

# The Nassau grouper *Epinephelus striatus* (Bloch, 1792): Monitoring of the spawning aggregation site ‘El Blanquizal’, southern Mexican Caribbean

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## Abstract

‘El Blanquizal’ was one of the most important Nassau grouper (*Epinephelus striatus*) spawning aggregation sites (SAS) in the Mexican Caribbean. However, the characteristics of the population that still uses this site for reproduction remain unknown. The objective of the present study was to monitor and evaluate the Nassau grouper spawning aggregation at El Blanquizal using passive acoustics and visual counts during 2022 and 2023. Based on the sound pattern related to reproductive behaviour (SRRB) and visual monitoring, we determined that the Nassau grouper spawning aggregation season at El Blanquizal occurs from January to March, with up to three reproductive events (one per month). Each event is synchronized with the lunar cycle (the highest reproductive activity occurs between the 9th and 12th days after the full moon), a specific temperature range (26.9–27.7°C) and a particular time of day (28–60 min before sunset). Visual counts estimated an abundance of at least 1700 groupers during the reproductive season, with 80% being adults (TL > 50 cm), reproductive behaviour (courtship) and the identification of colouration phases associated with the spawning event (bicolour phase). These observations confirm that passive acoustics is a highly promising complementary method for monitoring Nassau grouper spawning aggregations and that the El Blanquizal is one of the few sites where Nassau grouper reproduction currently occurs. Its abundance during the spawning aggregation likely places it among the two most important aggregation sites for the species in Mexico, highlighting the priority of continuous monitoring and the implementation of protective measures based on the present results.

## KEYWORDS

abundance, conservation, full moon event, passive acoustic, spawning season, visual counts

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## 1 | INTRODUCTION

The Nassau grouper (*Epinephelus striatus*) is a typically solitary marine fish inhabiting coral reefs in the Western Atlantic, from Florida and Bermuda to Guyana, including the southeastern Gulf of Mexico and the Caribbean Sea (Erisman et al., 2018). During certain months of the year, it forms spawning aggregations at specific times and locations, gathering thousands of individuals per reproductive event (Colin, 1992; Sadovy & Eklund, 1999). These spawning aggregation sites (SAS) have been used recurrently for decades and represent the species' entire annual reproductive effort (De Mitcheson et al., 2008). Such predictability makes SAS highly vulnerable to overexploitation (Sadovy de Mitcheson, 2020; Sala et al., 2001; Waterhouse et al., 2020).

Over the past four decades, more than half of these aggregations have been lost, and Nassau grouper populations have declined by 80%–90% throughout their range, including Mexico, the Bahamas and the Caribbean (Aguilar-Perera, 2006; Fulton et al., 2020; Sadovy & Eklund, 1999). In response, management measures such as fishing bans, seasonal closures and marine protected areas have been implemented (Benedetti, 2013; Sadovy & Eklund, 1999). However, the Nassau grouper remains critically endangered (Sadovy et al., 2018; Somma et al., 2021), with limited evidence of population recovery due to insufficient data on SAS status and weak enforcement of management strategies (Waterhouse et al., 2020).

To address these gaps, effective SAS monitoring is paramount to ensure the species' conservation and promote responsible fishing practices in the Mexican Caribbean. Passive acoustic monitoring has emerged as an essential tool for studying fish SAS, particularly for species like the Nassau grouper, as it offers a non-invasive and cost-effective alternative to traditional methodologies (Rowell et al., 2015). This approach enables the detection of species-specific vocalizations associated with reproductive behaviours (Ibrahim, Zhuang, et al., 2018), providing unique insights into SAS temporal patterns and variability without requiring continuous observer presence. Furthermore, passive acoustics minimizes disturbances to the natural behaviour of fish and facilitates long-term data collection, which is essential for assessing the reproductive dynamics of SAS (Chérubin et al., 2020; Ibrahim, Chérubin, et al., 2018; Rowell et al., 2012).

In addition to acoustic data, environmental conditions such as temperature play a crucial role in synchronizing spawning and ensuring reproductive success (Carter, 1986; Pankhurst & Porter, 2003). Integrating both data sources establishes a baseline for understanding the environmental factors that favour spawning aggregations, offering a more comprehensive perspective on species conservation (Nemeth, 2009; Rowell et al., 2015; Schärer et al., 2012).

In the Mexican Caribbean, at least 28 Nassau grouper SAS have been identified, but only 7 have been scientifically validated, and systematic monitoring has been lacking for over a decade (Aguilar-Perera, 1994; Fulton et al., 2020; Heyman et al., 2014). Among these, El Blanquizal stands out as one of the most historically significant SAS, hosting up to 5000 individuals per reproductive event (Medina-Quej et al., 2004). Similar abundances (between 1000 and 2000 fish per reproductive event) have been reported for Niche Habin in the Sian Ka'an Biosphere Reserve,

another known SAS in the Mexican Caribbean (Franquesa-Rinos & Loreto-Viruel, 2006; Fulton et al., 2020). Recent exploratory reports suggest that this site remains crucial for the species' reproduction, emphasizing the need for updated evaluations (Fulton et al., 2020).

Understanding why Nassau grouper selects specific SAS is critical, as these sites likely provide shelter during resting periods and access to cooler waters and oceanic currents that enhance reproductive success (Kobara & Heyman, 2008; Nemeth et al., 2007). Site selection may be influenced by generational inheritance and extensive migratory capacities (Bolden, 2000; Starr et al., 2007).

The colouration patterns of *E. striatus* are closely linked to its reproductive behaviour and social interactions within spawning aggregations. During aggregation events, individuals exhibit distinct colouration phases (such as barred, bicolor, dark and white belly) associated with specific behaviours, including courtship, territoriality and spawning readiness (Archer et al., 2012; Colin, 1992). These patterns provide valuable insights into the dynamics and structure of spawning aggregations, offering an indirect indicator of reproductive activity and aggregation composition (Archer et al., 2012; Nemeth, 2009).

Incorporating a detailed geomorphological analysis of El Blanquizal, including bathymetry, can further enhance this understanding by revealing the physical and environmental features that make it suitable as a reproductive site. Bathymetric data are particularly relevant for identifying key characteristics such as depth gradients, seafloor complexity and potential oceanographic processes that influence aggregation behaviour (Colin, 1992).

This study aims to monitor and describe the characteristics of the Nassau grouper (*E. striatus*) aggregation at El Blanquizal using non-invasive methodologies, including visual counts, passive acoustic monitoring and assessments of geomorphological and temperature conditions. By analysing the distribution and prevalence of colouration patterns, the study will assess the behavioural and reproductive phases of the aggregation, providing a detailed perspective on the dynamics of this critical spawning site.

