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Are the Coastal Waters of French Guiana a Source or Sink Habitat for Atlantic Goliath Grouper *Epinephelus itajara*?

Céline Artero ^{1,2,*}, Christopher C. Koenig ² and Jessica E. Marsh ^{3,4}

- ¹ Office Français de la Biodiversité (ex Office National de la Chasse et de la Faune Sauvage), CEDEX, 97338 Cayenne, French Guiana
- ² Coastal and Marine Laboratory, Florida State University, St Teresa Beach, FL 32358, USA; ckoenig@fsu.edu
- ³ Centre for Environment, Fisheries and Aquaculture Science (Cefas), Weymouth DT4 8UB, UK; jessica.marsh@cefas.gov.uk
- ⁴ Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole BH12 5BB, UK
- * Correspondence: artero.celine@gmail.com

Abstract: The coastal waters of French Guiana are amongst the most turbid and nutrient rich in the world, and as such, they favour the settlement and early development of several species of marine fish. Recent work has revealed a high abundance of Atlantic Goliath Grouper (*Epinephelus itajara*) in these waters, yet little is known about this species' reproductive biology, which this study aims to complement. During the period from 2010 to 2013, we surveyed Goliath Grouper at three rocky sites along the French Guiana coast and examined 602 individuals for evidence of maturation. Satellite tags were deployed on five individuals and an acoustic survey was conducted to identify potential spawning movements and activity. We found no evidence of sexually active individuals or local spawning aggregations. Most individuals showed high site fidelity, but one fish was located 1150 km away, near Trinidad and Tobago. We discuss these findings in the context of the wider literature and postulate that Goliath Grouper inhabiting French Guiana reefs originate from spawning sites in northern Brazil and disperse to westerly reefs with the onset of maturity. We propose that the Goliath Grouper populations could have wide-reaching impacts on Goliath Grouper stocks.

Keywords: reproduction; migration; South American fish stocks; fish management; maturity

Key Contribution: Multiple scientific approaches and local fishers' knowledge failed to show any reproduction activity of Goliath Grouper within French Guiana coastal waters. Satellite tags deployed on Goliath Grouper in French Guiana coastal waters not only confirmed the territorial behaviour of the species, but also revealed a >1000 km migration capacity, potentially for reproduction.

1. Introduction

The biology and life history characteristics of the Atlantic Goliath Grouper (*Epinephelus itajara* (Lichtenstein, 1822), hereafter, Goliath Grouper), a large, long-lived, and latematuring species, make them vulnerable to overexploitation [1,2]. Consequently, Goliath Grouper experienced large population declines during the late 1980s throughout their range [3] from North Carolina to southern Brazil in the western Atlantic, and from Senegal to Congo in the eastern Atlantic [4]. Despite some protection, mostly as moratoria on fishing in parts of its range [3,5,6], Goliath Grouper remain threatened. They are currently classified as 'Vulnerable' on the red list of the International Union for Conservation of Nature (IUCN; [7]) and are thought to be locally extinct off the west African coast [8]. Knowledge of reproductive biology and spawning areas are essential to inform management strategies such as stock assessments and the protection of key habitats [9], the latter being especially pertinent for Goliath Grouper, which form annual spawning aggregations [10,11]. However,



Citation: Artero, C.; Koenig, C.C.; Marsh, J.E. Are the Coastal Waters of French Guiana a Source or Sink Habitat for Atlantic Goliath Grouper *Epinephelus itajara*?. *Fishes* **2023**, *8*, 274. https://doi.org/10.3390/ fishes8050274

Academic Editors: Peter W. Sorensen and Felicia C. Coleman

Received: 16 March 2023 Revised: 11 May 2023 Accepted: 12 May 2023 Published: 22 May 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). most studies of Goliath Grouper biology and ecology have focused on habitats in the United States and Brazil, with limited knowledge of these aspects in other locations [12]. This includes coastal French Guiana, which is considered a productive marine ecosystem that supports an abundant Goliath Grouper population [13].

