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Fish spawning aggregations in the Gulf of Chiriqui, Panamanian Pacific: six years of monitoring

Yolani A. Robles P.[1]; https://orcid.org/0000-0003-4140-9235
Ángel J. Vega[1*]; https://orcid.org/0000-0002-9535-3348
Luis A. Montes S.[1]; https://orcid.org/0000-0002-8823-1991
Erasmo E. Sánchez-Carles[1]; https://orcid.org/0009-0006-6106-7745
Roberto C. Lombardo G.[1,2]; https://orcid.org/0000-0002-0279-8621

1. Centro de Capacitación, Investigación y Monitoreo de la Biodiversidad en el Parque Nacional Coiba (CCIMBIO-CRUV-UP), Universidad de Panamá, Santiago, Veraguas, Panamá; yolany.robles@up.ac.pa, angel.vega@up.ac.pa*, luis.montes@up.ac.pa, esanchezc157@gmail.com, roberto.lombardo@up.ac.pa (*Correspondencia)
2. Sistema Nacional de Investigación (SNI), Secretaría Nacional de Ciencia, Tecnología e Innovación, Panamá (SENACYT), Ciudad del Saber, Clayton Panamá, República de Panamá.

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ABSTRACT

Introduction: Fish spawning aggregations (FSAs) are temporary concentrations of individuals of the same species that form for the sole purpose of reproducing.

Objective: To document the species, times, and localities where FSAs occur in the Gulf of Chiriqui, Panamanian Pacific.

Methods: From 2020 to 2025, SCUBA surveys and photographic documentation were conducted to identify FSAs within Coiba National Park (CNP) and the Islas Secas Archipelago (ISA) in the Gulf of Chiriquí. Environmental data, including temperature, salinity, and pH were collected using a YSI EXO2 multiparameter probe, and temperature was continuously recorded with a HOBO Water Temperature Pro v2.

Results: The FSAs were recorded for three snapper species (*Lutjanus peru*, *Lutjanus colorado* and *Lutjanus aratus*); one jack (*Caranx sexfasciatus*); one grouper (*Cephalopholis colonus*); and one wrasse (*Thalassoma lucasanum*). Aggregations were observed at Bajo 20, Sacramento, Sueño del Pescador, and Montaña Rusa within CNP, and at Bajo Rizo in ISA. In the latter location, aggregations were recorded for *T. lucasanum*, *C. colonus*, and *L. colorado*. During aggregations, water column stratification was observed, associated with the intrusion of cold-water masses into the gulf, thermocline shoaling, and a decrease in dissolved oxygen concentrations, all correlated with temperature dynamics. Spawning events were most frequently observed in the morning hours.

Conclusion: The number of reported species forming FSAs in CNP increased from three to seven, and FSAs were documented for the first time in ISA for three species.

Key words: spawning; Coiba; Islas Secas; reproduction; snappers.

RESUMEN

Agregaciones de desove de peces en el Golfo de Chiriquí, Pacífico panameño: seis años de monitoreo

Introducción: Las agregaciones reproductivas de peces (FSAs, por sus siglas en inglés) son concentraciones temporales de individuos de la misma especie que se forman con el único propósito de reproducirse.

Objetivo: Documentar las especies, momentos y localidades donde ocurren las FSAs en el Golfo de Chiriquí, Pacífico panameño.
Métodos: Entre 2020 y 2025, mediante buceo autónomo y con el uso de cámaras fotográficas se documentaron las FSAs en el Parque Nacional Coiba (PNC) y en el archipiélago de Islas Secas (AIS), Golfo de Chiriquí. Las observaciones fueron complementadas con registros de temperatura, salinidad y pH con el uso de una sonda multiparamétrica YSI EXO2 y registro continuo de temperatura con un sensor térmico HOBO Water Temperature Pro v2.
Resultados: Se documentaron las FSAs en tres especies de pargos (*Lutjanus peru, Lutjanus colorado, Lutjanus aratus*), un carángido, *Caranx sexfasciatus*; un serránido, *Cefalopholis colonus*; y un lábrido, *Thalassoma lucasanum,* en las localidades: Bajo 20, Sacramento, Sueño del Pescador y Montaña Rusa, en el PNC y bajo Rizo, en AIS, en este último caso para *T. lucasanum*, *C. colonus* y *L. colorado*. Durante el periodo de agregaciones se presentó una estratificación en la columna de agua, por la presencia de masas de agua fría que entran al golfo, acercamiento de la termoclina a la superficie y una baja en la concentración de oxígeno disuelto, correlacionado con el comportamiento de la temperatura. La mayor frecuencia de desoves se observó en horas de la mañana.
Conclusiones: Se aumentó de tres a siete los reportes de especies que realizan FSAs en el PNC y se documentaron por primera vez en el AIS, para tres especies.

Palabras clave: desoves; Coiba; Islas Secas; reproducción; pargos.

INTRODUCTION

Fish spawning aggregations (FSAs) are temporary concentrations of individuals of the same species that form for the sole purpose of reproducing. These events, which are key to the survival of the species, are determined by adaptation to habitat characteristics and ocean dynamics (Erisman, Cota-Nieto et al., 2017; Erisman et al., 2018). These aggregations lead to large-scale, recurrent spawning events, and are considered a reproductive strategy that increases offspring survival probability (Domeier & Colin, 1997; Domeier, 2012). Spawning aggregations have been documented across several commercially important fish families, including snappers (Lutjanidae), seabass and groupers (Serranidae) (Choat, 2012).

Various fish species that form spawning aggregations are known to traverse great distances to specific sites, where they spawn seasonally over short time windows (Boomhower et al., 2010; Kobara et al., 2013; Kadison et al., 2006), while other species are resident and travel shorter distance (Domeir, 2012). For example, the kelp bass, *Paralabrax clathratus* (Girard, 1854), maintain small home ranges (few hundred m) where individuals repeatedly use reef habitats for spawning aggregations (Lowe et al., 2003). In contrast, the gulf weakfish, *Cynoscion othonopterus* (Jordan & Gilbert, 1882), migrates approximately up to ~ 150 km from widespread coastal habitats to aggregate and spawn in the Colorado River delta. (Erisman et al., 2012). At the extreme end, the bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758), travels transoceanic distances exceeding 4 000 km, from its foraging areas in the North Atlantic to spawning aggregation sites in the Gulf of Mexico and Mediterranean Sea (Block et al., 2005).

Spawning aggregations are critical for the sustainability of fisheries (Chollett et al., 2020; Kobara et al., 2013); however, their predictability also makes fish particularly vulnerable to fishing pressure, as fishermen exploit such predictability to locate and capture large numbers of individuals with relatively low effort (Pittman & Heyman, 2020; Erisman, Heyman et al., 2017; Sala et al., 2001; van Overzee & Rijnsdorp, 2015). In addition to fishing, environmental changes driven by climate change also pose serious threats for species that form transitory spawning aggregations. This is the case as the timing, success, and viability of aggregations are highly dependent on ecological conditions. Globally, climate change affects both breeding and non-breeding fish populations; however, the on-going change of oceanographic features at aggregation sites suggests that sea surface temperature and thermic gradients might significantly influence fish phenology, distribution and oceanic habitat suitability. In this scenario, species with narrow thermal tolerances are particularly at risk (Asch & Erisman, 2018; Sánchez-Hernández et al., 2022). For instance, groupers (Epinephelidae) may be more affected than snappers (Lutjanidae), as the latter generally exhibit broader thermal spawning thresholds, while groupers often rely on cooler waters for reproduction (Gokturk et al., 2022).