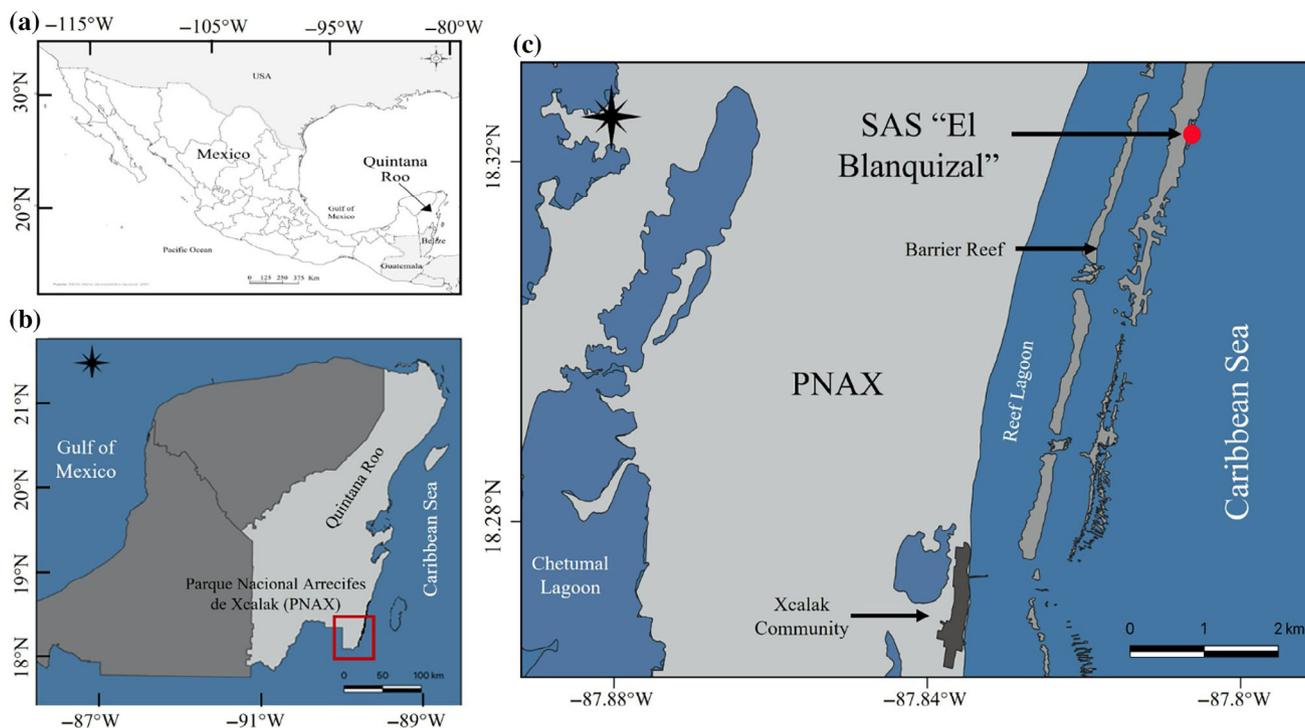
## 2 | METHODS

### 2.1 | Ethical considerations for the use of animals

The ethical policies do not apply to this study, as no organisms were manipulated or extracted from the natural environment to meet the objectives of this work. The study design employed only non-invasive methodologies. Access to the study area was authorized by the Comisión Nacional de Áreas Naturales Protegidas (CONANP), the responsible authority in Mexico. The permit granted has the following reference number: No F.00.9. DPNAX/122/2023.

### 2.2 | Study area

The SAS characterized in this study is locally known as 'El Blanquizal'. It is located in the southern Mexican Caribbean and is part of the



**FIGURE 1** Study site. (a) Geographic location of Quintana Roo. (b) Location of the Parque Nacional Arrecifes de Xcalak (PNAX). (c) The location of the spawning aggregation site (SAS), known as ‘El Blanquizar’, is represented by the red dot. Hard substrates and coral reefs are depicted in dark grey.

Parque Nacional Arrecifes de Xcalak (PNAX), Quintana Roo, Mexico (Figure 1a,b). It is  $\sim 1.5$  km from the beach shoreline and 400 m from the reef barrier ( $18^{\circ} 19' 24.3474''$  N and  $-87^{\circ} 48' 23.2922''$  W) (Figure 1c). In this area, there is a narrow continental shelf of  $\sim 1.8$  km, from the coastline to the edge ( $\sim 40$  m), after which the depth rapidly increases to 240 m (Carrillo et al., 2010). It has an average depth of 30 m and consists of large-sized coral patch reefs with high relief ( $\sim 8$  m in height). The patch has fractures that form channels and masses with sand in the central part of these; around this point, there are large sandy areas (Bolio-Moguel, 2007; Medina-Quej et al., 2004).

### 2.3 | Geomorphological characterization of the site

For the bathymetric characterization of the site a quadrant of  $1.2$  km<sup>2</sup> was established with four reference points: two points to boundaries adjacent to the reef barrier ( $18^{\circ} 19' 12''$  N– $87^{\circ} 48' 36''$  W and  $18^{\circ} 19' 47''$  N– $87^{\circ} 48' 36''$  W) and two points to boundaries offshore ( $18^{\circ} 19' 47''$  N– $87^{\circ} 47' 59''$  W and  $18^{\circ} 19' 12''$  N– $87^{\circ} 47' 59''$  W). Perpendicular transects to the coast were conducted, with an approximate distance of 100 m between each, covering the entire quadrant area. Bathymetric data were collected using a Lowrance HD5S Fish Finder and a Transducer (Airmar TM260 50/200 kHz) mounted on the stern of the boat. The unit recorded latitude, longitude and depth points (Fulton et al., 2016). Surfer 12.0 software was used to generate the bathymetric map, utilizing kriging interpolation due to its suitable

linear and unbiased prediction of intermediate values in spatial analysis (Papritz & Moyeed, 1999). The surrounding area of the aggregation point was also characterized based on bottom type, depth and the geomorphological structure of the site through in-situ observation using autonomous diving.

### 2.4 | Passive acoustics and temperature conditions

To monitor the dynamics of the Nassau grouper spawning aggregation at ‘El Blanquizar’, passive acoustic monitoring was conducted following established methodologies (Rowell et al., 2012; Schärer et al., 2012). The Nassau grouper sounds related to reproductive behaviour (SRRB) are identifiable based on their frequency range (51–206 Hz), mean duration ( $1.6 \pm 0.3$  s), mean maximum frequency ( $99 \pm 34$  Hz), call structure and tonal characteristics (Chérubin et al., 2020; Ibrahim et al., 2024; Ibrahim, Chérubin, et al., 2018; Schärer et al., 2012).

A SNAP-type hydrophone, equipped with an omnidirectional sensor capable of detecting sounds within this frequency range of up to 500 m, was deployed at a site  $\sim 100$  m from the core aggregation area, as determined through preliminary dives. The selected location minimizes extraneous noise interference, and prior surveys confirmed the absence of other Nassau grouper aggregations within a 1 km radius. The hydrophone was configured to record 20-s intervals every 5 min at a sampling frequency of 400 Hz. Data were collected from December to early April in 2022 and 2023, encompassing the Nassau

grouper's reproductive aggregation season in the Mexican Caribbean (Fulton et al., 2020; Medina-Quej et al., 2004; Sadovy & Eklund, 1999).

