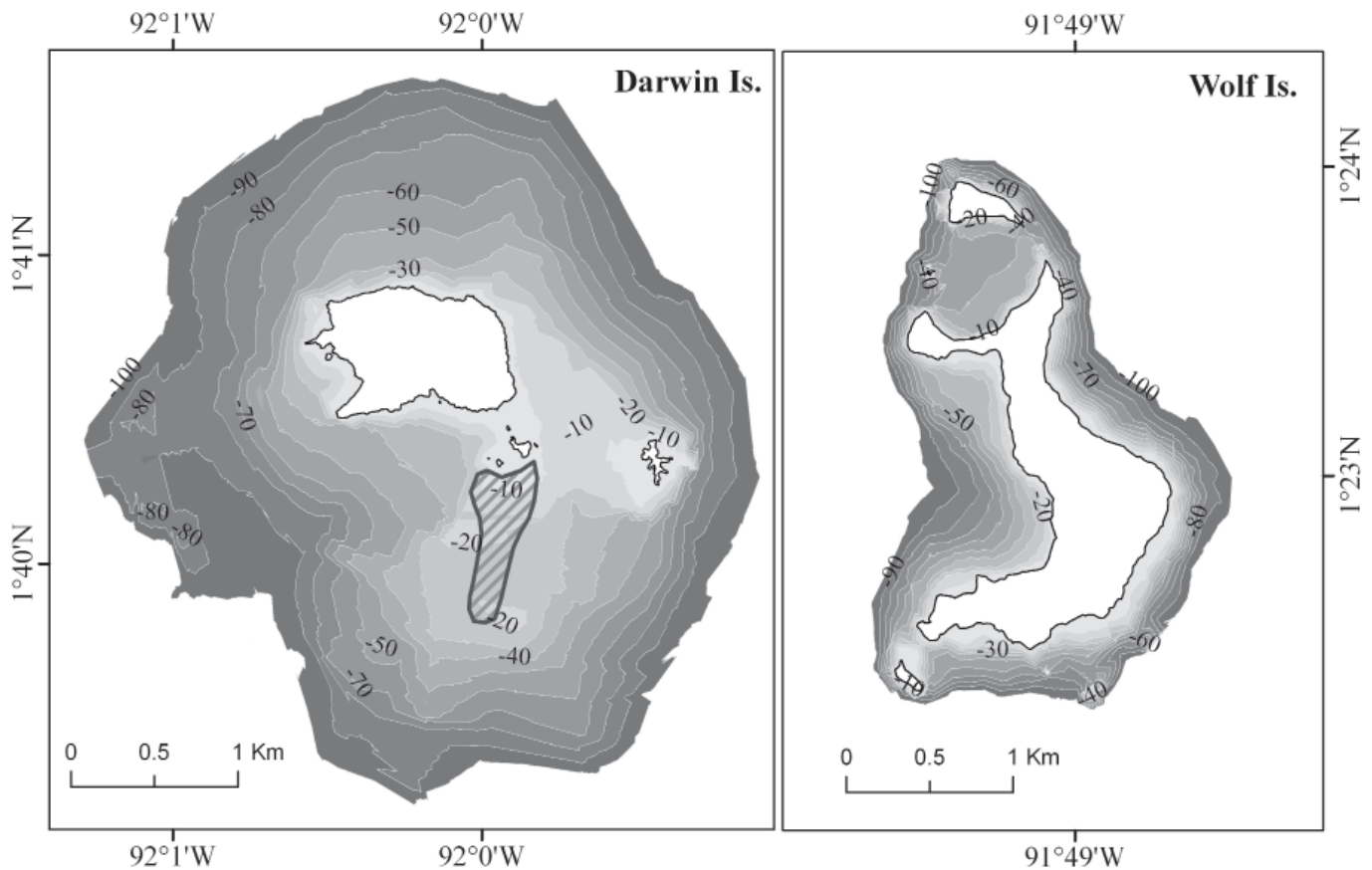


Figure 5. Contour maps of insular platform shield of Darwin and Wolf from 0 to 100 m depth. Dashed area on Darwin represents the unsampled area.

the coast all round. The rapid increase in depth off the eastern face of Darwin's Arch is quite different from the more gradual slope off the rest of the island (Fig. 6). Darwin's insular platform has an estimated volume of nearly 500 Mm³, with a planar area covering around 11.7 Mm² (Table 2). We estimate the amount of water covering the platform to be nearly 665 Mm³.