By 2014, 25 % of documented spawning aggregations were reported to be in decline, while 4 % had been considered lost (Russell et al., 2014). Of the documented aggregations, 52 % had not been evaluated, fewer than 35 % were under any form of protection, and only around 25 % had some degree of monitoring (Erisman et al., 2018). These proportions stand in stark contrast to the importance of spawning aggregations for the ocean's ecology and fisheries, as well-monitored and managed aggregations have been shown to enhance fishery performance, reflected in increased yields at nearby sites where fishing is permitted (Erisman, Cota-Nieto et al., 2017). Among the management strategies for spawning aggregations, the establishment of seasonal fishing closures have proven effective when they: a) reduce fishing mortality of the largest individuals, which are crucial to the reproductive potential of the population, b) protect spawning habitats, c) lower the risk of overexploitation in species that form large aggregations, d) mitigate the evolutionary effects on size at maturation and reproductive investment, and e) reduce the risk of overexploitation of specific spawning components (van Overzee & Rijnsdorp, 2015). This effectiveness translates into increased fish biomass, higher catch rate, and improved larval recruitment at fishing grounds (Erisman, Cota-Nieto et al., 2017).

Management requires science-based measures that can be provided to administrators and stakeholders, through scientific research and monitoring (Erisman, Cota-Nieto et al., 2017). In the Eastern Pacific, spawning aggregations have been reported for *Lutjanus argentiventris*, *Lutjanus novemfasciatus*, *Mycteroperca prionura* (Rosenblatt & Zahuranec, 1967), *Mycteroperca jordani* (Jenkins & Evermann, 1889), *Mycteroperca rosacea* (Streets, 1877), *Paranthias colonus* (Valenciennes, 1846), *Caranx sexfasciatus* (Quoy & Gaimard, 1825), *Seriola lalandi* (Cuvier &Valenciennes, 1833) (Sala et al., 2003), and *C. othonopterus* (Erisman et al., 2012) in the Gulf of California; *Tylosurus pacificus* (Steindachner, 1876) in Colombia (Correa-Herrera et al., 2017), *Dermatolepis dermatolepis* (Boulenger, 1895) in Costa Rica (Erisman et al., 2009); and *Lutjanus peru* and *Lutjanus guttatus* in Coiba National Park (CNP) Panama (Vega, Maté et al., 2016). The limited number and frequency of spawning aggregation reports in the Eastern Tropical Pacific likely reflects the lack of long-term monitoring programs, rather than a true absence of spawning aggregations (Sala et al., 2003). Therefore, it is in the public interest to develop research and monitoring plans to increase current knowledge on fish spawning aggregations in the region. Following the first report of fish spawning aggregations in Panama (Vega, Maté et al., 2016), and in recognition of their ecological importance and relevance to sustainable fisheries, a research and monitoring program was established in 2020. The objective of the present study is to document the species, timing, and locations where spawning aggregations occur, based on six years of monitoring (2020 - 2025) within CNP and the Islas Secas Archipelago (ISA), in the Panamanian Pacific.

MATERIALS AND METHODS

Study area: The CNP is a protected area in the Gulf of Chiriqui (GCH), Eastern Tropical panamanian Pacific. It extends a surface of 2 701.25 km^2, of which 2 165.43 km^2 corresponds to sea surface (Maté et al., 2015; Cardiel et al., 1997). The ISA consists of five main volcanic islands and a number of smaller islets located in the GCH, approximately 20 km off the Western coast of Panama (Angehr et al., 2021). During the dry season, the GCH is influenced by the shoaling of the thermocline to depths of up to 30 m due to trade winds, leading to cooling of surface waters and increased nutrient availability (D'Croz & O'Dea, 2007; D'Croz & O'Dea 2009). However, analyses of the vertical structure of the thermocline and halocline show greater stratification during the dry season (January and February), with these layers located at depths ranging from 15 m and 30-35 m (Olivera et al., 2023).

Dive sites: Vega, Maté et al. (2016) reported the presence of snapper FSAs at Parque Nacional Coiba (PNC) during full-moon periods in the dry season, between February and April. Research on FSAs resumed in 2020, and fieldwork to document the occurrence of aggregations was carried out during each dry season from January to April (2020-2025). Throughout this period, research was interrupted due to COVID-19 in March 2020, and in April 2022 the start of fieldwork was delayed due to budget setbacks.

The sites studied were: Bajo 20 (7°40'14.76" N & 81°40'55.32" W), a submarine rocky pinnacle with mats of azooxanthellate coral and patches of accumulated white sand. The shallowest part of this site is about 28 m deep according to the tide amplitude (Vega et al., 2019). Bajo 20 is one of the two sites in the CNP and the only one in the Eastern Tropical Pacific where spawning aggregations have been recorded for Pacific red snapper (*L. peru*) and spotted rose snapper (*L. guttatus*) (Vega, Maté et al., 2016). Sacramento (7°45'25.29" N & 81°40'51.43" W) is seamount located West of Bajo 20, with its shallowest point at a depth of 32 m. The bottom is densely covered with black corals, which host significant aggregations of reef fishes. Montaña Rusa (7°53'8.93" N & 81°48'50.41" W) consists of a rocky pinnacle, oriented North to South, with a minimum depth of 12 m at its summit. The surface is covered with algal mats, crustose coralline algae, and corals of the genus *Pocillopora*, along with octocorals, sponges, and other invertebrates. Sueños del Pescador (7°53'20.62" N & 81°48'50.46" W) is a rocky pinnacle that rises to about 8 m below the surface, also oriented North to South, similar to Montaña Rusa. The summit is covered with complex arrangements of scleractinian corals, and the rock walls are lined with a diverse sea fan (A. Vega, personal observation, May 13, 2023). In 2025, Bajo Rizo (7°55'1.43" N & 82°0'30.25" W) was included in the fieldwork campaigns. This site is located in the ISA, 17 km West of the Contreras Islands, outside the boundaries of CNP. Bajo Rizo lies at a depth of 26 m at its shallowest point and is characterized by a black coral forest scattered with sandy channels and rocky formations (L. Montes, personal observation, March 27, 2025) (Fig. 1).

Water column conditions: To correlate fish behavior with prevailing water column conditions, a YSI (EXO2) multiparameter probe was deployed upon arrival at each site.

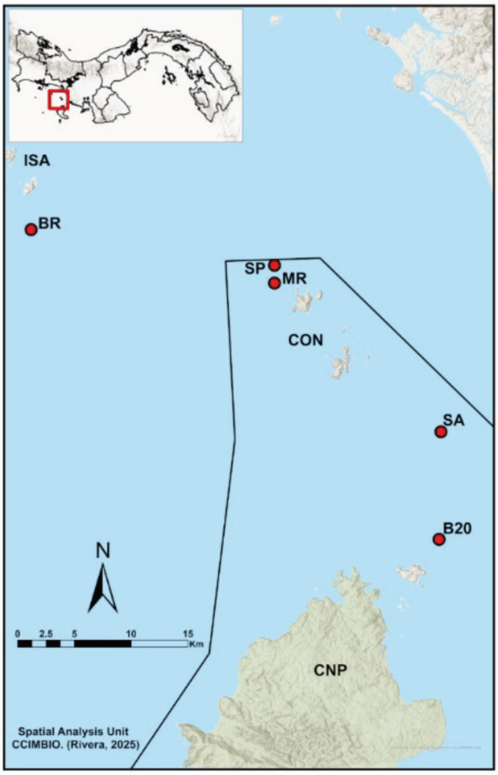

Fig. 1. Sampling sites for fish breeding aggregations in Coiba National Park, Panamanian Pacific. Coiba National Park (CNP), Islas Secas Archipelago (ISA), Contreras Islands (CON), Bajo Rizo (BR), Sueños del Pescador (SP), Montaña Rusa (MR), Sacramento (SA), Bajo 20 (B20). The black outline indicates CNP boundaries.