Acoustic data analysis employed the FADARV3 algorithm, which detects and classifies SRRB in the coastal region of Quintana Roo (Ibrahim et al., 2024; Ibrahim, Zhuang, et al., 2018). Recorded data included the number of SRRB per 20-s recording and the duration of each call. To analyse and graph the acoustic activity patterns during the 2022 and 2023 spawning aggregation seasons, the recorded SRRB were grouped into hourly intervals. Specifically, the sounds recorded at each hour of the day across all days of the study period were summed up, obtaining an accumulated value for each interval, from 00:00 to 23:00. This process generated what was referred to as the 'typical day' of the spawning aggregation season. The resulting data were analysed using a non-parametric Kruskal-Wallis ANOVA ( $\alpha = 0.05$ ) and Mann-Whitney  $U$  tests ( $\alpha = 0.05$ ). Additionally, Spearman's correlation coefficient ( $r_s$ ) ( $\alpha = 0.05$ ) was used to evaluate the relationship between SRRB production, time of day and temperature.

To characterize temperature variation during the aggregation season, a HOBO® U20 sensor was deployed alongside the hydrophone to record water temperature every 30 min from November 2021 to December 2023. Monthly average temperatures were analysed using Kruskal-Wallis ANOVA ( $\alpha = 0.05$ ) and Kolmogorov-Smirnov tests ( $\alpha = 0.05$ ). All statistical analyses were conducted using STATISTICA 10.0 software (TIBCO Software Inc., Palo Alto, CA, USA).

## 2.5 | Monitoring and visual survey

To characterize the biological dynamics of the El Blanquizar SAS, visual surveys were conducted during 2 months of the Nassau Grouper reproductive aggregation season in 2023 (January and March). Previous studies reported that the reproductive season of the Nassau Grouper in the Mexican Caribbean occurred from December to February (Aguilar-Perera, 2014; Bolio-Moguel, 2007; Medina-Quej et al., 2004). However, based on acoustic analyses from previous years, it was observed that this period has shifted, and the reproductive aggregation season now extends from January to March (unpublished data).

The visual survey dates were scheduled to coincide with the days of peak acoustic activity, identified as occurring between the 5th and 12th days after the full moon (DAFM). This timing was determined using unpublished acoustic data from another aggregation site in the Mexican Caribbean (Niche Habin) and corroborated by findings from the literature (Archer et al., 2012; Schärer et al., 2012). Although surveys were originally planned for the 2022 and 2023 reproductive seasons, unfavourable weather conditions in 2022 restricted data collection to January and March 2023.

Every day two dives were conducted to document fish activity within the aggregation: midday (12:00 to 2:00 PM) and dusk (5:00 to 7:00 PM). Midday dives focused on recording colouration pattern proportions, which are closely associated with the reproductive behaviour of *E. striatus* and provide insights into the sexual maturity and

behavioural states of individuals (Archer et al., 2012; Colin, 1992). This analysis helped differentiate between courting, territorial and spawning behaviours, thereby supporting the interpretation of reproductive dynamics observed within the aggregation. During each monitoring session, colouration patterns of Nassau grouper individuals were recorded visually by trained divers. Observations focused on four recognized patterns: barred (BA), bicour (BI), dark (DA) and white belly (WB) (Archer et al., 2012; Colin, 1992). These patterns were documented to infer behavioural states, as previous studies have linked specific colouration phases to reproductive activities, such as courtship (BI), dominance displays (DA) and spawning readiness (WB). Divers estimated the proportion of each colouration phase during peak aggregation abundance days in January and March.

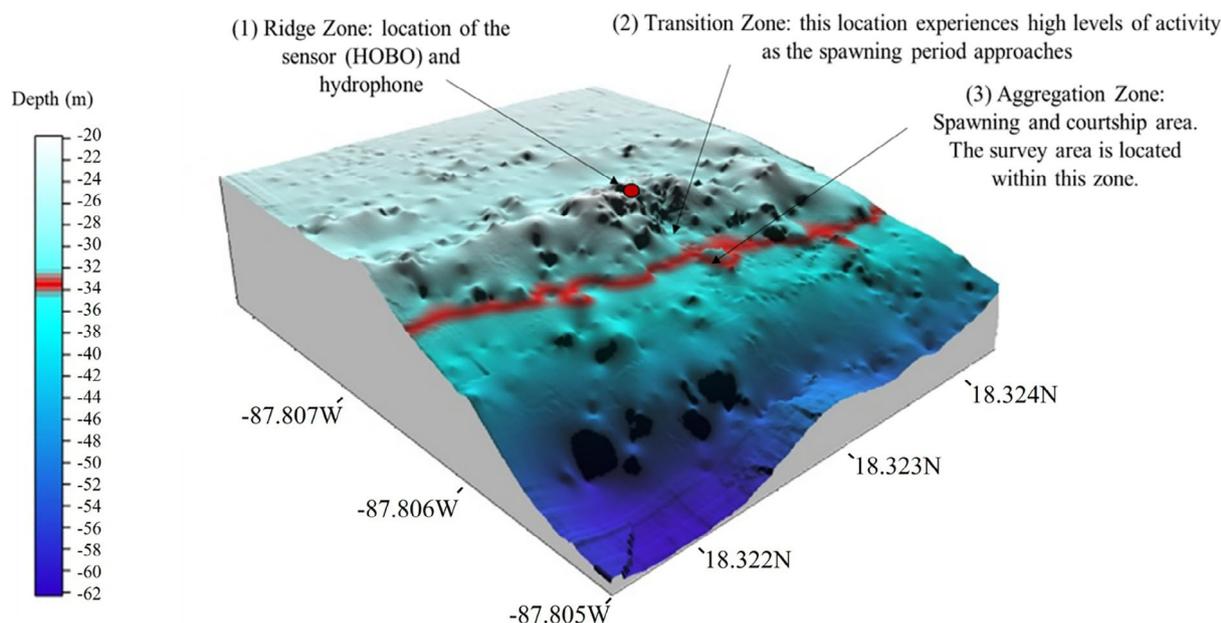
Dusk dives were conducted to estimate abundance, as peak reproductive aggregation activity typically occurs near dusk (Colin, 1992; Heyman et al., 2004; Rowell et al., 2012; Schärer et al., 2012). This dual approach enabled a detailed characterization of individual behaviours and population-level dynamics at 'El Blanquizar'.