Wolf's insular shield was observed to be narrower and smaller than Darwin's, extending < 1 km away from land in all directions. The slope of its seafloor is more abrupt, with depths rapidly increasing away from land, apparently following the shapes of the island's sub-aerial cliffs. Soundings also captured two reefs south of the main island, the first called "La Draga" and the second as yet unnamed (Fig. 7). The estimated volume for Wolf's insular platform is approximately 280 Mm³ and its planar surface area around 4.1 Mm² (Table 3).

DISCUSSION

Coastline corrections

The new coastlines developed through this assessment differ considerably from maps of Darwin and Wolf produced by The Nature Conservancy-CLIRSEN (2006). Those previous versions were produced using aerial photography with limited ground-truthing. Most errors

found were shadows areas over the sea that were mistakenly considered to be part of the land mass. Our new maps represent the integration of aerial photography,

Table 2. Area and volume estimations for Darwin's insular platform (0–100 m depth) based on the TIN interpolation method.

Site	Depth interval	Area (m ²)
Arch	exposed land	15,210
	0 to -10	107,904
Darwin	exposed land	661,051
	0 to -10	335,037
Darwin exposed rock	exposed land	69
Southern reef	exposed land	8,063
Stack	exposed land	1,087
Entire platform	-10 to -20	825,755
	-20 to -30	786,297
	-30 to -40	756,944
	-40 to -50	1,003,598
	-50 to -60	1,077,676
	-60 to -70	1,240,455
	-70 to -80	1,156,711
	-80 to -90	1,910,900
	-90 to -100	1,832,088
Darwin platform total area		11,718,843
Darwin platform total volume (m ³)		505,946,204
Water mass volume (m ³)		665,938,119

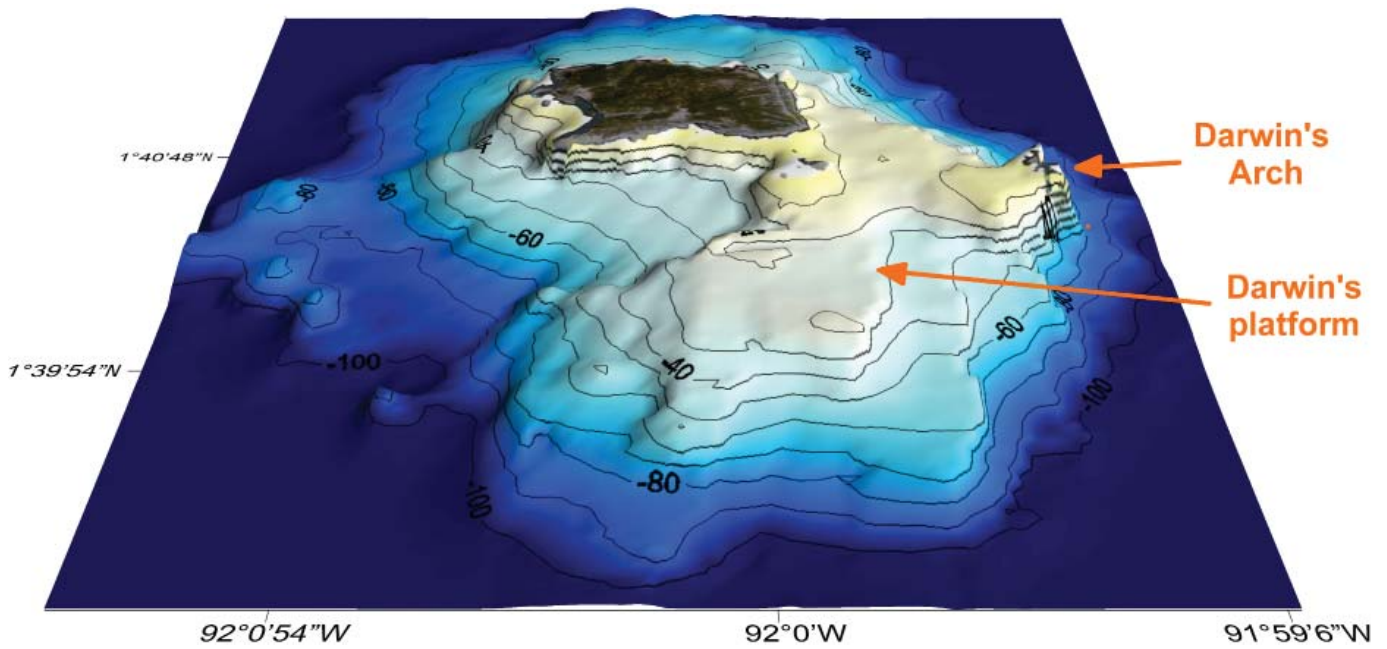


Figure 6. Three-dimensional view of Darwin and its platform from a smoothed TIN interpolation. Depth is exaggerated 3.8 times for illustrative purposes.