This instrument allowed the measurement of temperature (°C), salinity (ups), dissolved oxygen (mg/l) and pH from the surface down to 30 at 5 m intervals. In addition, the probe aided in thermocline depth estimation. Additionally, In July 2023, a temperature data logger (HOBO Pro v2) was installed at a depth of 28 m in Bajo 20. Temperature and depth values corresponding to fish aggregation and spawning events were obtained from both the logger and the dive computer. Water column were analyzed using the Pearson correlation. Differences between categorical variables, when expressed as proportions, were tested using a goodness-of-fit chi-squared test. Statistical significance was set at α = 0.05 (Zar, 2010).

Aggregation monitoring: Each field trip began two days prior to the new and full moons and concluded two days after those lunar phases. The presence of fish schools was confirmed prior to diving using a Garmin Echomap Ultra 106sv echosounder. During each dive, a team of three to four divers descended, equipped with two Sony Cyber-Shot DSC-RX100M6 cameras, housed inside Nauticam NA-RX100VI frames, one of which was fitted with a wide-angle lens (130°-67 mm). Additionally, two GoPro Hero 10 Black cameras were used. Horizontal visibility was estimated by the divers as the maximum distance at which a diving partner remained clearly visible. Dives took place in the morning (6:30-11:00 h) and afternoon (14:00-18:00 h), each lasting 30-40 min, with two dives completed in the morning and two in the afternoon. Monitoring activities at each site aimed to capture as much as possible of the present species, their behavior, and depth at which spawning occurred. In the laboratory, collected photographic and video materials were reviewed with Adobe Premier Pro (Adobe, 2019) to study the spawning behavior of each species in the observed aggregations (Heyman et al., 2004; Sala et al., 2003). To determine whether aggregations qualified as FSAs, we recorded the species forming the aggregation, the occurrence of spawning, and several indicators, including color changes in individuals, swollen abdomens, courtship behavior, the presence of spawn remnants, predator presence, and thermal stratification in the water column. In addition to these indicators, a spawning aggregation event in this study was defined as one occurring during either a low-tide or high-tide cycle.

RESULTS

Water column conditions: Significant correlation was found between temperature, salinity, dissolved oxygen and pH (Pearson, p < 0.05). Dissolved oxygen and temperature had the strongest correlation (R = 0.84), while correlation between the other variables was lower yet significant (Table 1).

The greatest variations in temperature and dissolved oxygen between the surface and 30 m depth occurred between January and April. During this period, the water column was stratified into three main layers. In the first layer, the water was clearer and warmer in the upper 10-12 m, with roughly 25 m of visibility. This was followed by a denser and more turbid second layer extending to about 20 m depth, where visibility dropped to roughly 7 m. The third layer, reached the bottom, and was clearer again (~ 15 m visibility) but significantly colder, at 16 °C.

These variations were driven by the intrusion of a cold-water mass into the GCH during dry season, causing the thermocline to raise closer to the surface, especially between February and mid-April. This resulted in thermal stratification, with surface waters exceeding

Table 1

Pearson correlations (r) between the different para m recorded in Bajo 20, Panamanian Pacific, during 2024.

		DO (mg/l)	S (ups)	pH
S (ups)	R	-0.38*		
	n	1 914		
pH	R	0.39*	-0.10*	
	n	1 755	1 755	
T (°C)	R	0.84*	-0.28*	0.32*
	n	1 914	1 914	1 755

Salinity (S), temperature (T), and dissolved oxygen (DO). Asterix represents significance.

30 °C and relatively cooler waters below 20 m depth (Fig. 2). This change in the water column structure coincided with fluctuations in dissolved oxygen concentrations, which dropped below 3 mg/l and were associated with the thermocline between 20-30 m depth; this was particularly evident in March, when thermal minima were also recorded at that depth (Fig. 3).

Salinity showed minor variation at all depths in March across all monitoring years, coinciding with the presence of the cool water mass that flows through the PNC, with its influence being most pronounced between 20-30 m depth (Fig. 4). The pH held between 7.5 and 8.5, with the highest values observed at the surface in March, compared to those at the 20-30 m depth interval, particularly in 2021 and 2024 (Fig. 5).

Continuous temperature records at Bajo 20, from January and April 2024, show daily oscillations ranging from 16 to 30 °C at approximately 28 m depth (Fig. 6). During this period, the lowest temperatures were associated with full and new moon phases, coinciding with a turbid water mass rich in organic matter and low dissolved oxygen.

Aggregation monitoring: A total of 187 dives were completed, representing approximately 122 diver-hours. Between 2020 to 2025, spawning aggregations were observed during full and/or new moon phases. The six species confirmed to form spawning aggregations in CNP were *L. peru*, *Lutjanus colorado*, *Lutjanus aratus* (Günther, 1864), *C. sexfasciatus*, *Cephalopholis colonus*, and *Thalassoma lucasanum* (Gill, 1862) (Table 2). Aggregations were documented at Bajo 20, Sacramento, Sueño del Pescador and Montaña Rusa in CNP, and Bajo Rizo in the ISA. In the latter, aggregations were

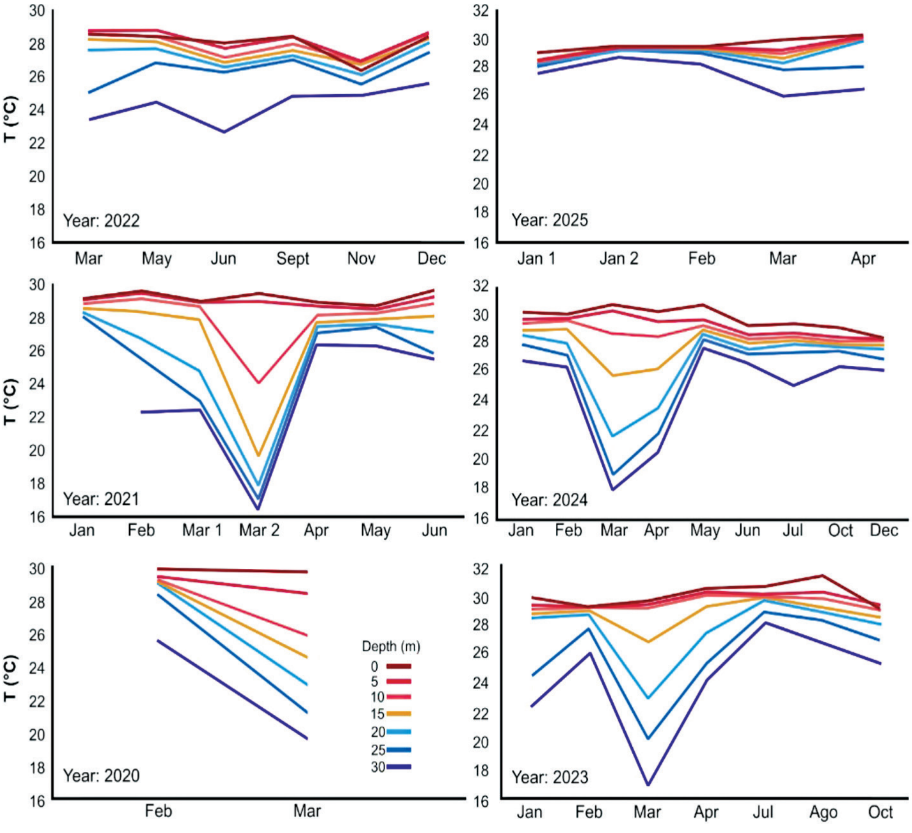

Fig. 2. Temperature records in Bajo 20, between surface and 30 m depth, Coiba National Park, Panamanian Pacific.