Three experienced divers conducted the surveys, having been previously trained to identify *E. striatus*, record colouration patterns (Archer et al., 2012) and estimate total length (TL) and aggregation size (abundance). TL was estimated visually using 10-cm intervals, following established protocols and manuals (Colin et al., 2003; Heyman et al., 2004; Samoilys, 1997). The proportion of colouration patterns was calculated based on the day of maximum observed abundance each month. Diver training for TL and abundance estimation was conducted to ensure consistency and reliability in the data collection process. The surveyed area was determined from previous exploratory dives, which identified the site with the largest number of fish concentrated during the aggregation. To define the polygon, four points were marked with a rope tied to a weight at the bottom and a small buoy at the top. A total of 2400 m<sup>2</sup> was delineated, measuring 60 m in length (parallel to the coast) and 40 m in width (perpendicular to the coast). All dives started at the same point (where the hydrophone and temperature/pressure sensor were placed). Once reaching a depth of 25 m, the divers advanced 100 m in a straight line to reach the middle of the front edge of the polygon. One diver remained at this point, another moved 15 m to the right and the last 15 m to the left. Once in position, the divers synchronized their stopwatches, and the survey began along a 40-m transect in a straight line to the back limit of the polygon, standardizing the monitoring time to 10 min. Each diver counted the fish in ~1200 m<sup>2</sup> (40 × 30 m). The counts of each diver were averaged and extrapolated to the total delineated area, assuming a uniform distribution of the fish. The density calculation was performed using the following equation (Samoilys & Carlos, 2000):

$$\text{Density} = \frac{n}{y},$$

where  $n$  is the number of fish counted by diver 'a' and  $y$  is the surveyed area (m<sup>2</sup>).

The day with the highest number of fish was considered to determine the maximum abundance and length structure of the Nassau



**FIGURE 2** Bathymetry and morphology of the spawning aggregation site (SAS) 'El Blanquial'. The red dot marks the location of the sensor and hydrophone deployment. The depth scale is shown in meters (on the left side of the figure). The red strip indicates the area with the highest concentration of groups observed during the monitoring sessions.

groupers during each monitored month. Differences in estimated abundances between divers and between months were evaluated using a non-parametric ANOVA Kruskal-Wallis test ( $\alpha = 0.05$ ) and a Mann-Whitney  $U$  test ( $\alpha = 0.05$ ), respectively. All statistical tests were performed using STATISTICA 10.0 software.

### 3 | RESULTS

#### 3.1 | Geomorphology of the SAS

'El Blanquial' site is situated at an average depth of 31 m, with the shallowest area at 18 m and the deepest reaching up to 45 m; beyond this point, the depth increases abruptly to over 100 m (Figure 2). For the characterization, the area was divided into three zones (Table 1).

#### 3.2 | Passive acoustics and temperature conditions

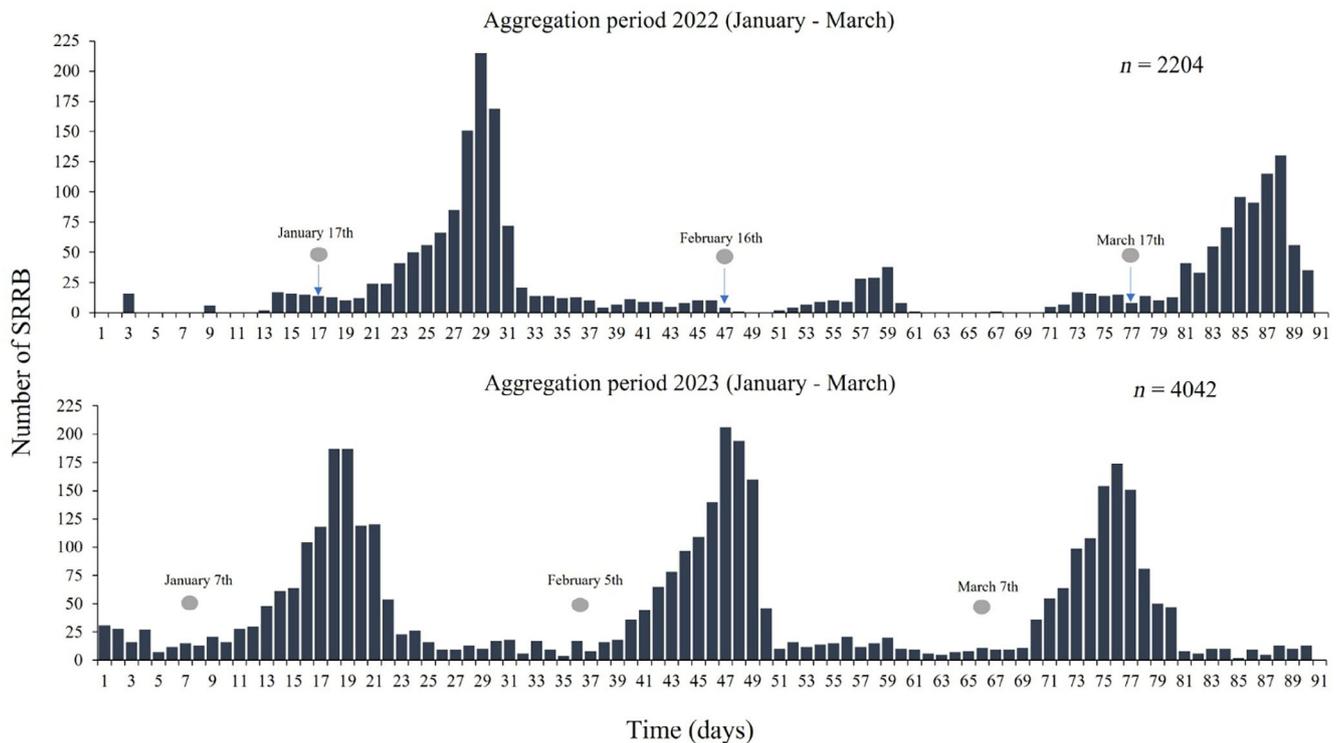
Acoustic activity was significantly higher during the 2023 season compared to 2022, with 4042 sounds recorded versus 2204, respectively ( $U = 2491$ ,  $p < 0.05$ ). January registered the highest number of SRRB in both years, with 1054 sounds in 2022 and 1447 in 2023. SRRB increased after each full moon event, peaking between the 9th and 13th DAFM, with a 27 to 28 day periodicity between activity peaks. The pattern of sounds identified during February 2022 was lower than that of the other months (Figure 3). No clear SRRB pattern was detected in December and April, suggesting that these months may

