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Mapping bathymetric and hydrographic features of Glover's Reef, Belize, with a REMUS autonomous underwater vehicle

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Abstract

We used an autonomous underwater vehicle (AUV) to survey bathymetry and water mass properties at Glover's Reef atoll in Belize as part of a multidisciplinary study of population connectivity of Nassau grouper (*Epinephelus striatus*). Nassau grouper populations are declining dramatically throughout its range in the Caribbean because of overfishing. In response, Marine Protected Areas have been established at several spawning aggregation (SPAG) sites. However, effectiveness of these measures is presently unclear, as the regional patterns of transport and recruitment of grouper larvae have not been measured in extensive field studies. As part of a pilot study to relate oceanographic processes with transport and recruitment of Nassau grouper larvae, we used a Remote Environmental Monitoring Unit(S) (REMUS) AUV to measure the bathymetry, stratification, current velocity, and chlorophyll *a* fluorescence around Glover's Reef. The portability of the REMUS system enabled comprehensive oceanographic data collection in a remote location with minimal infrastructure. Using REMUS, we were able to effectively map the bathymetry of the reef and the shelfbreak. These data were merged with historical bathymetric data to develop a new chart of the atoll margin. A distinct contrast in the width of the shelves on the eastern and western sides of the atoll was demonstrated, with the widest shelf coinciding with the SPAG site. Water mass structure in the vicinity of SPAG site was also markedly different from other locations on the reef, suggesting an offshore advective influence on eggs and early-stage larvae released there.

Many species of coral reef fishes aggregate to spawn at specific times and locations (Claydon 2004). This behavioral strategy makes species that aggregate to spawn particularly susceptible to overfishing. Nassau grouper (*Epinephelus striatus*) is perhaps the best-known example. It historically formed particularly large aggregations of up to 100,000 individuals at locations throughout the Caribbean (Smith 1972), but declined rapidly in the 1990s and was assigned an "endangered" status by the World Conservation Union (IUCN) in 1996. At least nine Nassau grouper aggregations were present in Belize before 1990, each with at least 30,000 fish. Currently, only three of these aggregations remain, but at abundance levels at least an order of magnitude lower than pre-1990 numbers (Sala et al. 2001). Protection of these aggregations is consequently a critical conservation imperative. There is also an urgent need to determine the degree to which larval replenishment from the remaining aggregations is sufficient to maintain current population levels and supply individuals to other heavily fished areas.

Glover's Reef (Fig. 1a), an atoll located approximately 45 km east off the coast on the edge of the continental shelf, harbors one of the three remaining significant aggregations of Nassau grouper in Belize (Starr et al. 2007). West of the atoll the continental shelf is relatively flat, with a mean depth of 400 m. On the east side of the atoll, the continental slope starts just beyond the reef and drops to over 3,000 m into the southern Yucatan Basin. The spawning aggregation (SPAG) site of Nassau grouper is located approximately 1 km east of the northeastern corner of the reef (Sala et al. 2001; Starr et al. 2007).

Glover's Reef has been designated a marine reserve by the government of Belize in an attempt to protect populations of Nassau grouper and other threatened and endangered marine species. However, the effectiveness of these measures cannot be determined without demonstrating larval replenishment from the protected areas. Although several recent studies have used coupled biophysical models to examine larval fish dispersal from Belizean atolls and barrier reef (Heyman et al. 2005; Cowen et al. 2006; Tang et al. 2006), none of the physical models used had the requisite spatial resolution to capture submesoscale physical processes that significantly affect population connectivity (Gawarkiewicz et al. 2007). Moreover, there is little detailed bathymetric data on which a high-resolution model can be built, and little hydrographic observations with which it can be validated (Heyman et al. in press).

The work presented here was part of a larger effort to provide basic bathymetric and hydrographic information necessary for studies of larval dispersal from Nassau grouper SPAGs in Belizean waters. We conducted comprehensive mapping of bathymetry and water mass distributions using an autonomous underwater vehicle