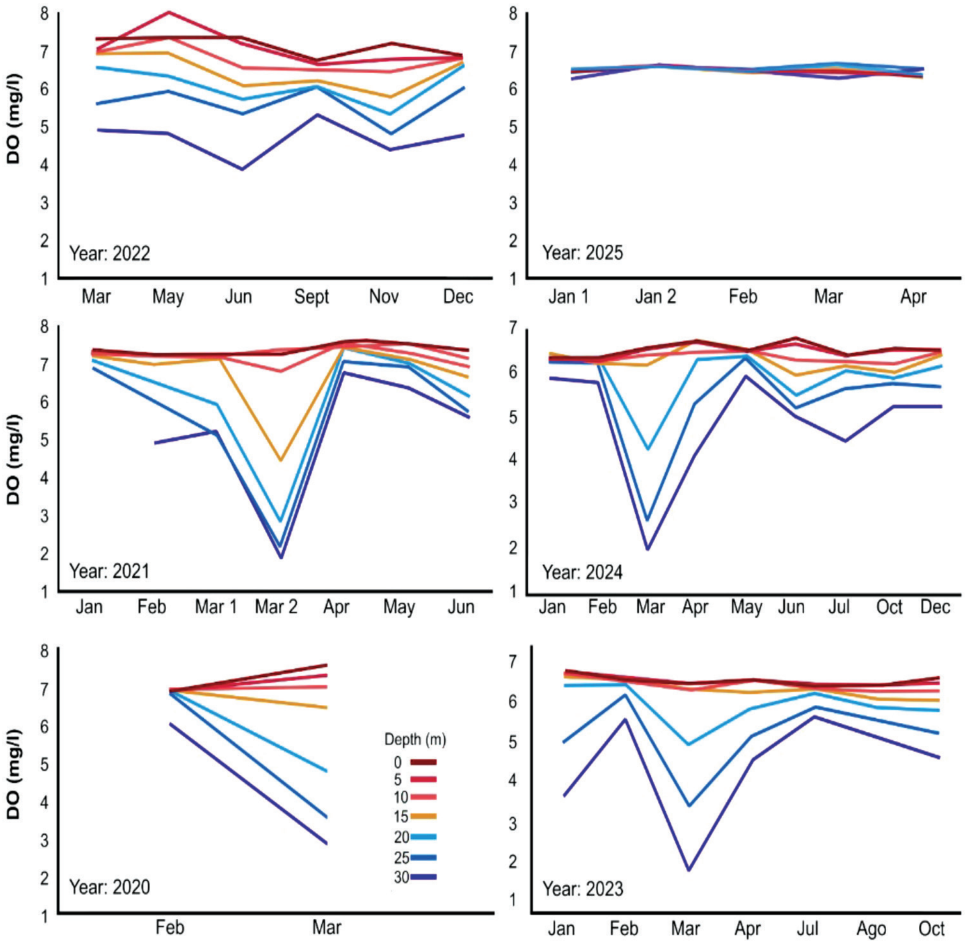

Fig. 3. Dissolved oxygen (mg/l) profiles, between the surface and 30 m depth in Bajo 20, Coiba National Park, Panamanian Pacific.

recorded for *T. lucasanum*, *C. colonus*, and *L. colorado* (Jordan & Gilbert, 1882).

Between 2020 and 2025, 61 aggregation events were recorded, where 32 events culminated in spawning, while 29 showed signs of reproductive activity but did not end in spawning. During the morning at low tide, 21 spawning events were recorded and 11 in the afternoon at high tide. On a full moon, 17 events were recorded and 15 during a new moon (Table 2). There was no difference in the proportions among these categories (spawn vs. no spawn: $\chi^2 = 0.15$, $p = 0.70$; spawning at low vs. high tide: $\chi^2 = 3.13$, $p = 0.08$; full vs. new moon: $\chi^2 = 0.13$, $p = 0.72$).

The six species spawned during both full and new moons, and during both high and low tides, except for *T. lucasanum*, which spawned only during low tide. Within the snapper group, *L. peru* spawned two days apart in 2025, on the evening of 12 March at Sacramento and the morning of 14 March at Bajo 20, two sites approximately 10 km apart within PNC. *L. aratus* spawned on consecutive days, 7 and 8 April 2025, with afternoon and morning events recorded at Bajo 20. A similar pattern occurred

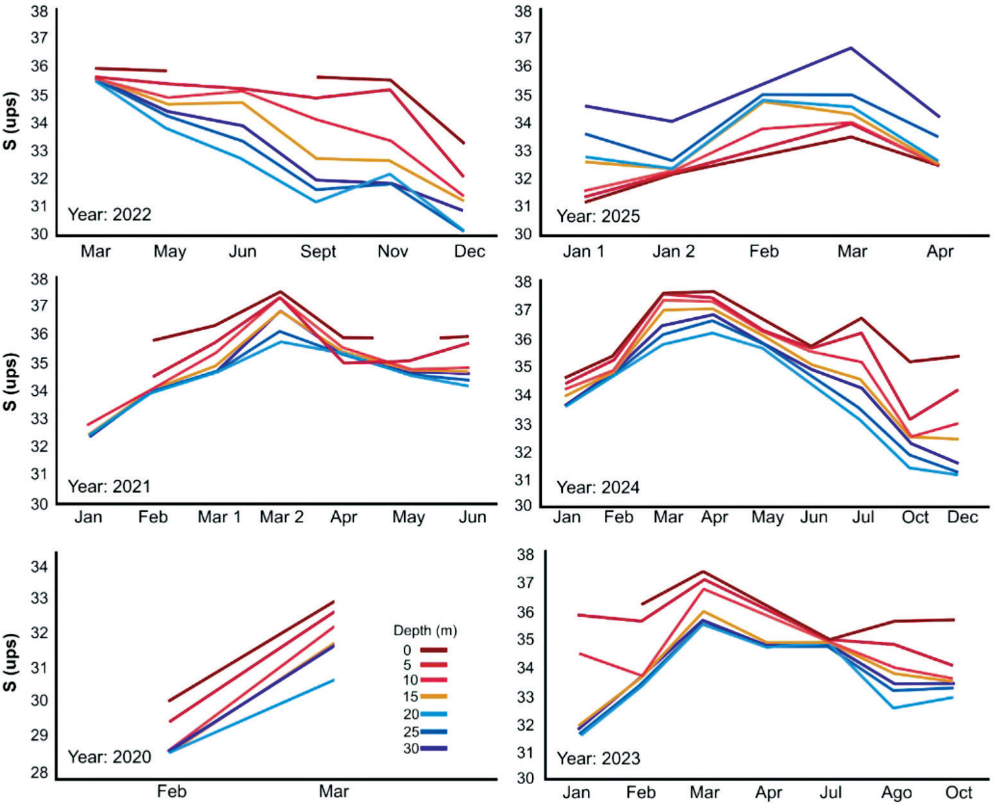

Fig. 4. Salinity (ups) records between surface and 30 m depth in Bajo 20, Coiba National Park, Panamanian Pacific.

in *C. sexfasciatus* (Carangidae), which spawned on 24 and 25 March 2025, with morning and afternoon events documented at Bajo 20 and Sacramento (Table 2).