Throughout their range and life cycle, Goliath Grouper inhabit bays, estuaries, shallow coastal waters, and natural or artificial reefs offshore [4,6,14–18]. Complex coastal structures, such as mangroves, are beneficial habitats for juveniles [15,17,19,20] because they provide protection from predators and food resources [17]. Juveniles stay in this habitat for five to six years until they reach maturity (approximately at lengths > 1.1 m, [11,21]) and migrate toward offshore rocky sites [16,17,22]. There, individuals are found at depths of up to 90 m in habitats with varying topography, such as walls and wrecks [16,18,23].

Goliath Grouper is a territorial species throughout its life cycle, except during the reproduction period, when mature individuals can migrate up to 436 km to join aggregation sites composed of 20 to 100 individuals [10,11]. These aggregations appear annually, but the timing varies by area: from August to October in Florida [11,23–25]; September to October in Colombia [16]; and from December to February in southern Brazil [6,18,26]. Spawning aggregation sites are difficult to find and are generally reported by fishers or divers [18,27]. In lieu of direct observations of spawning, indirect evidence of reproduction may be used, such as changes in physiology (e.g., body shape of females due to egg production [18]), pigmentation of the head [27], and behaviour (e.g., rapid vertical movements [28]). Furthermore, Goliath Grouper are noisy during spawning, producing numerous low-frequency (60 Hz) sounds [28], and therefore acoustic surveys could be used to identify reproductive aggregations of Goliath Grouper and to estimate abundance of spawners [11].

The coast of French Guiana extends 320 km, but knowledge of its marine fish populations is lacking [29]. This is partly due to strong coastal currents [30,31] and to the very limited visibility of these extremely turbid, nutrient-rich waters [32]. Both of these factors render the deployment of static scientific equipment useless. As such, marine species, such as Goliath Grouper, are exploited in French Guiana without prior assessment of the impact of this exploitation on the population. Unlike other Goliath Grouper populations, such as in Florida, the character of French Guiana's marine environment has led the species to establish a unique spatial dispersion whereby small (<1.2 m) and large (>1.2 m) individuals occupy the same coastal and offshore rocky habitats [13], and the fish undergo an ontogenetic dietary shift, which may be the adaptation that enables the coexistence of conspecifics [33]. Furthermore, Goliath Grouper in French Guiana grow at relatively rapid rates, attaining a larger mean size at age than populations in southwestern Florida [34] this is likely due to the highly productive coastal waters of French Guiana [35,36]. Areas in French Guiana have been identified as potential Goliath Grouper reproduction sites due to the high abundance of Goliath Grouper regularly observed around October [13,37]. However, to date, evidence of spawning activity has not been observed in French Guiana.

The aim of our study was to determine whether or not Goliath Grouper reproduces in the coastal waters of French Guiana. As turbidity prevented any direct observation of animals underwater, a variety of survey techniques were used: firstly, non-lethal methods (observation of genital openings and external sampling of gametes) were employed to determine whether or not reproductively active Goliath Grouper were present in the study area; secondly, acoustic surveys were used to record and detect low-frequency sounds that are emitted during spawning activity; thirdly, satellite tags were attached to a sample of large (mature) Goliath Grouper, which are known to migrate each year toward aggregation sites for reproduction, in order to follow their movements around the year; and fourthly, local fishers' knowledge of potential spawning activity was used to identify the timing and location of reproduction of Goliath Grouper in French Guiana.

To complement the field surveys, we analysed the historical landings of Goliath Grouper (1990–2011) of a commercial fisher to inform our discussions on the life cycle of Goliath Grouper in French Guiana and on the potential consequences of the management of Goliath Grouper in French Guiana's coastal waters. Based on our findings, we postulate

that French Guiana represents a feeding habitat (or sink) for Goliath Grouper originating from the coastal waters of Brazil.

2. Materials and Methods

All coastal rocky areas off eastern French Guiana were surveyed, which consisted of three areas (Figure 1): Îlets de Rémire, Battures du Connétable, and the Île du Grand Connétable, which is a marine reserve (hereafter, 'marine reserve'). The closest inshore area is Îlets de Rémire (located near the Mahury Estuary), which contains shallow rocky habitats of 2 to 5 m depth approximately 7 km offshore. Battures du Connétable, located 22 km offshore, has the deepest rocky sites ranging from 5 to 20 m depth. The marine reserve (Île du Grand Connétable) is 14 km offshore, opposite the River Approuague Estuary, and has rocky habitats 6 to 9 m deep. The reserve was established in 1992, primarily to protect breeding bird populations on the islands, but includes a two-nautical-mile margin around the islands where fishing and anchorage are prohibited (decree ENVN9200079D, adopted on 8 December 1992).