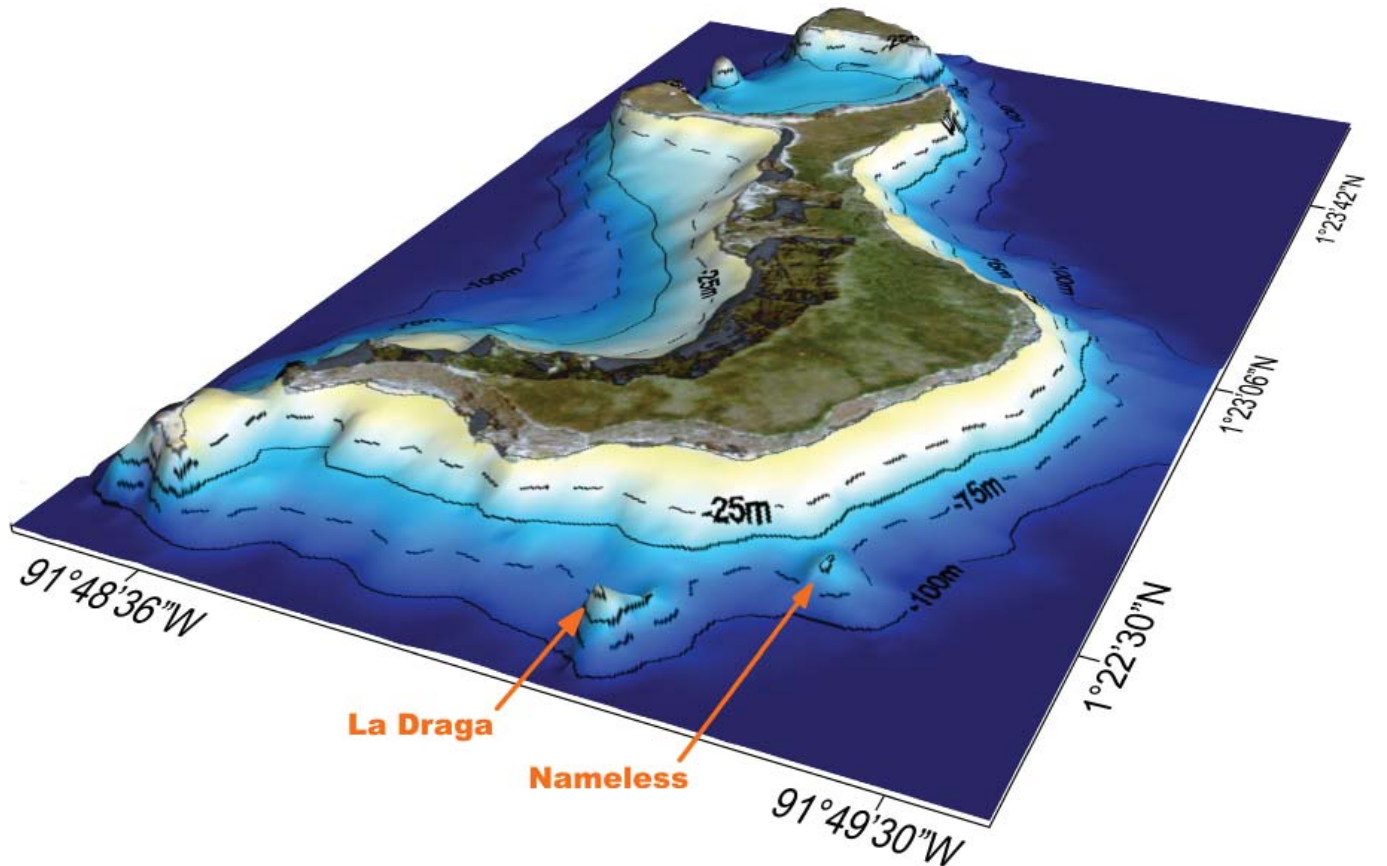


Figure 7. Three-dimensional view of Wolf, showing La Draga and Nameless reefs, from a smoothed TIN interpolation. Depth is exaggerated 3.8 times for illustrative purposes.

Table 3. Area and volume estimations for Wolf's insular platform (0 to 100 m depth) based on the TIN interpolation method.