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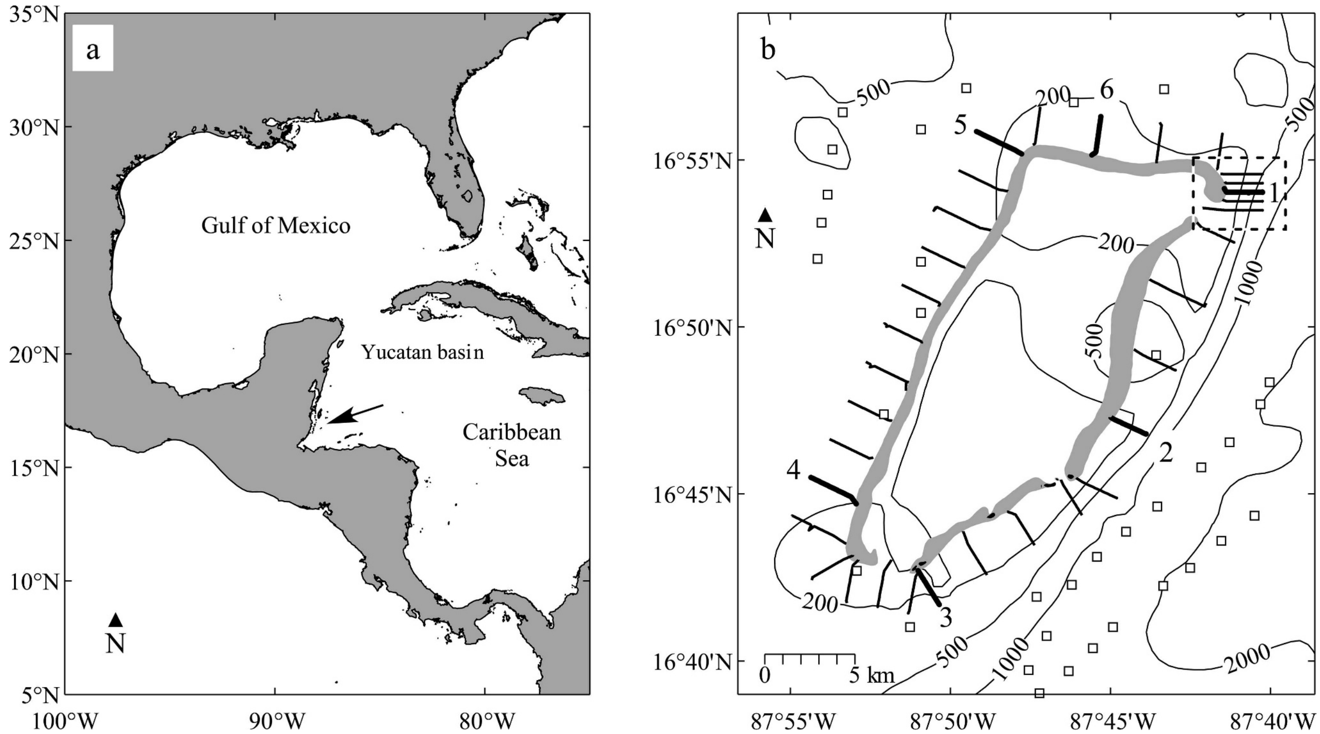

Fig. 1. (a) A map of the Caribbean Sea, showing the location of Glover's Reef atoll (black arrow). (b) Some of the AUV REMUS transects occupied during the bathymetric and hydrographic surveys of Glover's Reef 02–07 May 2006 and 10–15 February 2007. Bathymetry along selected transects (numbered bold lines) is shown in Fig. 4. Gray and black shading indicate shallow reef area and islands, respectively. Contour lines represent best available large-scale bathymetry before the survey (Claire Paris pers. comm.). Squares mark the bathymetry soundings from the British Admiralty (1992) chart. The protected Nassau grouper SPAG zone at the northeast corner of the atoll is marked by a dashed rectangle.

(AUV) during two consecutive years. The first survey (02–07 May 2006) was targeted at obtaining measurements of fore-reef bathymetry, whereas the second survey (10–15 February 2007) focused on temporal and spatial hydrographic changes. The AUV operations were based at the Glover's Reef Marine Research Station managed by the Wildlife Conservation Society, which provides infrastructure for ongoing research at Glover's Reef.

AUV surveying—Comprehensive surveying of bathymetry and hydrography outside the Glover's Reef atoll were performed using a specially equipped Remote Environmental Monitoring Unit(S) (REMUS 100). REMUS (Fig. 2) is a compact light-weight self-propelled AUV designed for operation in shallow water environments (Moline et al. 2005).

The configuration and equipment of the AUV REMUS used in the present study has been optimized to enhance its long-range hydrographic and bathymetric surveying capabilities. The vehicle carried a high-accuracy pumped Seabird conductivity–temperature–depth (CTD) probe, sampling continuously at the rate of 5 Hz. Chlorophyll *a* (Chl *a*) fluorescence was continuously monitored with a WET Labs ECO BB2F meter. Observed fluorescence values have been converted to the units of chlorophyll concentration (mg m^{-3}) using factory-provided coefficients. Since the plankton taxonomy at Glover's Reef was likely different from that used for the instrument calibration, the chlorophyll concentration values obtained in this study should be treated as relative, not absolute.

A dual-head RDI Workhorse Navigator 1,200-kHz acoustic Doppler current profiler (ADCP) measured the

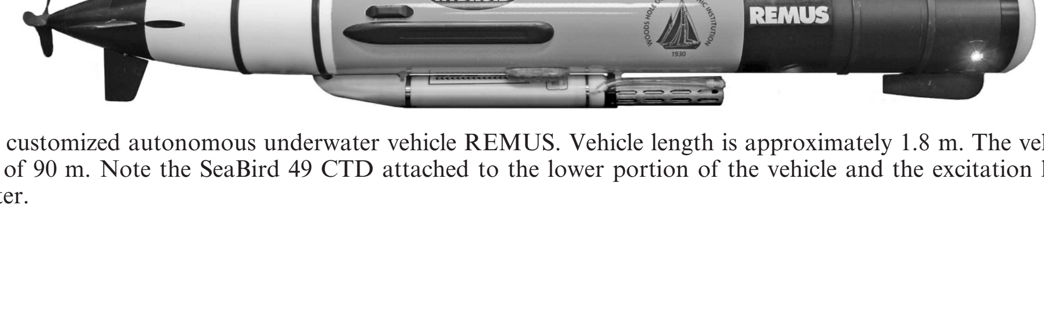

Fig. 2. The customized autonomous underwater vehicle REMUS. Vehicle length is approximately 1.8 m. The vehicle is capable of reaching depths of 90 m. Note the SeaBird 49 CTD attached to the lower portion of the vehicle and the excitation light of the BB2F fluorescence meter.

water velocity relative to the vehicle in a swath, extending approximately 15 m above and below the path of travel. Because of unforeseen interference with the experimental navigational equipment, some of the water velocity data were affected by higher-than-usual noise levels. As a result, only the transect averages of the flow velocity were analyzed in this study. Downward-looking ADCP also operated in bottom-tracking mode, providing reliable vehicle altitude and speed-over-ground data used for navigation, automatic obstacle avoidance, and bottom following.