**TABLE 1** Description and characteristics of the zones comprising the spawning aggregation site (SAS) 'El Blanquial'.

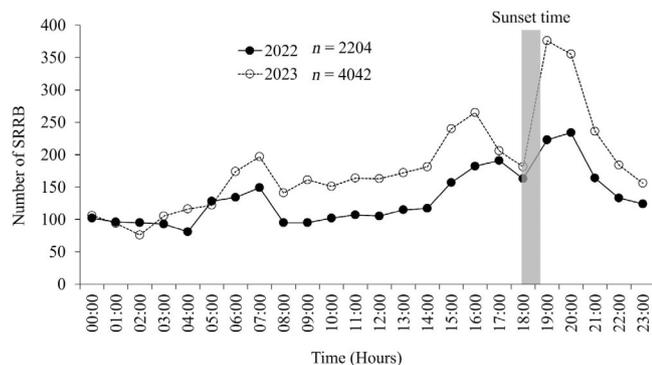
Zone	Characteristics	Use during aggregation
1 (Ridge)	Coral patches with heights reaching up to 9 m. Features channels and caves between the coral formations. Max. depth 30 m.	Refuge, resting and feeding place.
2 (Transition)	Delimited by the end of the ridge zone, with depths ranging from 30 to 38 m. Bottom with medium-sized rocks isolated on the sand.	Resting zone, when there is little reproductive activity. Very crowded area as sunset approaches, especially after the fifth day following the full moon event.
3 (Aggregation)	Bottom is mostly composed of sand and small isolated patches of coral up to 2 m in height. Depth ranges from 38 to 45 m.	Aggregation, courtship and likely spawning.

not correspond to the peak of reproductive activity. The daily pattern of SRRB production was consistent across both seasons, showing a progressive increase as sunset approached [ $r_S$  (2022) = 0.4,  $p < 0.05$ ;  $r_S$  (2023) = 0.72,  $p < 0.05$ ], reaching its maximum between 7:00 and 8:00 PM (Figure 4).

The temperature at 'El Blanquial' showed interannual variation. In 2022, temperatures ranged from 25.9 to 30.05°C, with an average



**FIGURE 3** Periodicity and abundance of sounds related to the reproductive behaviour (SRRB) of Nassau grouper (*Epinephelus striatus*), detected during the aggregation seasons of 2022 and 2023 at the spawning aggregation sites (SAS) 'El Blanquizal'. The y-axis represents the total SRRB accumulated per day. Grey circles represent the full moon event of each month.



**FIGURE 4** Pattern of SRRB (sounds related to reproductive behaviour) of Nassau grouper (*Epinephelus striatus*) during a typical day of the reproductive aggregation season (1 January to 31 March 2022 and 2023) at the spawning aggregation site (SAS) 'El Blanquizal'. The data represent hourly accumulated SRRB. The grey bar indicates the sunset time during the study period.

of  $28.42 \pm 0.85^\circ\text{C}$ , whereas in 2023, they ranged from  $26.58$  to  $31.06^\circ\text{C}$ , with an average of  $28.79 \pm 1.25^\circ\text{C}$ . Monthly significant differences were observed ( $H = 694.72$ ,  $df = 23$ ,  $N = 730$ ,  $p < 0.05$ ). August, September and October were the warmest months in both years, with average temperatures of  $29.39 \pm 0.21^\circ\text{C}$  in 2022 and  $30.37 \pm 0.41^\circ\text{C}$  in 2023. Conversely, the coldest months were January, February and March, averaging  $27.23 \pm 0.24^\circ\text{C}$  in 2022 and  $27.22 \pm 0.17^\circ\text{C}$  in 2023 (Figure 5a). Significant differences between

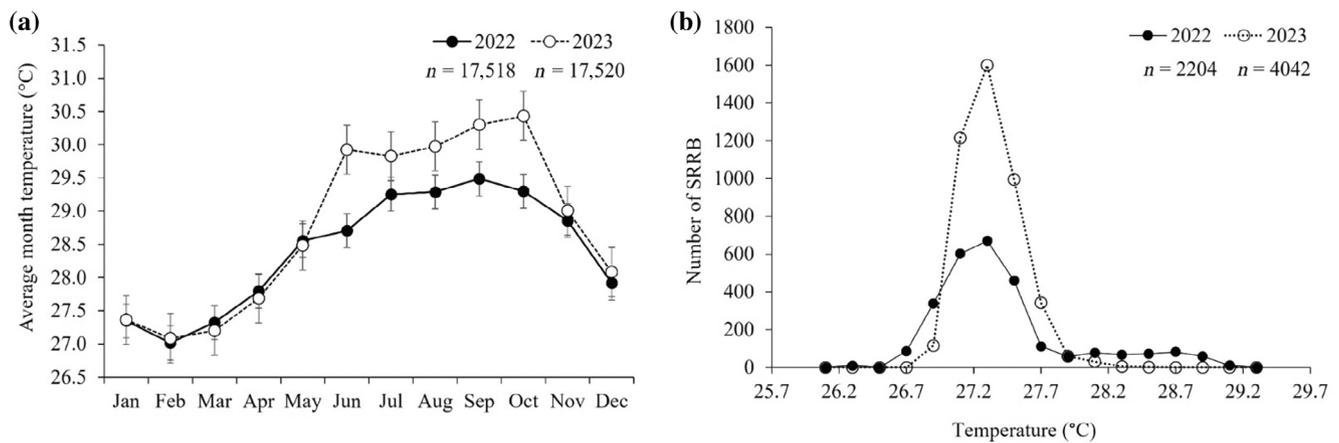
years were detected ( $U = 53,984$ ,  $p < 0.05$ ), primarily due to warmer conditions from June to October 2023 compared to the same period in 2022.

Daily average temperature patterns during the reproductive aggregation months were consistent across both seasons. In January, temperatures gradually decreased, with variations of  $1.02^\circ\text{C}$  in 2022 and  $0.44^\circ\text{C}$  in 2023 from the beginning to the end of the month. February exhibited relatively stable temperatures, with variations of  $0.84^\circ\text{C}$  in 2022 and  $0.44^\circ\text{C}$  in 2023. In contrast, March was characterized by an increasing temperature trend in both years, with variations of  $0.62^\circ\text{C}$  in 2022 and  $0.73^\circ\text{C}$  in 2023.

A significant correlation between average temperature and the number of SRRB recorded was identified only in January 2022 and February 2023 ( $r_{\text{January}_2022} = -0.49$ ,  $p < 0.05$ ;  $r_{\text{February}_2023} = -0.48$ ,  $p < 0.05$ ). In both cases, the number of SRRB increased as temperatures reached a specific range between  $26.9$  and  $27.7^\circ\text{C}$  (Figure 5b).

### 3.3 | Monitoring and visual surveys

Ten monitoring sessions (five per month) were conducted to estimate aggregation abundance, with visibility at survey depths exceeding 15 m. No significant differences were observed between diver counts (Table 2), but significant differences were detected between days ( $H = 40.47$ ,  $df = 9$ ,  $N = 210$ ,  $p < 0.05$ ). Aggregation



**FIGURE 5** (a) Annual temperature pattern at the spawning aggregation site (SAS) 'El Blanquizar' based on monthly average temperatures recorded during 2022 and 2023. The plot highlights interannual variations and seasonal trends. (b) Temperature range (26.9–27.7°C) associated with the highest acoustic activity of Nassau grouper (*Epinephelus striatus*) during the reproductive aggregation season (January to March) in 2022 and 2023.