Figure 1. Main panel shows map of survey sites located off the coast of French Guiana; top inset map shows the location of survey sites within French Guiana; bottom inset map shows the location of French Guiana in South America.

From April 2010 to December 2013, daytime fishing trips were carried out four times per month minimum on recreational vessels using hook and line to survey Goliath Grouper. Each captured individual (the eyes were covered with a wet towel and gills were irrigated with sea water from a pump) was released following measurement of their total length $(\pm 1 \text{ cm})$ using the straight-line distance from the tip of the upper jaw to the end of the tail [33] and clipping of fin rays five and six from the second dorsal fin (as close as possible to the articulation point) for age determination [34,38]. The maturation status of fish was estimated based on size (1.1 m) and age (6 years) at sexual maturity relationships established for Florida Goliath Grouper [11,21]. To assess reproductive condition, the state of genital openings was examined—these are red and swollen in actively spawning females, whereas males typically leak white sperm when gentle pressure is placed on the area around the genital opening [11,39]. To obtain gamete biopsies, a plastic tube (3 mm diameter) was inserted into the genital openings, followed by suction with a hand-held vacuum pump (methods described in [40]. Reproductive migrations were evaluated from five individuals (Fish1–5) between June and December 2013 that had been tagged with Mk10-PAT satellite tags (Wildlife computers Inc., Redmond, WA, USA). A sixth satellite tag (Tag6), which was intended to track a sixth individual and reconstruct movement pathways, sank to the bottom before it could be attached to the fish. The tagged fish ranged in total length from 1.4 to 1.5 m, with four tagged in the marine reserve and one tagged at Battures du Connétable (Table 1).

Table 1. Information on capture and satellite tag survey of five Goliath Groupers (*Epinephelus itajara*) (Fish1–5) and unattached tag (Tag6) along the coast of French Guiana at two sites: Battures du Connétable, and the marine reserve of Île du Grand Connétable.

	Fish1	Fish2	Fish3	Fish4	Fish5	Tag6
Length (m) Tagging site	1.4 Reserve	1.5 Reserve	1.4 Reserve	1.5 Reserve	1.5 Battures	NA Reserve
Geographic coordinates (tagged)	4°49.432′ N 51°56 117′ W	4°55.154′ N 51°57 176′ W	4°49.432′ N 51°56 117′ W			
Tagging date Programmed duration (days)	21/06 30	21/06 63	02/08 38	30/08 81	14/09 85	29/11 94
Effective duration (days)	30 4852 740/ NI	63 4850 460/ NI	79 10822 440/ N	81	18 (*22.252/ N	94 4850 422/ N
Geographic coordinates (pop-up)	4 52.740 N 52°04.500' W	51°55.740′ W	60°38.535′ W	52°00.153′ W	54°45.306′ W	51°56.381′ W
Distance from release site (km)	16	2	1150	14	360	2
Min depth (m)	0–2	0–2		0–2	0–2	4
Max depth (m)	15-20	25-30		8-10	25-30	6
Min temperature (°C)	27	27		27	27	27
Max temperature (°C)	29	30		30	30	30

The sampling period was chosen because it included the most likely season for spawning in the southern part of the northern hemisphere—as derived from the species' spawning season in Florida, which is August to October [24]. The tags, which were attached with a tether inserted in the muscle between the two dorsal fins, were programmed to release from the fish at selected times and float at the surface whilst transmitting a summary of the recorded data via Argos satellite transmission. The tags had three sensors: light level, temperature, and pressure. Tags were set to record every 15 min for a duration of one-to-three months, so as to maintain sufficient battery life to transmit data via satellite. Because Goliath Grouper are larger in French Guiana for a given age relative to other neighbouring populations [33], only individuals larger than the known length at sexual maturity (≥ 1.4 m) were selected for tagging.