Bathymetric data were inferred from the combination of CTD and ADCP measurements. Vehicle altitude above the bottom was tracked by the downward-looking ADCP; its depth below the surface was calculated from the synchronous CTD pressure record. The sum of the two, corrected for vehicle attitude and relative sensor distance, gave bathymetry along the vehicle track. Nominal accuracy of ADCP bottom ranging, continuously corrected for local sound speed, is on the order of 0.1 m (Gordon 1996), which is also the accuracy of CTD depth measurements. Bottom roughness within the ADCP footprint (four 0.8- × 1.0-m ellipses in a 7-m-wide cross pattern at 10 m altitude) far exceeded these accuracies because of the presence of several-meter-high coral heads. Consequently, the bathymetry measurements represent average depth of the coral tops over a roughly 10-m length scale. This effective footprint could potentially be reduced to about 1 m by postprocessing the data of each of the four ADCP beams separately (Trump and Marmorino 1998). This approach, however, was not necessary for the present study, which was focused on characterizing bathymetry at a 100-m scale. Along-track resolution (1.1 m at 3.5 knots) was also higher than required. Consequently, REMUS bathymetric record was averaged and subsampled to approximately 40-m horizontal spacing between data points.

A typical REMUS mission for the present study was a straight cross-shelf section extending from the reef outward for approximately 2 km (Fig. 1). In bathymetry surveying mode, the vehicle was programmed to fly at constant altitude of 5–10 m, depending on the anticipated bottom roughness. This type of trajectory is optimal for maintaining continuous acoustic contact with the bottom and maximizing bathymetry coverage. On the other hand, optimal sampling of vertical hydrographic structure can be achieved in a "seesaw" surveying mode, when the AUV follows an undulating path between the surface and the bottom (Fig. 3). The first survey (2006) consisted chiefly of bathymetric (constant altitude) missions, whereas the second one (2007) emphasized hydrographic (seesaw mode) observations.

AUV surveying in the vicinity of extremely steep bottom slopes (up to 45°), characteristic of coral atolls, presented unique challenges. The vehicle used in the present study was not equipped with a forward-looking sonar, and thus was incapable of avoiding head-on collisions with the coral when heading into the shallow reef from offshore: the sharp shelfbreak at the periphery of the atoll would amount to a hazardous wall for the approaching vehicle. Consequently, for safety reasons, REMUS was always directed toward deep water. On the outward track, the collision danger was avoided at the expense of the survey coverage: since the maximum downward glide angle of the REMUS trajectory is about 15°, the vehicle is not capable of following steeper bathymetry. Since the bottom quickly dropped beyond the reach of ADCP bottom tracking, bathymetric data could not be obtained beyond 30–50-m depth. This range could potentially be increased to about 120 m (90 m maximum vehicle depth plus 30-m bottom-tracking range) by directing the vehicle at an oblique angle to anticipated isobaths. For the purpose of the present study, however, the gain in horizontal coverage would have been negligible.

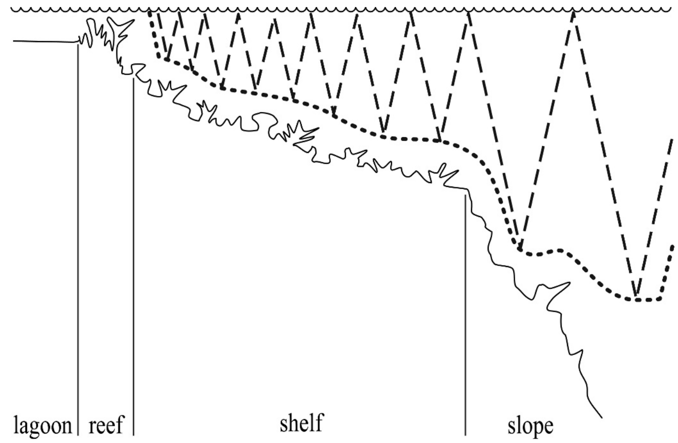

Fig. 3. Schematics of bathymetric (dotted line) and hydrographic (dashed line) REMUS missions during the Glover's Reef survey (not to scale).

The chief strength of AUV-based surveying lies in its ability to provide simultaneous characterization of multiple parameters of the physical environment (temperature, salinity, current speed, fluorescence, turbidity, bathymetric profile, and others, depending on the vehicle configuration). Having a single highly portable instrument capable of such suite of measurements allows comprehensive observations to be carried out in remote navigationally challenging locations with minimal infrastructure, minimal resources, and minimal manpower available. Glover's Reef is an excellent example of such a location.