***Lutjanus peru*:** With the arrival of the cold-water mass, *L. peru* concentrates on or around underwater mounds at depths between 25-40 m, and as the cold-water mass moves to shallower depths, individuals follow it to begin the reproductive process. A total of two events were recorded during the new moon (January 25, 2020; January 22, 2023) and six during the full moon (March 09, 2023; February 23 and March 23, 2024; February 12, March 12 and 14, 2025) (Table 2). Spawning aggregations generally occurred in the early morning hours, although two afternoon events were also observed. As the cold-water mass ascended, the school separated off the rock pinnacle where smaller groups of 5-200 individuals formed. These groups began courtship behavior characterized by chasing, where some individuals interacted with the lead fish. During the chase, fish clustered and circled, while swimming turned slow rising in the water column while nipping and rubbing against the leader until it spawned. When the leader spawned, nearby individuals were stimulated to spawn as well, leaving behind a cloud of eggs and sperm in the water column (Fig. 7).

Depending on the size of the aggregation, spawning groups ranged from as few as ten to as many as 200 individuals; however, in large spawning groups, not all individuals were able to release their gametes. Those located at the periphery of the spawning core regrouped with other fish to carry out a subsequent episode

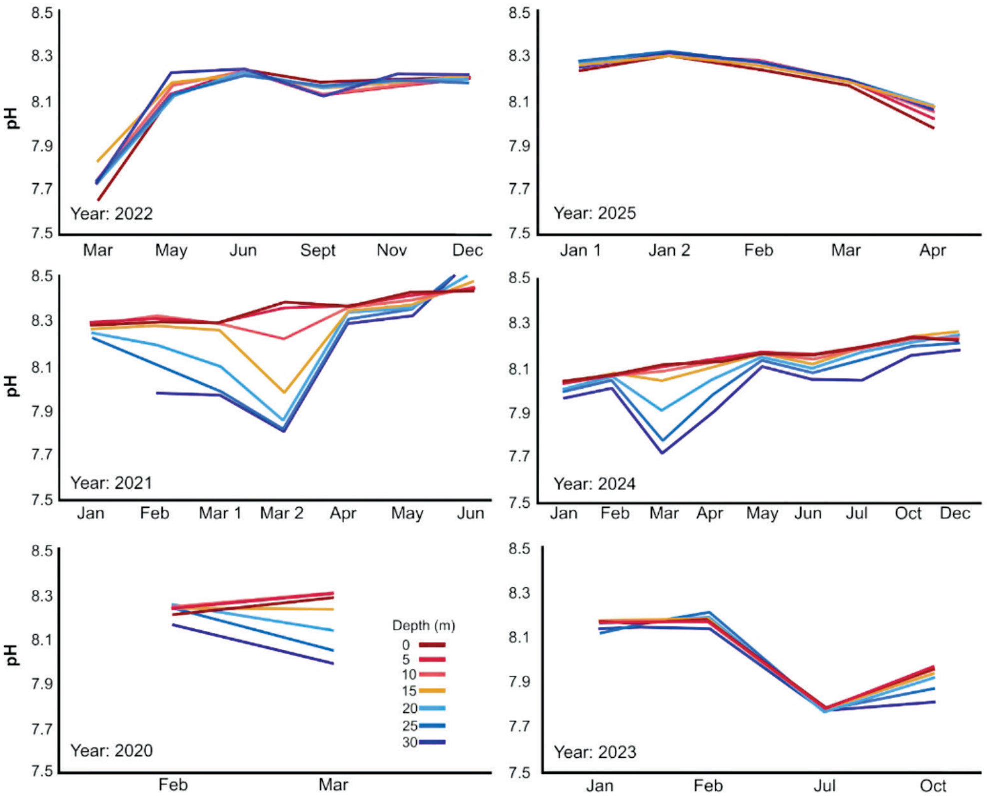

Fig. 5. pH records from the surface to 30 m depth at Bajo 20, Coiba National Park, Panamanian Pacific.

of gamete release. The end of spawning was signaled when individuals swam downslope to rejoin the main aggregation. These processes occurred at the interface between cold and warm water masses. Observations indicate spawning individuals were over 50 cm in total length, although smaller individuals were present, they did not participate in the spawning process. *L. peru* spawning aggregations were documented at Bajo 20 and Sacramento in CNP.

***Lutjanus colorado*:** This species was observed forming schools consisting of hundreds of individuals around or near underwater pinnacles. In some cases, fish are aggregated at the interface between warm and cold water, between 10-20 m depth. Within the school, spontaneous spawning, either by individual fish or as a mass event, occurred without segregation into spawning subgroups. Spawning was observed in both the morning and afternoon, with two events during the new moon (April 9, 2024; March 28, 2025) and one during the full moon (March 31, 2024) (Table 2). Aggregations were recorded at Sueño del Pescador (SP) and Montaña Rusa (MR) in Coiba National Park, and at Bajo Rizo (BR) in Islas Secas (ISA), outside the park boundaries (Fig. 8).

***Lutjanus aratus*:** Similar to what was observed in *L. colorado*, *L. aratus* formed schools of hundreds of individuals around submarine mounds or in open water column at depths between 10-20 m. Spawning pulses were observed within schools, one during full moon (March 26, 2024) and three in new moon (March 12, and April 6 and 7, 2024) in both

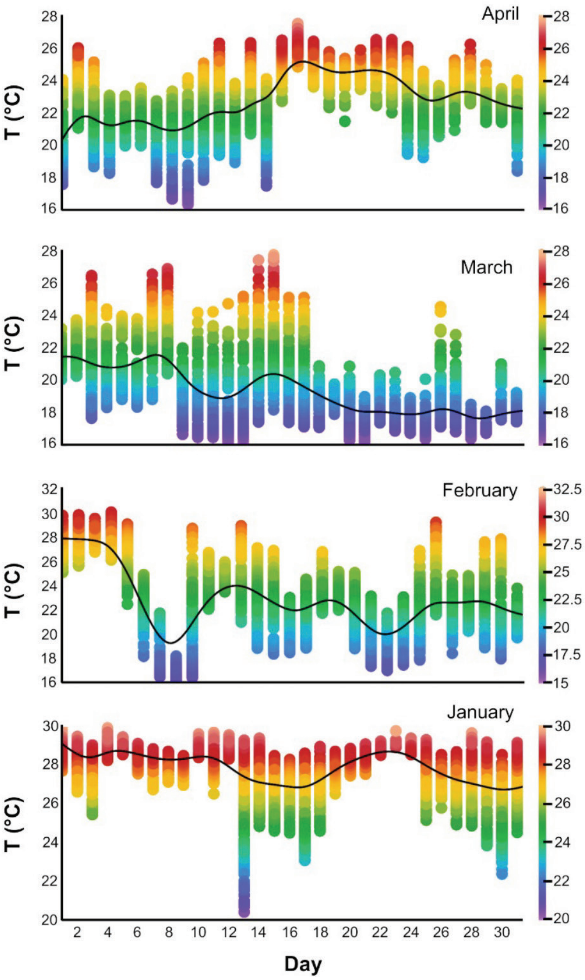

Fig. 6. Daily thermal profile in Bajo 20 between January and April 2024 at Coiba National Park, Panamanian Pacific. Data corresponds to records from a fixed sensor at 28 m depth. Black line is the daily average temperature.