Site	Depth interval	Area (m ²)
Banana	exposed land	62,100
	0 to -10	9,040
	-10 to -20	8,830
	-20 to -30	9,330
	-30 to -40	11,100
La Draga reef	-40 to -50	34,600
	-10 to -20	1,460
	-20 to -30	763
	-30 to -40	1,172
	-40 to -50	1,809
Elephant	-50 to -60	4,940
	exposed land	11,000
	0 to -10	18,700
Exposed pinnacle	-10 to -20	9,960
	exposed land	346
	0 to -10	1,390
	-10 to -20	763
	-20 to -30	825
Nameless reef	-30 to -40	969
	-40 to -50	4,430
	-40 to -50	520
Wolf	-50 to -60	2,870
	exposed land	1,230,000
	0 to -10	271,000
	-10 to -20	209,000
Wolf-Elephant	-20 to -30	197,000
	-30 to -40	250,000
Wolf-Elephant-Banana-Exposed pinnacle	-40 to -50	337,000
	-50 to -60	410,000
Entire platform	-60 to -70	327,000
Entire platform	-70 to -80	333,000
Entire platform	-80 to -90	382,000
Wolf platform total planar area		4,142,917
Wolf platform total volume (m ³)		279,182,502
Water mass volume (m ³)		135,109,160

satellite imagery and field observations. Although a differential GPS could be used in the future to achieve a more accurate coastline, the many inaccessible cliffs around the islands may continue to cause problems. Shorelines of both islands are mainly cliffs that reach more than 100 m above sea level in some places.

Spatial analysis

Kriging interpolation methods are usually considered to be the best, as they use quantifiable error and uncertainty to estimate un-sampled areas (Issaks & Srivastava 1989). Nevertheless, both kriging methods produced higher RMSE and MAD values in comparison to IDW, Spline and TIN. This situation might be produced by the particularities of the sampling tracks. IDW is an exact interpolator when no smoothing factor is used, but has a tendency to create "bull's-eye" contour maps around outlier sample points, with extreme values surrounded by

several concentric circles (Sterling 2003). Abrupt changes between data points are thus easily misrepresented by this interpolator, as was observed in test contour maps of Darwin, for which reason IDW was not assessed further. In the case of Spline, its error and variance values were good, but not lower than those of TIN. Indeed, RMSE and MAD values calculated for Wolf with TIN were very low (< 1 m of error and 0.14 of variance). TIN interpolations performed better than any other method for both data sets. It produced the smallest error and absolute variance, which means that it generated the least uncertainty in predicting the values in the un-sampled areas. As a result, contour maps and area calculations were produced using TIN.

Bathymetric models

The present bathymetric maps provide a good start for Darwin and Wolf islands, although some areas could be improved by additional soundings. In the south part of Darwin, a large, shallow platform extension was mapped less accurately than other areas. The rough swell usually present over this area hampered navigation, yet results from the few tracks available provide a good general perspective. On Wolf, small pinnacles along the east border of the crater are not visible due to the inaccuracy of the interpolation method and equipment limitations. Smoothing methods were used over TIN interpolations for both islands in order to diminish the noise produced by the rugged rocky bottom, but this also precluded the possibility of producing a detailed view of some small but potentially important features. Present output cannot therefore be used for navigation purposes, as more soundings are needed to represent all near-surface features properly. Nevertheless, the use of these sampling and interpolation techniques presents several advantages over some others, including: the ability to produce a rapid image of the seafloor without the use of specialized software (sampling took *c.* 5 h per island); a cheap technique compared to other methods; mapping of shallow areas where bigger vessels cannot navigate and thus acquisition of bathymetric data very close to shoreline areas of biological importance.

The present results have greatly improved the resolution of the topography of both islands, changing even the perception of their relative size. Darwin was thought to be the smaller, but its insular platform is actually about twice that of Wolf. Darwin therefore has a wider seafloor area exposed to currents and light, which could produce a greater biomass of benthic and reef species. Area and volume estimations provide a first insight on the island mass and the water mass covering both platforms, which could help in marine life density estimations. Depth should be taken as an approximation of the actual profile, as tidal variation and sampling method could affect estimates. No data were collected on tidal height variation, so the results are not corrected for this.

The next task will be to link this bathymetric information to other oceanographic variables in order to

understand biodiversity patterns on and around the islands. Concentrations of zooplankton and fish around seamounts are often driven principally by the interactions of seafloor topography with ocean currents (Genin 2004). Darwin and Wolf host the largest coral reefs in the GMR (Vera & Banks 2009) and harbour fish and apex predator aggregations associated with strong currents on their southeast faces (Hearn *et al.* 2010). We anticipate that the new bathymetric data will help to understand these biological phenomena better.