It should be noted that each of the parameters can potentially be measured more effectively with a dedicated instrument with which REMUS capabilities need to be compared. For example, shipboard multibeam sonars (Hughes-Clarke et al. 1996) are capable of swath bathymetric mapping with the cross-track coverage of up to seven times water depth and angular resolution of 1.5°. Airborne LIDAR systems (e.g., scanning hydrographic operational airborne lidar survey [SHOALS], http://shoals.sam.usace.army.mil/) allow even faster surveying of large areas (up to 25 km^2 h^{-1}) with the resolution of several meters, but are limited to water depth of less than 60 m. Inexpensive single-beam surveying systems can also be built using off-the-shelf components. One of such systems built on the base of a fishfinder sonar was used in the present study, whereas others were described by Heyman et al. (2007) and the references therein. The accuracy and resolution of such systems are affected by the wide beam

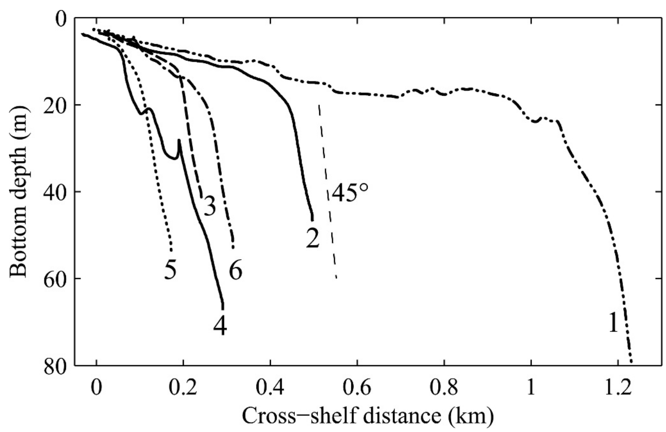

Fig. 4. Cross-shelf bathymetric profiles at various locations around Glover's Reef atoll. Numbers correspond to the survey layout shown in Fig. 1. Cross-shelf distance was measured from the outer margin of the barrier reef. Note the strong variation of the shelf width and steep dropoff (45° slope angle shown by the dashed line for reference).

angles of consumer sonars (20° in our case) exacerbated by steep topography (*see* Heyman et al. 2007 for full error analysis). REMUS bathymetric capabilities exceed those of single-beam shipboard systems because of the vehicle's proximity to the bottom. Similar results can be potentially achieved with a towed instrument, provided it can be operated in a shallow coral reef environment.

The hydrographic payload of REMUS has the same accuracy and resolution as the conventional ship-based systems. It has an added benefit of unattended surveying at a cost of somewhat increased uncertainty of horizontal coordinates (due to the lower accuracy of underwater dead reckoning compared with global positioning system-aided surface navigation). The mobility of an AUV also allows continuous surveying along complicated trajectories (e.g., undulating, bottom-following, etc.), unattainable with other platforms.

Bathymetry mapping—The AUV survey of the atoll bathymetry revealed distinctly different shapes of the transition from the shallow fore-reef to the shelf slope at various locations around Glover's Reef atoll (Fig. 4). The width of the shelf varied from under 100 m southwest of the atoll to 1.2 km toward the northeast.

The SPAG site at the NE corner of Glover's Reef was characterized by the widest expanse of relatively flat bottom (slope less than 1°) outside the reef. This area is also relatively flat in the north–south direction. The shelf along the rest of the eastern boundary of the atoll, bordering the continental slope, is similarly flat but only half as wide. On the other hand, the western shelf is narrow and remarkably steep. Despite a factor-of-10 difference in shelf width, the shelfbreak is found at around the 20-m isobaths both east and west of the atoll. The southern shelf is narrow (less than 100 m extent), but also shallow (less than 10 m).

To create the most accurate rendition of the atoll bathymetry, several different data sources were used. The reef-to-shelfbreak region was covered by the REMUS, providing a total of 34 km of bathymetric trackline (approximately 850 data points subsampled at 40-m horizontal spacing). Additional shallow water data were also collected with an improvised over-the-side (OTS) bathymetric surveying system consisting of a recreational-use Humminbird [sic.] 767c fishfinder sonar interfaced with a logging laptop computer (net trackline length was 112 km, equivalent to 2,800 data points at 40-m horizontal spacing). Bathymetry of the atoll interior and immediate vicinity at 1-km horizontal resolution (379 data points) was provided by D'Agrosa and Hoare (pers. comm.). Outlines of the shoaling barrier reef and the islands ("cays") were digitized from a paper navigation chart (British Admiralty 1992) and Landsat-7 satellite imagery (Millennium Coral Reef Landsat Archive, NASA-Johnson Space Center, http://oceancolor.gsfc.nasa.gov/cgi/landsat.pl).

Bathymetrical mapping in a complex multiply connected domain created by barrier reefs is most efficiently done on an unstructured grid (Fig. 5a). Resolution of such a grid can be arbitrarily increased in the areas adjacent to the reef, allowing more accurate representation of the local bathymetry and coastline configuration. At the same time resolution can be relaxed in deeper water to save computational resources. The grid used for combining bathymetric data at the SPAG site at the northeastern corner of the atoll (Fig. 5a) contained about 1,300 vertices, with the resolution varying from about 70 m near the reef to about 600 m at the periphery of the domain. The grid was constructed to follow the boundaries created by shoaling barrier reefs. Mesh generation and bathymetry mapping is an important step toward potential future numerical modeling of the reef environment (Pietrzak et al. 2005).

The data from all available sources were pooled together, controlled for quality, and interpolated onto an unstructured grid. Interpolation was performed using two-pass objective mapping, where the first pass (with an isotropic 2-km Gaussian covariance function) established the large-scale trends and the second (with 200-m Gaussian covariance) mapped local deviations from this trend. To prevent interpolation across the reef boundaries, the mapping was done separately for several convex subregions. Interpolation within each region was based only on the data relevant for this region.