**TABLE 2** Abundance estimates from monitoring of Nassau grouper (*Epinephelus striatus*) reproductive aggregation in 2023.

Date	Start-end time count (GMT-5)	Abundance diver 1	Abundance diver 2	Abundance diver 3	Mann-Witney U test p-value	Average abundance $\pm$ SD	Density (fishes/m <sup>2</sup> )
17 Jan	17:20–17:30	1076	1024	994	0.74	1031 $\pm$ 94.4	0.86
18 Jan	18:10–18:20	1193	1182	1206	0.84	1194 $\pm$ 68.3	1
19 Jan	18:35–18:45	1305	1302	1306	0.84	1304 $\pm$ 78	1.1
20 Jan	17:50–18:00	890	877	950	0.94	906 $\pm$ 106.2	0.75
21 Jan	17:17–17:27	508	493	434	0.9	478 $\pm$ 85.4	0.4
12 Mar	17:10–17:20	92	89	98	0.97	93 $\pm$ 7.3	0.08
13 Mar	18:35–18:45	127	125	137	0.79	130 $\pm$ 10.9	0.1
14 Mar	18:11–18:21	285	298	298	0.89	294 $\pm$ 19.9	0.24
15 Mar	17:44–17:54	327	322	326	0.88	325 $\pm$ 29.9	0.27
16 Mar	18:01–18:11	383	406	398	0.84	396 $\pm$ 25.6	0.33

Abbreviation: SD, standard deviation.

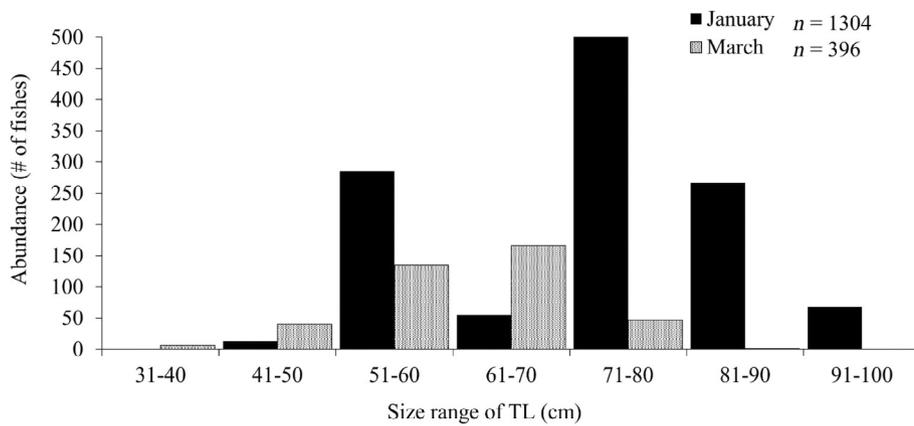
abundance peaked in January (19th: 1304  $\pm$  78 groupers) and was significantly higher than in March (16th: 396  $\pm$  25.6 groupers) ( $H = 32.8$ ,  $df = 1$ ,  $N = 210$ ,  $p < 0.05$ ) (Table 2). The highest densities were recorded on the 12th DAFM in January and the 9th DAFM in March.

The estimated size range during the surveys was 30 to 100 cm TL (Figure 6). More size groups and larger organisms were identified during the January aggregation compared to the March aggregation ( $U = 107,461$ ,  $p < 0.05$ ). The average size in January was 73.04  $\pm$  11.85 cm TL, and in March it was 60.3  $\pm$  8.95 cm TL.

Four colouration patterns were identified during both months of monitoring: BA, BI, DA and WB (Figure 7). The predominant colouration pattern on the day of peak abundance in both months was BI, comprising 51% of the total abundance in this phase during January and 45% in March. The proportion of fish in the other colouration phases was as follows (with the first value corresponding to January and the second to March): BA = 16% and 20%; DA = 22% and 21%; WB = 11% and 10%.

## 4 | DISCUSSION

The conservation and recovery of Nassau grouper SAS in Mexico require strategies that validate and continuously monitor spawning sites, as emphasized by Fulton et al. (2020), Sadovy de Mitcheson (2020) and Waterhouse et al. (2020). However, understanding the current conditions and establishing population reference points for this species remain challenging due to logistical constraints. These aggregations often occur at sites far from the coast, at depths exceeding 30 m and near the edges of coastal platforms (Sadovy de Mitcheson, 2020). Additionally, the short duration of the reproductive aggregations and adverse weather conditions complicate annual monitoring efforts (Fulton et al., 2020). In this context, our study describes and monitors the reproductive population at 'El Blanquizar' during two consecutive seasons (2022 and 2023). We documented population size, length structure and behavioural dynamics by integrating passive acoustics to identify the optimal time for visual surveys. This approach addresses key logistical challenges and establishes a baseline



**FIGURE 6** Estimated size structure from monitoring of the reproductive aggregation of Nassau grouper (*Epinephelus striatus*) at the spawning aggregation site (SAS) 'El Blanquizal' during 2023.



**FIGURE 7** Colouration patterns of maximum abundance of Nassau grouper (*Epinephelus striatus*) were identified during the reproductive aggregation season of 2023 at the spawning aggregation site (SAS) 'El Blanquizal'. Barred (BA), bicolour (BI), dark (DA) and white belly (WB).

for understanding the reproductive population's dynamics, offering critical insights for the long-term conservation and management of this species in the Mexican Caribbean.

#### 4.1 | Geomorphological characterization of the site

'El Blanquizal' is part of a reef zone facing the open ocean, characterized by a narrow shelf (1 to 2 km wide) and depths of 25–45 m, with steep descents into deep waters (>200 m) just 150 m offshore. These geomorphological features align with those reported for Nassau grouper aggregation sites in other regions of its distribution, such as the

Bahamas, Virgin Islands, Honduras, Mexico, Belize and the Cayman Islands (Aguilar-Perera & Aguilar-Dávila, 1996; Colin, 1992; Heyman et al., 2007; Kobara & Heyman, 2008; Medina-Quej et al., 2004; Olsen & LaPlace, 1978).

The bathymetric and geomorphological characterization of El Blanquizal was conducted to confirm whether this site meets the criteria associated with SAS described in previous studies (Kobara & Heyman, 2008; Nemeth et al., 2007). This analysis revealed that the site shares key physical attributes, such as proximity to deep waters and high seafloor complexity, which are hypothesized to influence site selection by Nassau grouper (Sadovy & Domeier, 2005). During monitoring, groupers were observed sheltering in zone 1 (Ridge),

particularly during periods of low aggregation activity, suggesting the site provides adequate refuge during resting periods, as proposed by Kobara and Heyman (2008) and Nemeth et al. (2007).