The new data provide a significant improvement in resolution of seafloor bathymetry. Nevertheless, the mapping needs to be extended to deeper areas. The new data will complement further side-scan sonar surveys in order to achieve a greater resolution for benthic habitat maps and subsequent use in ecological, biological, and geological studies. Final bathymetric contour maps will be available at <www.migramar.org> and <www.darwinfoundation.org>.

ACKNOWLEDGMENTS

We thank WWF-Galapagos, Friends of Galapagos Switzerland and Lindblad Expeditions for funding the Shark Research Project of the Charles Darwin Foundation and its subsequent programs which include the bathymetric mapping presented here. We acknowledge National Science Foundation support for geological field work around Darwin and Wolf. The present work could not have been done without the invaluable help of Captain Tito Franco, the crew of the *Arrecife* and the captains and crew of M/V Sierra Negra from the Galapagos National Park. We acknowledge the time spent by Matthias Wolff, Alex Hearn, James Ketchum, Rodolfo Martínez and Verenitze Valencia in revising and commenting on this work. This is Contribution number 2066 of the Charles Darwin Research Station.

LITERATURE CITED

- Collins, F.C., Jr 1995. A Comparison of Spatial Interpolation Techniques in Temperature Estimation. Doctoral Dissertation. Virginia Polytechnic Institute and State University, Blacksburg, VA.
- Cressi, N.A.C. 1993. *Statistics for Spatial Data*. Wiley, New York.
- Davis, J.C. 1986. *Statistics and Data Analysis in Geology*. Wiley & Sons, New York.
- DMA. 1944, 1947, 1979, 1984, 1985. South Pacific Ocean, Archipiélago de Colón (Galápagos Islands). Defense Mapping Agency: Hydrographic/Topographic Center, Washington, DC.
- Genin A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Science* 50: 3–20.
- Golden Software 2009. Surfer 9© (Demo Version) Help. Golden Software, Golden CO.
- Hamner, W.M. & Hauri, I.R. 1981. Effects of island mass: water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. *Limnology and Oceanography* 26: 1084–1102.
- Harpp, K. & Geist, D. 2002. Wolf–Darwin lineament and plume–ridge interaction in northern Galápagos. *Geochemistry, Geophysics, Geosystems* 3(11): 1–19.
- Hearn, A.R., Ketchum, J.T., Klimley, A.P., Espinoza, E. & Peñaherrera, C. 2010. Hotspots within hotspots? Hammerhead movements around Wolf Island. *Marine Biology* 157: 1899–1915.
- INOCAR. 1985, 1988, 1991, 1992, 1983, 2000. Cartas de Navegación del Archipiélago de Colón (Provincia Insular de Galápagos). Instituto Oceanográfico Militar (INOCAR). Quito, Ecuador.
- Issaks, E.H. & Srivastava, R.M. 1989. *An Introduction to Applied Geostatistics*. Oxford University Press. New York.
- Johnston, S. 2002. *Uncertainty in Bathymetric Surveys*. Coastal Hydraulics Engineering Tech. Note CETN-IV, U.S. Army Corp of Engineers Research and Development Center, Vicksburg, MS.
- Lam, N. 1983. Spatial interpolation methods: a review. *The American Cartographer* 10: 129–149.
- McBirney, A.R. & Williams, H. 1969. Geology and petrology of the Galapagos Islands. *Geological Society of America Memoir* 118: 1–197.
- Michaud, F., Collot, J-Y., Alvarado, A., López, E. & personal científico y técnico del INOCAR. 2006. *Batimetría y Relieve Continental e Insular*. Instituto Oceanográfico de la Armada (INOCAR), Guayaquil.
- Sterling, D.L. 2003. A comparison of spatial interpolation techniques for determining shoaling rates of the Atlantic Ocean Channel. M.Sc. Thesis, Virginia Polytechnic Institute and State University, Blacksburg VA.
- The Nature Conservancy-CLIRSEN. 2006. *Cartografía de Galápagos 2006, conservación en otra dimensión*. CLIRSEN, Quito.
- Tomczak, M. 1998. Spatial interpolation and its uncertainty using automated anisotropic Inverse Distance Weighting (IDW) – Cross validation/Jackknife approach. *Journal of Geographic Information and Decision Analysis* 2: 18–33.
- Vera, M. & Banks, S. 2009. Health status of the coral communities of the Northern Galapagos Islands Darwin, Wolf and Marchena. *Galapagos Research* 66: 65–74.
- Witman, J. & Smith, F. 2003. Rapid community change at a tropical upwelling site in the Galapagos Marine Reserve. *Biodiversity and Conservation* 12: 25–45.