Water mass distribution and circulation around Glover's Reef—The shallow shelf surrounding Glover's Reef atoll is embedded in the relatively thick surface mixed layer of the open Caribbean Sea. Dynamics of this layer is set by the balance of strong surface heating and vertical mixing, resulting in weak and variable stratification in the upper 100 m.

The mean vertical stratification observed during both AUV surveys in May 2006 and February 2007 showed a general temperature decrease and salinity increase with depth (Fig. 6). The relatively high surface salinity (35.8–35.9) and low temperature (27–28°C) (Fig. 6) were substantially different from those of the Caribbean surface water (salinity <35.5, temperature >28°C according to

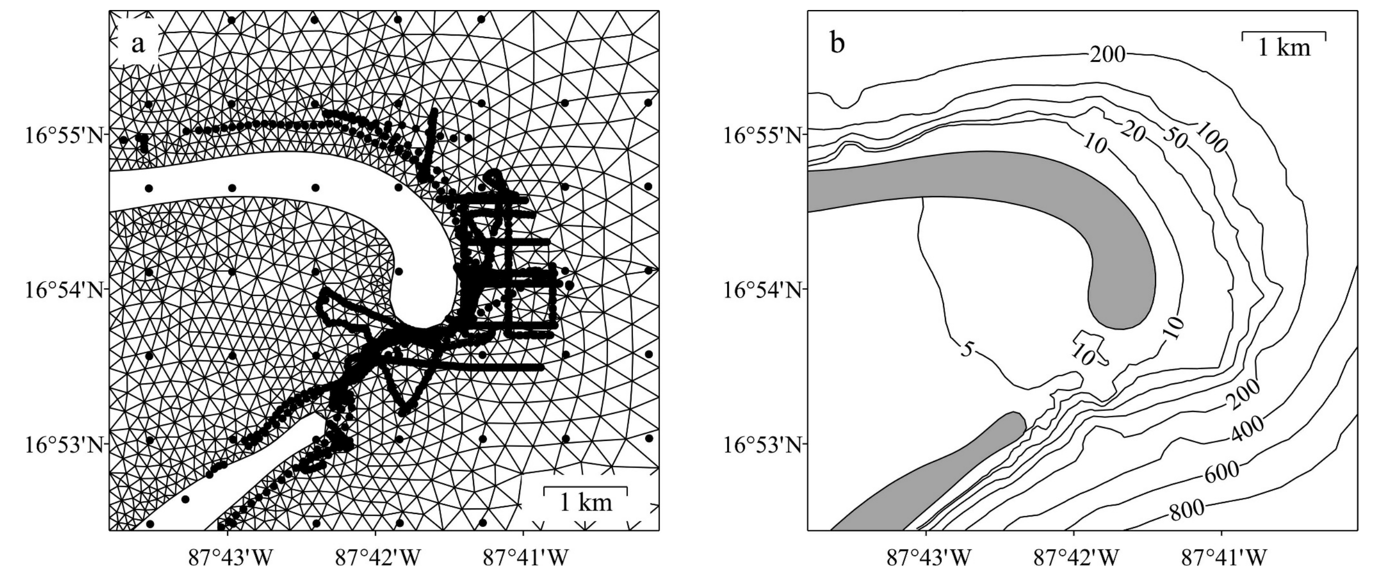

Fig. 5. Constructing detailed bathymetry of the SPAG site at the northeastern corner of Glover's Reef on the basis of a combination of AUV, OTS, and historic data. (a) Unstructured boundary-fitted grid used for interpolation. Black dots show data locations. (b) Final bathymetry product. Gray shading indicates shoaling (<1 m) reef areas.

Wüst [1964] and Hernández-Guerra and Joyce [2000]) during both surveys. These observations confirmed that Glover's Reef is located south of the zone of influence of the Caribbean Current, within the Gulf of Honduras cyclonic recirculation gyre, as suggested by models (Ezer et al. 2005; Tang et al. 2006; Chérubin et al. 2008) and surface drifter observations (Centurioni and Niiler 2003; Richardson 2005). Individual vertical profiles observed during both AUV surveys were composed of a series of remnant mixed layers (Fig. 7). This structure was likely created by a succession of storms, each homogenizing the water column to a different depth. At the same time, strong surface heating led to fast restratification after each storm and resulted in overall stable stratification of the surface layer. It should be noted that the observed layered structure cannot be attributed to double-diffusive processes, since the