Additionally, our findings confirm that El Blanquizal serves as a functional reproductive aggregation site for Nassau grouper. The bathymetric data support the interpretation of observed aggregation dynamics by contextualizing fish behaviour, such as movement patterns and spatial distribution within the site (Colin, 2011; Heyman & Kjerfve, 2008). For example, aggregations were concentrated near the shelf edge during peak activity, likely taking advantage of oceanographic features that enhance reproductive success, such as cooler waters and strong currents (Nemeth et al., 2008; Whaylen et al., 2006).

This study highlights the relevance of detailed geomorphological and bathymetric analyses for understanding the environmental and physical characteristics that define Nassau grouper SAS (Bolden, 2000; Colin, 1992). These findings not only validate the ecological importance of El Blanquizal but also contribute critical information for developing spatially explicit management strategies (Fulton et al., 2020; Sadovy de Mitcheson, 2020).

## 4.2 | Passive acoustics and temperature conditions

In this study, the exact moment of spawning could not be observed directly. However, the analysis of SRRB revealed three key variables directly associated with this behaviour: temperature, lunar cycle and time of day. These factors were evaluated in the context of the observed patterns at El Blanquizal to establish a baseline for understanding the conditions under which Nassau grouper exhibits reproductive activity.

### 4.2.1 | Temperature

Across both years, SRRB were predominantly recorded within a temperature range of 26.9–27.7°C, a consistent range where at least 80% of the reproductive sounds were detected. This suggests that specific thermal conditions facilitate reproductive behaviour, consistent with previous studies (Colin, 1992; Schärer et al., 2012). However, anomalies, such as the abrupt temperature change of 0.9°C observed in February 2022, may disrupt synchronization and reduce reproductive activity, as evidenced by fewer SRRB recorded during that period.

The seasonal pattern observed at El Blanquizal, characterized by relatively stable conditions and a gradual temperature decrease during the first quarter of the year, aligns with reports from other latitudes where reproductive aggregations occur under similar temperature regimes (Aguilar-Perera, 2006; Colin, 1992; Sadovy & Eklund, 1999; Schärer et al., 2012). From a physiological standpoint, the synchronization of spawning with specific temperature ranges likely influences hormonal activation in spawners and enhances larval survival. Spawning at the optimal thermal threshold reduces the time from fertilization to first feeding, thereby increasing larval fitness and potentially

enhancing larval recruitment (Carter, 1986; Pankhurst & Porter, 2003).

However, the role of environmental disturbances, such as temperature anomalies induced by extreme weather events, may have significant implications for the synchronization of reproductive events. The observed temperature fluctuation of 0.9°C in February 2022 suggests that sudden thermal changes could disrupt reproductive behaviour, reducing the frequency of SRRB and potentially diminishing reproductive success. This is consistent with findings from other studies showing that environmental stressors, including abrupt temperature shifts, can impair spawning synchrony and negatively affect larval survival (Brulé et al., 2022; Mellin et al., 2016).

Additionally, seasonal or storm-induced fluctuations could create windows of temperature instability that might interrupt the optimal thermal conditions required for spawning. Such disruptions are especially concerning for species like Nassau grouper, whose reproductive success depends on precise environmental cues. In tropical and subtropical marine ecosystems, storms and shifts in the thermal regime could be increasing in frequency and intensity due to climate change, adding another layer of unpredictability to the reproductive dynamics of vulnerable species (Mellin et al., 2016). The understanding of these thermal thresholds and the potential impact of climatic fluctuations is crucial for the development of effective conservation strategies. These strategies should account for the increased vulnerability of Nassau grouper to environmental disturbances, particularly in light of ongoing climate variability and extreme weather events (Brulé et al., 2022).

### 4.2.2 | Lunar cycle

The observed temporal pattern of aggregation events at El Blanquizal, occurring thrice per year and lasting approximately 8–10 days, aligns with findings from other Nassau grouper aggregation sites (Archer et al., 2012; Kadison et al., 2010; Schärer et al., 2012). Peak reproductive activity was recorded consistently between the 9th and 12th DAFM, suggesting a strong influence of lunar periodicity on spawning behaviour. The gradual increase in SRRB starting on the fifth DAFM likely reflects a behavioural strategy aimed at attracting and concentrating spawners before spawning events. This synchronization is intricately linked to physiological processes like egg hydration, which involves the uptake of water into the oocytes to achieve the buoyancy required for pelagic fertilization and early larval development (Kobayashi et al., 1988; Pankhurst & Porter, 2003). Environmental factors such as temperature and lunar cues may regulate this process, ensuring optimal timing for fertilization success.

Acoustic signals, which intensify during pre-spawning periods, likely play a dual role in facilitating synchronization and enhancing reproductive efficiency. They not only help aggregate individuals but may also act as social triggers that coordinate physiological readiness among spawners, including egg hydration and gamete release (Rowell et al., 2012; Schärer et al., 2012). These findings

emphasize the interplay between behavioural, acoustic and physiological processes, highlighting the importance of lunar and environmental drivers in shaping Nassau grouper reproductive dynamics. Incorporating these variables into long-term monitoring efforts is essential to better understand aggregation patterns and develop conservation strategies tailored to the species' reproductive ecology.

#### 4.2.3 | Time of day

During peak reproductive activity, the highest production of SRRB occurred near sunset, between 28 and 60 min after sunset. This daily pattern has been reported for Nassau grouper aggregations in other regions, such as Puerto Rico and Belize, and is thought to enhance reproductive success while minimizing predation risk (Heyman et al., 2005; Schärer et al., 2012). Spawning under low-light conditions may reduce predator detection of both adults and eggs, while also synchronizing larval hatching with favourable conditions for dispersal and survival (Colin, 1992; Sadovy & Domeier, 2005). This behaviour was investigated within the context of the study's objectives, which aim to identify the key environmental factors influencing aggregation and reproductive success. Specifically, understanding the timing of aggregation relative to sunset provides insight into the ecological drivers of reproductive synchronization. It highlights the adaptive significance of these temporal patterns for maximizing fertilization success and larval survival.

#### 4.2.4 | Environmental context

Seasonal temperature variation at El Blanquial is likely influenced by atmospheric processes, as the site's depth (20–45 m) generally remains within the mixed layer. This results in a direct interaction between heat transfer at the air-sea interface and oceanographic processes (Carrillo et al., 2009; Sánchez-Hernández et al., 2022). Despite interannual differences in mean water temperature, the consistent pattern of gradual cooling during the first quarter aligns with the observed reproductive season, reinforcing the importance of stable temperature regimes in shaping aggregation dynamics (Aguilar-Perera, 2006; Fulton et al., 2020).

These results highlight how the environmental context interacts with behavioural and reproductive dynamics. Specifically, the gradual cooling during the first quarter of the year at El Blanquial coincides with the observed aggregation and spawning patterns, emphasizing the role of stable thermal regimes in reproductive success. The evidence generated in this study underscores the complementary role of acoustic monitoring and environmental data in understanding the dynamics of Nassau grouper reproductive aggregations. This integrated approach helps identify critical conditions for spawning and informs conservation strategies aimed at protecting the species and its habitats (Nelson et al., 2011; Schärer et al., 2012).