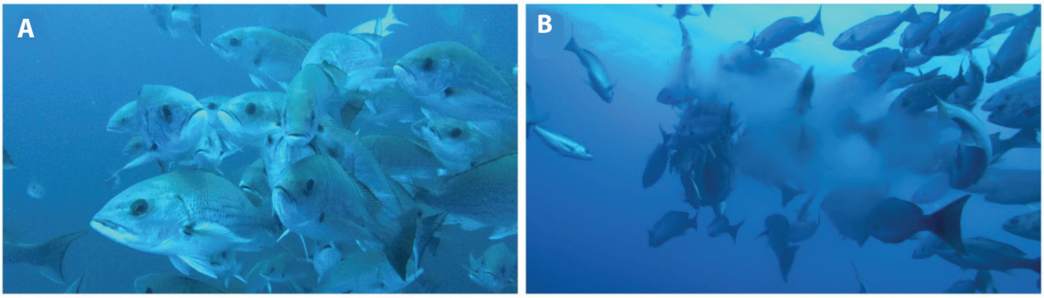

Fig. 7. Fish spawning aggregations in Pacific Red Snapper *Lutjanus peru* in Bajo 20, Coiba National Park. **A.** Spawning group in pursuit. **B.** Spawning group.

Table 2
Summary of species observed in spawning aggregations from 2020 to 2025 in Coiba National Park, Pacific Panama.

Species	Date	Lunar phase	Site	Time of day	Tide
Lutjanus peru	Jan 25, 2020	N	B20	a.m.	L
	Jan 22, 2023	N	B20	a.m.	L
	Mar 9, 2023	F	SA	a.m.	L
	Feb 23, 2024	F	SA	p.m.	H
	Mar 23, 2024	F	B20	a.m.	L
	Feb 12, 2025	F	B20	p.m.	L
	Mar 12, 2025	F	SA	p.m.	H
	Mar 14, 2025	F	B20	a.m.	L
Lutjanus colorado	Mar 31, 2024	F	SP	a.m.	L
	Apr 9, 2024	N	SP	p.m.	H
	Mar 28, 2025	N	BR	p.m.	H
Lutjanus aratus	Mar 12, 2024	N	B20	a.m.	L
	Mar 26, 2024	F	B20	a.m.	L
	Apr 6, 7, 2024	N	B20	p.m., a.m.	H, L
Caranx sexfasciatus	Jan 27, 2021	F	B20	a.m.	L
	Mar 14, 2021	N	B20	a.m.	L
	Jan 23, 2023	N	B20	a.m.	L
	Feb 3, 6, 2023	F	B20, SA	a.m., p.m.	L, H
	Mar 24, 25, 2024	F	B20, SA	a.m., p.m.	L, H
	Feb 25, 2025	N	BR	a.m.	L
	Mar 13, 2021	N	SP	p.m.	H
Cephalopholis colonus	Mar 29, 2021	F	SP	p.m.	H
	Jan 21, 2023	N	B20	a.m.	L
	Jan 15, 2025	F	B20	a.m.	L
	Feb 25, 2025	N	BR	a.m.	L
Thalassoma lucasanum	Apr 26, 2021	F	MR	a.m.	L
	Jan 16, 2025	F	B20	a.m.	L
	Apr 13, 2025	F	MR	pm	H
	Jan 31, 2025	N	B20	a.m.	L

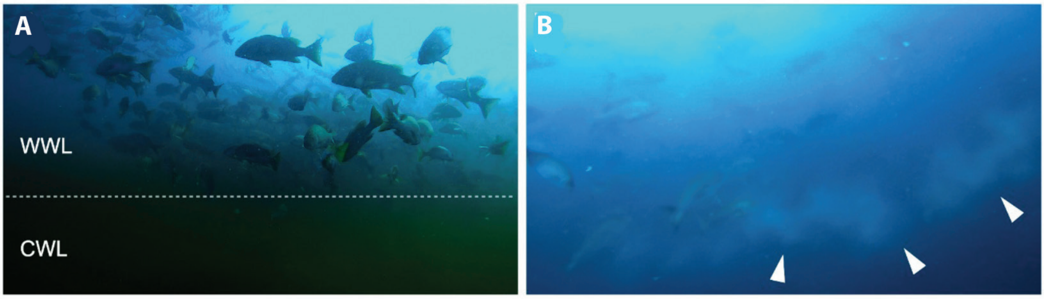

Fig. 8. Red snapper (*Lutjanus colorado*) spawning aggregation in Bajo 20 and Sueño del Pescador, Coiba National Park. **A.** Note difference between the warm-water layer (WWL, ~27 °C) and the cold (CWL, ~18 °C) water in Bajo 20. **B.** White arrows point to released gametes from spawning fish at Sueño del Pescador.

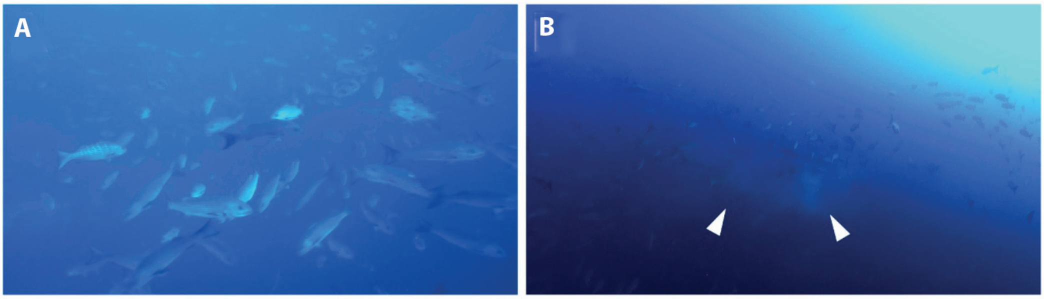

Fig. 9. A. Aggregation of mullet snapper (*Lutjanus aratus*) at Bajo 20. **B.** Spawning activity at Sueño del Pescador, indicated by white arrows.

morning and afternoon, all in Bajo 20 (Table 2, Fig. 9).

***Caranx sexfasciatus*:** This species formed schools of hundreds to thousands of individuals, especially in the warm, clearer water layer. While swimming over or around submarine mounds in the colder water layer, the fish, in response to an unknown stimulus, ascended vertically in mass toward the warmer layer. Within the school, dark-colored individuals were observed separating from the group and chasing lighter-colored individuals in a courtship ritual, positioning themselves beneath their partner. Spawning occurred individually, leaving a trail of gametes after the pair. Five spawning events were observed during full moon (January 27, 2021; January 3 and 6, 2023; March 24 and 25, 2024) and three in new moon (March 14, 2021; January 23, 2023 and February 25, 2025) (Table 2, Fig. 10).