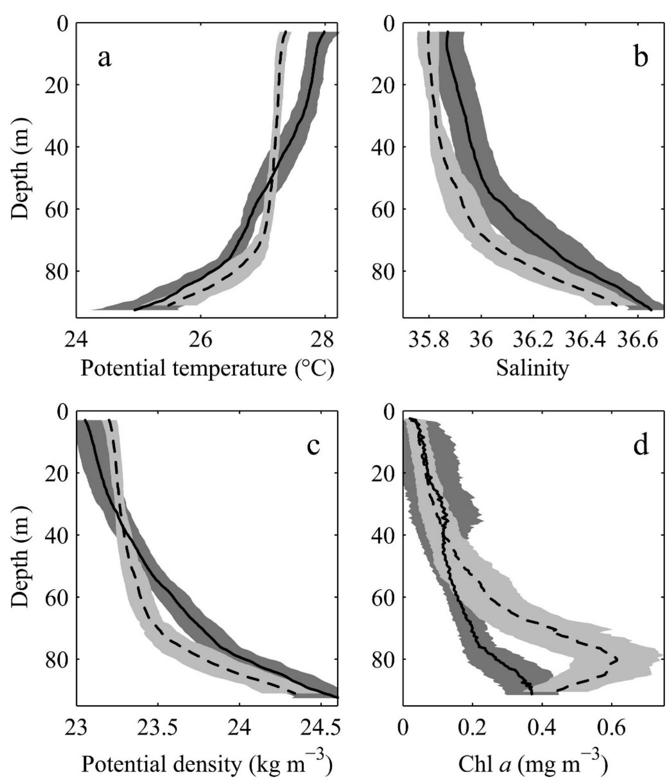

Fig. 6. Mean vertical distribution of (a) potential temperature, (b) salinity, (c) potential density, and (d) chlorophyll a fluorescence in the vicinity of Glover's Reef in May 2006 (solid lines) and February 2007 (dashed lines). Shading represents 1 SD about the mean.

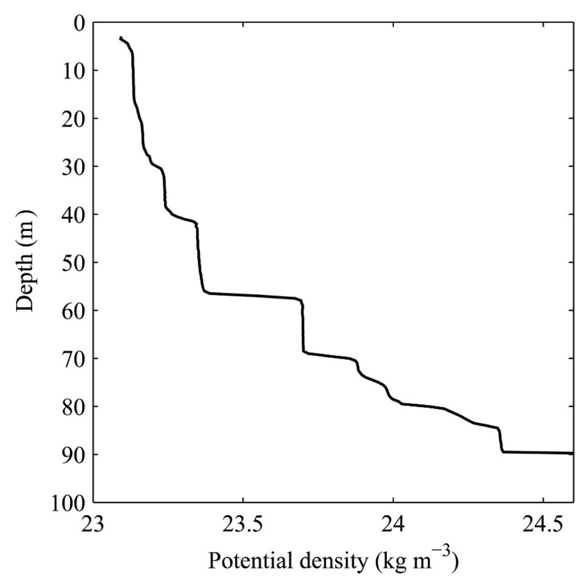

Fig. 7. Typical profile of vertical density distribution off Glover's Reef. Note multiple remnant mixed layers.

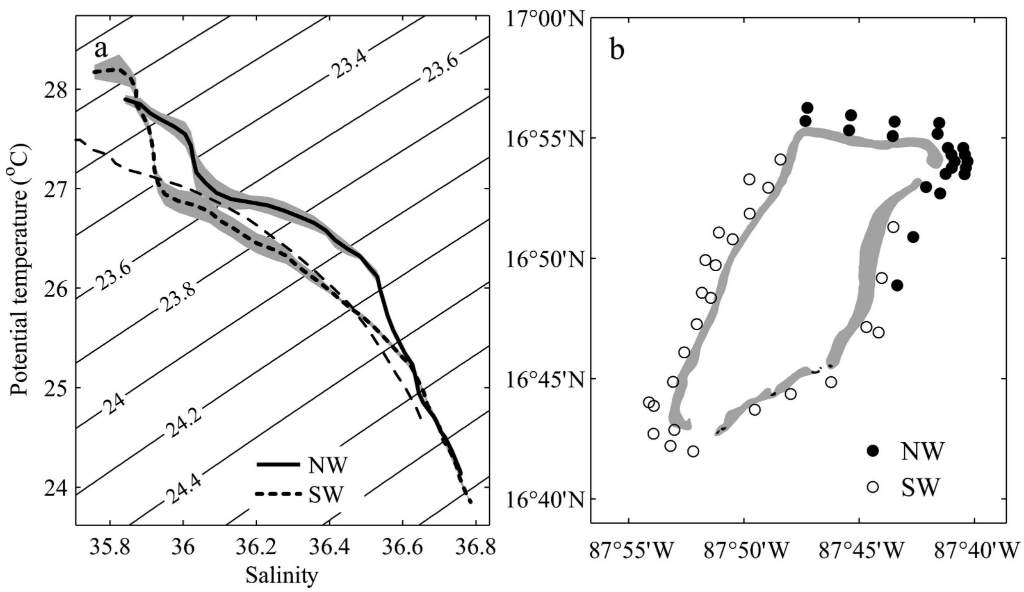

Fig. 8. Bimodal water mass structure on the Glover's Reef shelf in May 2006. (a) Mean T-S characteristics of northern (NW, solid line) and southern (SW, dotted line) stratification modes. Light shading shows 1 SD within each mode. Thin dashed line shows T-S characteristics from the February 2007 survey for the reference. (b) Geographic distribution of the northern (NW, solid circles) and southern (SW, open circles) stratification modes.

stratification was stable in both the temperature and salinity (Fig. 6).

Vertical hydrographic profiles showed substantial variability between the surveys. In May 2006 the water column was more stratified than in February of the following year: the mean buoyancy frequency in the upper 60 m was 9.3×10^{-3} s^{-1} vs. 5.5×10^{-3} s^{-1}. The difference could be attributed to the stronger heating and weaker mixing in May compared with February, resulting in surface water being 0.6°C warmer. Interannual variability of the large-scale water mass structure may have also played a role, judging by the 0.3°C temperature and 0.12 salinity difference in the upper thermocline (90 m) where seasonal changes of surface forcing have little direct effect.