### 4.3 | Monitoring and visual surveys

In the present study, the maximum abundance of Nassau grouper at the SAS was estimated at 1700 individuals during 2023 (1304 in January and 396 in March). Although no counts were conducted in February, it is likely that the total number of fish attending the SAS that year was higher, a hypothesis supported by acoustic data indicating greater reproductive activity during that month. This observation underscores the importance of integrating visual surveys with acoustic monitoring to obtain a more comprehensive understanding of aggregation dynamics. Unlike previous reports where SAS rarely exceeds 3000 individuals (Aguilar-Perera, 2006; Fulton, 2023; Fulton et al., 2020), the results from this study suggest that El Blanquial maintains a significant abundance, reinforcing its importance as one of the key sites for the species along the Mexican coastline.

Similar abundances (between 1000 and 2000 fish per reproductive event) have been reported for Niche Habin in the Sian Ka'an Biosphere Reserve, another known SAS in the Mexican Caribbean (Franquesa-Rinos & Loreto-Viruel, 2006; Fulton et al., 2020). This supports the relevance of aggregations in the region, consistent with the findings of this study. However, the size of any aggregation can vary annually due to the movement of reproductive individuals (Sala et al., 2001). Continuous monitoring of SAS is, therefore, essential to capture these fluctuations. Based on abundance and size structure, El Blanquial is likely one of the most critical SAS for the species along the Mexican coastline.

Another supporting factor is the size structure of the aggregations, where at least 80% of the individuals observed during the 2023 aggregation events exceeded 50 cm in TL, indicating that the majority had reached sexual maturity (Olsen & LaPlace, 1978; Colin et al., 1987; Sadovy & Colin, 1995). This contrasts with observations from heavily exploited SAS, where smaller fish, including juveniles, are frequently captured (Espinosa, 1980; Sadovy & Colin, 1995; Thompson & Munro, 1978). In such sites, differences of up to 10 cm in average TL have been reported when compared to non-exploited aggregations (Espinosa, 1980; Sadovy & Eklund, 1999).

Behavioural patterns and colouration phases observed in this study also support the existence of active spawning. The higher proportion of individuals in the bicolor phase suggests that visual counts were conducted during periods close to spawning events (Archer et al., 2012; Colin, 1992; Smith, 1972; Whaylen et al., 2006). This pattern was more evident from the eighth DAFM, consistent with studies reporting spawning between the 1st and 10th DAFM, during which most fish exhibit bicolor phases associated with gamete release (Archer et al., 2012; Colin, 1992; Smith, 1972; Whaylen et al., 2006). Combined with passive acoustics, these observations are vital for designing monitoring protocols, assessing aggregation dynamics and predicting spawning events (Mesa-Avila & Molina-Borja, 2007; Shumway, 1999).

Visual surveys were conducted between 17:00 and 19:00 to align with periods of increased activity when groupers transition from resting areas to mid- and upper-water columns in preparation for spawning (Colin, 1992; Heyman et al., 2004; Schärer et al., 2012). This

schedule ensures a representative estimate of abundance by targeting a period when fish are highly visible and evenly distributed in the water column.

Although SRRB exhibits two main daily peaks, with the highest occurring between 19:00 and 20:00, these signals primarily characterize reproductive behaviours rather than abundance (Mann et al., 2010; Rowell et al., 2012; Schärer et al., 2012). Adjusting visual surveys to coincide with this peak could potentially increase observed counts. However, the current schedule balances methodological rigour, diver safety and logistical considerations avoiding night-time dives while ensuring consistent and reliable data collection (Nemeth, 2005; Sadovy & Eklund, 1999).

Each monitoring approach presents inherent limitations that, when considered in isolation, can constrain the interpretation of spawning aggregation dynamics. Visual surveys provide critical data on abundance, size structure and behaviour but are limited by logistical and temporal factors, including diver safety and restricted coverage of night-time activity (Colin, 1992; Nemeth, 2005; Sadovy & Eklund, 1999). Passive acoustics, on the contrary, captures continuous behavioural data, such as the timing and intensity of SRRB, but does not directly quantify abundance or individual contributions to the recorded sounds (Mann et al., 2010; Rowell et al., 2012; Schärer et al., 2012). Combining these methods bridges these gaps, offering a more holistic understanding of aggregation dynamics. For example, acoustic data can complement visual surveys by identifying periods of heightened reproductive activity, such as the peak in February detected in this study (Archer et al., 2012; Whaylen et al., 2006). Together, these methods improve the accuracy of monitoring efforts and inform conservation strategies for critically endangered species (De Mitcheson et al., 2008; Sadovy & Domeier, 2005). This approach, coupled with complementary passive acoustic data, is essential for understanding population dynamics and informing the management of this critically endangered species.

## 5 | CONCLUSIONS

The periodicity of the Nassau grouper spawning aggregation season at El Blanquizal is from January to March, lasting approximately 9–10 days each month, between the 5th and 14th DAFM. Information on the prevailing temperature conditions during the highest acoustic/reproductive activity days was obtained, and some population characteristics of the 2023 aggregation were determined. These included an approximate abundance of 1700 groupers during the spawning season, a higher proportion of individuals that have reached sexual maturity (80% of fish with at least 50 cm TL), reproductive behaviour (courtship) and the identification of colouration phases associated with the spawning event. These observations confirm that El Blanquizal is one of the few sites where Nassau grouper reproduction currently occurs. Additionally, this SAS hosts a considerable abundance compared to other aggregations in the Caribbean and is likely one of the two most important reproductive sites for the species in Mexico.

Given that El Blanquizal is part of the Arrecifes de Xcalak Natural Protected Area (ANP) and is subject to a partial fishing ban (from 1 February to 31 March), the results from this study underscore the importance of expanding or adjusting protection measures. The current fishing ban only partially covers the Nassau grouper's reproductive period. To enhance conservation efforts, it is recommended that fishing closures be extended to encompass the entire spawning season from January to March, providing comprehensive protection during this critical reproductive window. Continuous monitoring of this site is essential for generating accurate, representative data on reproductive dynamics, which will inform effective conservation and management strategies. These efforts are crucial for conserving and recovering the Nassau grouper population in the Mexican Caribbean.

## AUTHOR CONTRIBUTIONS

Luis Salgado Cruz: conceptualization, data generation, data analysis, manuscript preparations, manuscript review and editing. Oscar F. Reyes Mendoza: conceptualization, funding, data generation, manuscript review. Karla A. Camacho-Cruz: conceptualization, data generation, data analysis, manuscript review and editing. Jacobo A. Caamal Madrigal: data generation, data analysis. Johnny O. Valdez Iuit: data generation, funding. Carlos I. Pérez-Quñonez: manuscript review. Daniel Arceo-Carranza: conceptualization, funding, manuscript review.

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