***Cephalopholis colonus*:** This species was observed forming schools over coral reefs and

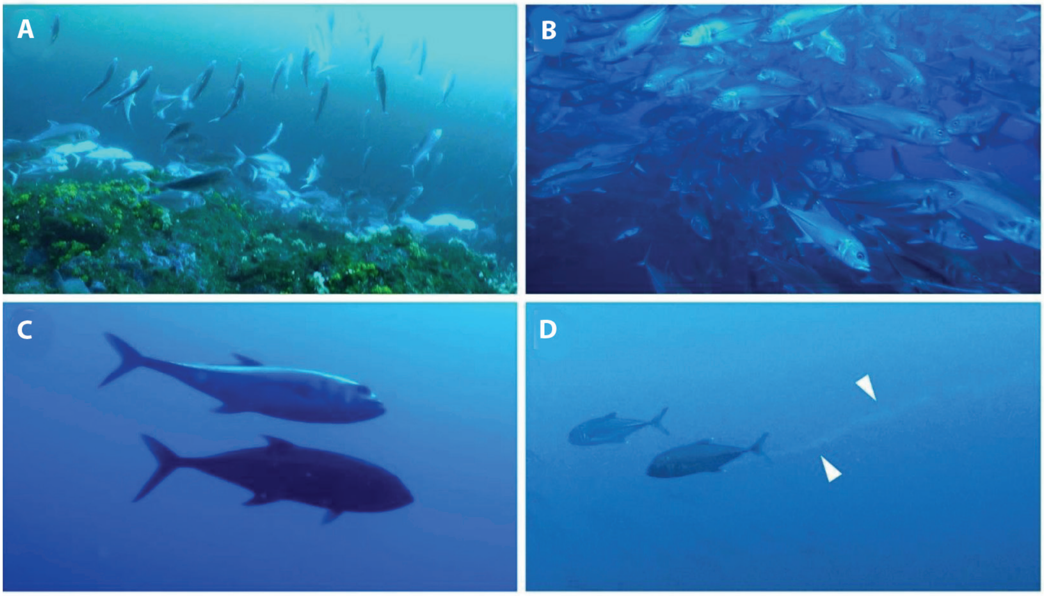

Fig. 10. Bigeye crevalle-jack (*Caranx sexfasciatus*) aggregation in Bajo 20, Coiba National Park. **A.** Specimens moving vertically from the bottom to the water column, moving from cold to warm water. **B.** Aggregation. **C.** Pair with dimorphism in courtship. **D.** Spawning pair in Bajo 20. Note the linear trail (white arrows) of gametes.

rocky mound pinnacles. The spawning aggregation segregated into multiple smaller groups of about 12 individuals that swam vertically to spawn. It was also observed forming large school in the open water column, from which smaller groups detached to carry out simultaneous spawning pulses. Two spawning events occurred during the full moon (March 29, 2021 and January 15, 2025) and tree during the new moon at Sueño del Pescador (March 13, 2021), Bajo 20 (January 21, 2023), and Bajo Rizo, the latter located outside the CNP boundaries (February 25, 2025) (Table 2, Fig. 11).

Thalassoma lucasanum**:** Spawning aggregations of this small fish formed groups of 10-60 individuals, over coral or rocky reef habitats. Individuals ascended into the water column where females released eggs, followed by males releasing sperm. Thee spawning events were observed during full moon in Montaña Rusa (April 26, 2021), Bajo 20 (January 16, 2025) and Montaña Rusa (April 13, 2025) and one during new moon at Bajo 20 (31 January, 2025) (Table 2, Fig. 12).

Spawning aggregation indicators: During spawning aggregations distinct water column stratification was observed between surface layers down to 30 m depth. The top layer was warm and clear followed by a cooler, turbid layer with copious sediment and organic matter. The bottom layer was cold and visibility improved. Turbidity was associated to suspended particles of organic origin, as well as plankton, cnidarians and sediment (Fig. 8A). Another noteworthy aspect was the presence of predators in the water column such as *Seriola rivoliana* (Cuvier & Valenciennes, 1833), *Seriola peruana* (Steindachner, 1881), *Caranx melampygus* (Cuvier & Valenciennes, 1833), *Decapterus* sp. (Bleeker, 1851), *Elagatis bipinnulata* (Quoy & Gaimard, 1825), *Triaenodon obesus* (Rüppell, 1837), *Carcharhinus falciformis* (Müller & Henle, 1839),

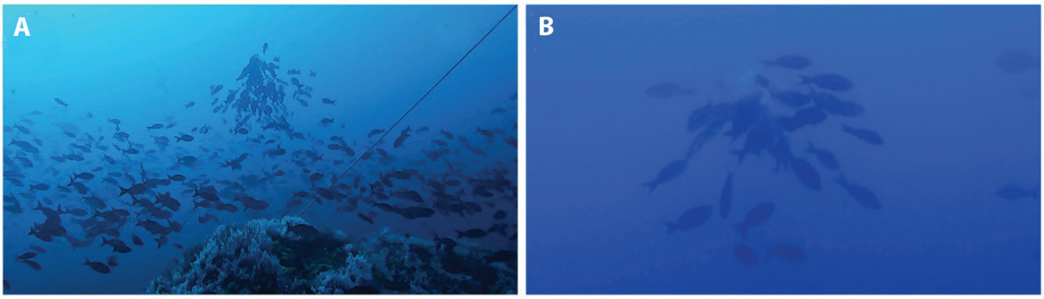

Fig. 11. Pacific creole fish (*Cephalopholis colonus*) aggregation at Bajo Rizo, Islas Secas Archipelago, Panamanian Pacific. **A.** Vertical movement of congregated fish. **B.** Spawning group.

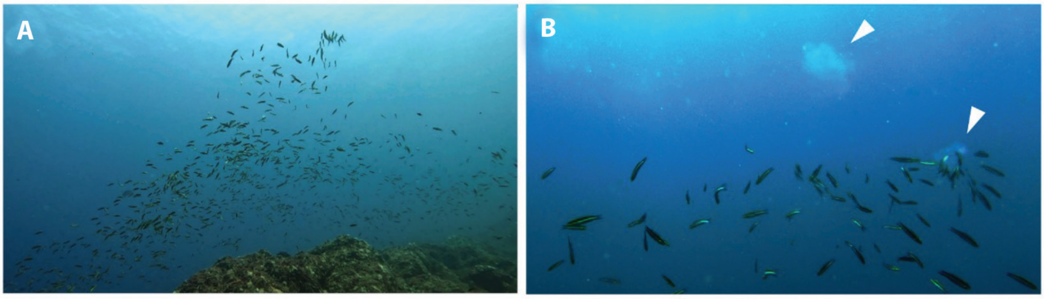

Fig. 12. Aggregation of Cortez rainbow wrasse (*Thalassoma lucasanum*) at Bajo 20, Coiba National Park, Panamanian Pacific. **A.** Vertical movement of spawning group. **B.** Spawning event with patches of released gametes (white arrows).

Hypanus longus (Garman, 1880), *Aetobatus laticeps (*Gill, 1865), and *Carcharhinus limbatus* (Valenciennes, 1839). Whale sharks, *Rhincodon typus* (Smith, 1828), common CNP visitors, were occasionally observed during the dry season, feeding at the spawning sites.

DISCUSSION

Since 2012, when spawning aggregations of *L. peru* and *L. guttatus* were first reported (Vega, Maté et al., 2016), no further monitoring had been conducted. In 2020, monitoring activities resumed and continued through 2025. This effort has made it possible to document the spawning aggregations of six additional species in the region, expanding the known group. Additionally, four new aggregation sites within CNP and one in the ISA were identified, all located within GCH.