Vertical distribution of phytoplankton biomass was also qualitatively different between the two surveys, as evident from the mean profiles of Chl *a* fluorescence (Fig. 6d). The 2007 survey showed a prominent fluorescence peak at 80-m depth, which was likely associated with the base of the active mixed layer present during that period. In contrast, only a hint of fluorescence increase toward 90 m was observed during the 2006 survey, when the surface layer was strongly stratified. Observed correlation between the surface-layer mixing and the deep chlorophyll maximum location and strength can be expected in oligotrophic (nutrient-limited) tropical waters (Huisman et al. 2006), but further clarification of the processes involved would require a full study of the biochemical environment of the reef.

In May 2006, Glover's Reef was surrounded by two distinct water masses, clearly separated in space and in properties (Fig. 8). The more ubiquitous of these water masses ("southern") was present along the western, southern, and southeastern sides of the atoll; the other ("northern") was found only at the northern and northeastern shelves. The northern water mass was slightly warmer (by 0.25°C), or, equivalently, saltier (by 0.1) at all potential density levels between 23.2 and 24.4 (Fig. 8a). The most distinct separation occurred near the potential density of 24.1 (roughly corresponding to a depth of 80 m); temperature values at this isopycnal were used to segregate northern and southern stratification modes in Fig. 8.

In February 2007 no bimodality in stratification was observed. All the profiles obtained at various locations on the Glover's Reef shelf during that survey generally followed the "southern" temperature–salinity (T-S) relationship (Fig. 8a). A notable discrepancy between the 2007 and 2006 "southern" T-S curves at potential densities below 23.4 (roughly corresponding to depths less than 45 m) can be attributed to the effect of seasonal warming.

The structure of the flow past Glover's Reef was also different during the two surveys (Fig. 9). In May 2006, the flow was relatively weaker (on the order of 10 cm s^{-1}) and was predominantly directed eastward. In February 2007, stronger currents reaching 25–30 cm s^{-1} were observed off the northeastern and southwestern corners of the atoll. General flow direction was more southward than during the previous year.

Circulation and water mass structure in the vicinity of Glover's Reef is strongly influenced by mesoscale eddies of the Caribbean Current. Modeling studies of Ezer et al. (2005) have demonstrated that presence of a cyclonic Caribbean eddy (associated with negative sea-surface anomaly) intensifies the Gulf of Honduras gyre and strengthens the southward flow along the Meso-American Barrier Reef. On the other hand, anticyclones weaken the gyre and may reverse the along-reef flow.

The flow structure observed in the present study further supports the model of the influence of eddies on reef flow proposed by Ezer et al. (2005). During the May 2006 survey, the eddy activity in the region was relatively low

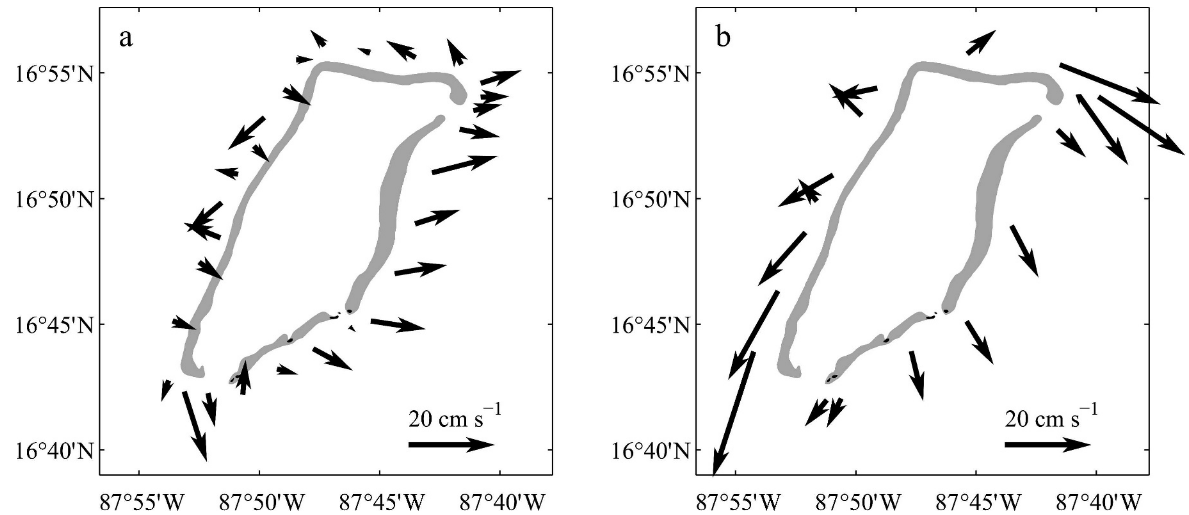

Fig. 9. Flow around Glover's Reef in (a) May 2006 and (b) February 2007 on the basis of REMUS surveying. Mean water velocity vectors for each transect are shown.

(Fig. 10a), resulting in a weaker alongshore flow past Glover's Reef. In contrast, during the following year survey, the area was affected by several strong cyclonic eddies (Fig. 10b), and southward flow was accordingly more pronounced. Note also that the observed flow direction was distinctly different from westward advection predicted by Tang et al. (2006) on the basis of their model of monthly mean velocity fields (*see* their fig. 12).

Wind forcing was similar during the two surveys and was not a likely cause of the observed differences in the circulation and water mass structure. On the basis of National Centers for Environmental Prediction (NCEP) reanalysis data for 02–07 May 2006 and 10–15 February 2007 (not shown), the wind direction in the vicinity of Glover's Reef was generally westward (from 88° and 77° true). Wind speeds were 7.7 ± 0.6 m s^{-1} and 4.5 ± 1.4 m s^{-1}, respectively.