Spawning aggregations have been linked to oceanographic conditions, and the importance of thermal stratification in the water column has been highlighted by many studies, in fact deepening of the thermocline, reduced vertical mixing, and rising temperatures, disrupt the spawning habitat suitability for Pacific cod, *Gadus macrocephalus* (Tilesius, 1810), with severe consequences for the fishery (Laurel & Rogers, 2020). In contrast, during the dry season, a cold-water mass enters the GCH system, causing the thermocline to rise (D'Croz & O'Dea, 2009). This process appears to promote fish aggregation for spawning on or near submarine mound pinnacles during the new and/or full moon.

According to Russell et al. (2014), snapper species exhibit the highest spawning frequency during full moon and at sunset. While this all aligns with our findings regarding lunar phase, it differs in the time of day, as most of the recorded spawning events occurred in the morning. Nevertheless, our results suggest thermal stratification of the water column is critical given that fish species that form spawning aggregations exhibit behavioral adaptations to spawn in habitats with temperatures that optimize egg-larval development, highlighting the importance of thermal regimes in reproductive success (Laurel & Rogers, 2020; Pankhurst & Munday, 2011).

L. peru is the primary species in catches from the GCH, accounting for 60 % of total landings and approximately 90 % of the snapper catch. It is fished at depths between 20-100 m, with the highest frequency around 50 m. Gonad analysis showed the species reproduces year-round with peaks in May, July and November (Vega, Robles-P et al., 2016). Spawning aggregations for *L. peru* were originally described between February and April (Vega, Maté et al., 2016), a period confirmed by our monitoring from 2020 to 2025, which also includes January as part of the spawning aggregation season. Reproduction in *L. peru* through spawning aggregations may be associated with the thermal profile of the GCH, implying that oceanographic conditions, particularly temperature, influence the reproductive aggregation process. According to Kobara et al. (2013), changes in water temperature, current velocity, tidal cycles, and ambient light operate at intermediate spatial scales (regional to local). These same criteria can be applied to explain the reproductive process of *L. peru* congeners: *L. colorado* and *L. aratus*, species that form spawning aggregations at the same sites and periods as *L. peru*, although their aggregation behavior and density differ.

Furthermore, *C. sexfasciatus* was frequently observed at high density, hundreds to thousands of individuals, in the first m of the water column where the water was warmer. This species displayed sexual dimorphism and distinct courtship behavior, which has been reported from other localities, for example in the Gulf of California (Sala et al., 2003) and Thailand, associated to an oil and gas platform (Madgett et al., 2022). Both report male color change and fast spawning, a scenario in line with the spawning aggregations observed at CNP. Interestingly, this same behavior pattern was also observed in congeners from the Caribbean and other species within the Carangidae (Graham & Castellanos, 2005). For *C. colonus*, reproduction was described by Sala et al. (2003) in the Gulf of California, where spawning-related behaviors such as group formation, color changes, and spawning events were reported. In Cabo Pulmo, Rowell et al. (2019) reported groups of 12 to 34 individuals spawning in multiple bouts. These same behaviors were observed in CNP and the ISA, where groups of approximately 12 individuals gathered to spawn at depths between 12-25 m, ascending through the stratified water column after separating from the main school. The pattern of ascension from the cold to the warm water layer was also observed in *T. lucasanum*, which is a species associated with coral communities, and rocky mounds (Robertson et al., 2024). Its spawning aggregations were reported at Bajo 20 in CNP (Vega et al., 2019), consistent with observations of *Thalassoma bifasciatum* (Bloch, 1791) in the U.S. Virgin Islands. In both cases, females were observed rapidly swimming upward for 1-2 min to release eggs, followed by accompanying males that released sperm (Warner, 1995).

The ascent of fish into warmer layers may facilitate gamete release through thermal contrast, a mechanism known to regulate reproduction. In the tropics, environmental regulation of aggregating species appears to operate across a hierarchy of variables with temperature and photoperiod as primary drivers (Pankhurst & Porter, 2003). The observed temperature stratification may explain the upward swimming behavior of aggregating fish as they enter the warm layer to spawn. Importantly, the formation of spawning aggregations appears to be facilitated by the seasonal intrusion of cold-water masses, which raise the thermocline and bring the fish closer to the warm surface layer. This interface likely provides optimal conditions for gamete fusion, egg development, and overall offspring survival (Domeier & Colin, 1997; Domeier, 2012). During new and full moon periods, a cold-water mass rises from the bottom toward the coast, bringing the thermocline closer to the surface. This causes spawning fish groups to move into shallower areas, where they enter the warm surface layer to spawn, likely induced by the associated thermal and pressure changes. The spawned products are rapidly dispersed by surface currents, which increase in intensity as the tidal stage changes. According to Sánchez-Hernández et al. (2022), shifts in oceanographic conditions at spawning aggregation sites can be used by various species to release gametes, promote fertilization, and facilitate subsequent egg dispersal, thereby reducing predation.

Fish spawning aggregations present a challenge for both fishers and managers, as fishing during these reproductive events might be economically profitable in the short term, but often leads to overfishing and population collapse (Tobin et al., 2013). For example, the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), has undergone severe reductions in number and density of its spawning aggregation across its distribution range, and it is now considered a threatened species (De Mitcheson et al., 2008). In this context, among the species in this study, snappers (especially *L. peru*), represent the primary target of the fisheries in CNP (Vega, Robles-P et al., 2016). These species are protected under the park's fishing regulations, which include a seasonal closure during the spawning aggregation period and an absolute ban on fishing within one nautical mile of any island, islet, or emergent area inside the park (Maté et al., 2015). This implies the spawning aggregations are protected by mechanisms of control and surveillance; nonetheless, landings continued between January and April 2024, a year in which both registered and unregistered fishing vessels were observed operating at night within the protected area (A. Vega, personal observation, March 12, 2024).

In 2025, the panamanian ministry of environment increased its personnel and started radar surveillance within the protected area. These management measures might significantly improve control over illegal fishing in the park. This is particularly important given that fish spawning aggregations can result from long-distance migratory patterns, concentrating spawning events at specific sites which are repeated in time and space (transient aggregations), or they can be resident, involving short-range migratory patterns (Domeier & Colin, 1997; Domeier, 2012). For the spawning aggregations described in the present study, further research is needed, particularly for snappers due to their commercial value, to determine whether these spawning aggregations are transient or resident, and whether reproduction occurs exclusively within CNP or also in other areas of the GCH or the Panamanian Pacific. Such research could help identify future candidate sites requiring special protection and management.

Heidmann et al. (2024) recommended increasing the protection of *Lutjanus analis* (Cuvier, 1828) spawning aggregation sites in St. Croix, U.S. Virgin Islands, by modifying existing regulations, improving enforcement, and involving fishers in co-management actions. In this context, the current regulations in CNP for snapper species include both spatial and temporal protection during the spawning season; however, much work remains regarding co-management. Therefore, it is critical to improve the efficacy of these regulations, particularly during nighttime hours, when illegal fishing targeting spawning aggregations occurs. Moreover, engaging communities within the park's area of influence is essential to raise awareness about the importance of conserving these reproductive events to ensure the reproductive potential of the species and the long-term sustainability of snapper fisheries and other associated species.

The next steps involve acoustic studies to track individuals from species that form FSAs, in order to determine their origins and movements between aggregation sites and the localities where they are caught by artisanal fisheries in the Gulf of Chiriquí, as documented by onboard observer programs (Vega, Robles-P et al., 2016). Acoustic tracking would refine our understanding of aggregation dynamics and occurrence patterns, particularly whether the same individuals spawn at nearby sites within a one- to two-day window or whether distinct groups contribute to the observed spatio-temporal patterns.

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