It is presently not clear whether the observed changes in water mass properties can be explained by the influence of the Caribbean eddies. Taking into account the limited data obtained during the 2006 and 2007 surveys, we speculate that the southern mode represents the typical stratification in the vicinity of the atoll. The northern stratification mode indicates intermittent and localized admixing of a foreign water mass. This relatively warmer and saltier water extending to about 80-m depth could have been brought

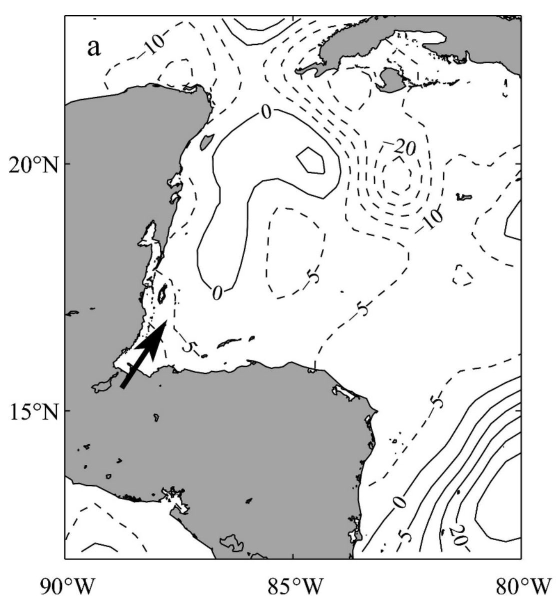

Fig. 10. Caribbean Sea surface height anomaly in centimeters over the 7-yr climatological mean on (a) 03 May 2006 and (b) 14 February 2007 on the basis of Aviso altimetry (http://www.aviso.oceanobs.com). Isolines are drawn every 5 cm, negative contours are dashed. Arrows mark the Glover's Reef location.

into the area by the anticyclonic eddy, remnants of which can be seen in Fig. 10a. The source of this water cannot be presently determined.

Discussion

In the course of two surveys, AUV REMUS proved itself as a capable tool for combined bathymetric and hydrographic mapping of a remote coral reef. The shallow shelf area surrounding Glover's Reef atoll was only accessible via the research station's small (5 m long) boats. Consequently, any surveying system used needed to be highly portable, compact, low maintenance, and incur low operating and maintenance costs. REMUS fulfilled these requirements and allowed us to conduct simultaneous observations of key hydrographic parameters while mapping the bathymetry of the atoll. Additionally, the high degree of autonomy of the vehicle permitted us to conduct additional biological and hydrographic OTS operations while the survey was underway.

Construction of an accurate bathymetric description of Glover's Reef, focusing specifically on the Nassau grouper SPAG site, was the first goal of this study. As Monismith (2007) discusses, cross-shelf gradients in wave radiation stresses arising from interaction with the bottom slope drive mean flows in many reef systems. We found that the depth of the shelfbreak around Glover's Reef varies in places from as shallow as 10 m to as deep as 40 m. Thus we would anticipate complicated flows driven around the regions in which the depth of the shelfbreak changes substantially as a result of pressure gradients imposed by spatial gradients in the wave radiation stresses.

The shape of the reef promontory where the aggregation site is located may have significant implications for larval transport. A similar topography adjacent to Gladden Spit is currently an important SPAG site of Cubera snapper (Heyman et al. 2005), and was also used historically by Nassau grouper. Heyman et al. (2005) found that model particles released from the Gladden Spit aggregation site moved eastward during periods of light winds where they became entrained in cyclonic mesoscale eddies. During strong trade winds from the northeast, the particles tended to either return to the lagoon or are blown further onshore to the continental shelf off Belize. It is presently unclear whether similar processes operate at Glover's Reef. Our study confirmed that the grouper SPAG site off Glover's Reef is situated at a unique location characterized by maximal shelf width between the reef crest and the shelfbreak with a large and relatively flat section of spur and groove reef in the vicinity.

The second goal of the study was description of hydrographic properties of the water mass(es) surrounding Glover's Reef. Our initial observations suggest that Caribbean Current mesoscale eddies have a pronounced effect on the circulation around the reef, corroborating the results of the previous modeling studies (Ezer et al. 2005). Strong southward flow observed during the February 2007 survey could be explained by the effect of several strong cyclonic eddies on the study area. No such eddies were present in May 2006, when the flow was relatively weaker and more zonal.

At the same time, the influence of local processes on the water mass structure was also evident. Staircase stratification of the upper ocean observed during both surveys indicated complex and variable balance of surface heating and mixing. Vertical chlorophyll distribution was, in turn, highly dependent on the surface boundary layer structure.

Two distinct water masses were found at the opposite corners of the atoll in 2006 (but not in 2007). One of them, the warmer and saltier "northern mode," was present in the direct vicinity of the SPAG site. Further observational or modeling studies are necessary to identify the origin of this water mass and the pathways of its advection to the SPAG site. The processes responsible for creating the distribution of water masses and the flow structure observed in the present study are likely to affect the fate of the Nassau grouper larvae. Consequently, resolving these processes (among others) is vital for future population connectivity models and could be used for their validation. If the presence of the northern-mode water mass is a seasonal feature contemporaneous with winter spawning events, it could provide a useful correlate to Nassau grouper larvae. Observing water mass properties would then help tracking the larvae as they travel away from Glover's Reef.

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