Transmitted data were decoded and analysed by a private institute, "Collecte Localisation Satellites" (CLS,, a subsidiary of the French Space Agency (CNES) that provides surveillance and monitoring solutions to understand, protect and manage resources sustainably. They help scientists processing environmental and positions data.). They estimated movement trajectories with a model combining fish movement, light level, temperature and pressure (depth) data [41]. The model used was for a benthic species [33]; therefore, the recorded depth was set to correspond to the local bathymetry, with an error of ± 10 m.

To monitor for sounds produced by Goliath Grouper during spawning activity [28], 20 acoustic listening stations were set up around Îlets de Rémire (4 to 5 around each island). The listening stations consisted of HTI-96-MIN hydrophones (High Tech, Inc., Long Beach, MS, USA) at a 5 m depth, directly linked to an onboard recorder (MicroTrack II, M-Audio, Cumberland, USA). The listening stations were visited twice a month (two 5 min recordings at each station) during September and October 2011, months during which the abundance of Goliath Grouper around rocky sites in French Guiana has been shown to increase in previous studies [13,37].

Historical captures of Goliath Grouper were acquired from one of the few commercial fishers of French Guiana skilled in the species' captures from 1990 to 2011. His fishing journal was used to estimate historical trends in the Goliath Grouper population of French Guiana. The date, fishing site and number caught were recorded for each fishing trip. This information enabled us to calculate the capture per unit effort (CPUE) over time: CPUE = Number of Goliath Grouper caught/number of fishing trips. Fishers are often knowledgeable of the reproductive biology of their targeted species (e.g., [42], in particular,

the reproductive period when gonads are developed and easily identifiable when the fish is cleaned for market. So, we also conducted informal interviews to obtain information from local fishers (n = 70) on the landings of reproductively active female Goliath Grouper and the timing of their captures.

3. Results

3.1. Reproduction

A total of 602 Goliath Groupers were captured between April 2010 and December 2013, with the majority of fish caught at the marine reserve (n = 361), followed by Battures du Connétable (n = 149), and Îlets de Rémire (n = 92). The lengths of Goliath Grouper caught at the marine reserve (mean = 125 cm; range = 55 to 189 cm) and Battures du Connétable were similar (mean = 120 cm; range = 45 to 212 cm), whereas fish caught around Îlets de Rémire were smaller (mean = 101 cm; range = 38 to 168 cm). A large range of size classes were caught at each site throughout the sampling period, and there was no clear trend in the mean size of fish over time at any site (Figure 2).



Figure 2. Mean length of Goliath Grouper caught at each site in each month between 2010 and 2013. Points show the mean length (error bars showing \pm standard deviation) with the size of point denoting the number of fish caught at each site and month.

A total of 407 (68%) fish exceeded the mean size at maturity, and 50 (8.2%) fish exceeded the mean age at maturity. A large majority (76%) of fish caught in the marine reserve were classed as mature, as well as 66% of fish caught at Battures du Connétable (Figure 3), whereas only 36% of fish caught at Îlets de Rémire were classed as mature (Figure 3). However, across all sites, no caught individual showed the external features of spawning fish—that is, no females had a swollen or reddened genital orifice and no sperm excretion was observed during gentle pressure on the ventral area. The genital openings were tightly closed as in non-spawning fish, so we could not insert the biopsy tube to attempt to sample gametes.



Figure 3. Distribution of length classes of Goliath Grouper caught at each site across the entire

study period (2010–2013). Vertical red line highlights the size at maturity (1.1 m) of Goliath Grouper reported in the literature [11,21].

3.2. Tagging, Acoustic and Historical Fisher Data

Jumber of goliath groupe

Of the five deployed satellite tags, three popped up on schedule and two others popped up with some lag—the duration of tracking surveys ranged from 30 to 85 days (Table 1). However, once at the surface, all tags transmitted their location, which provided the fish's location at the time of pop-up tag release (Figure 4). Temperature, pressure and light-level data recorded for Fish1, Fish2 and Fish5 were usable, whereas the others had corrupted data. The unattached satellite tag, Tag6, remained activated for 94 days from 29 November 2013, after which it reached the surface 2 km away from where it was dropped. The geolocation analysis suggested that the tag moved out of the marine reserve and came back to its original location (Figure 5), which seems unlikely.



Figure 4. Popped-up locations (black stars) of the satellite tags deployed on Goliath Grouper in French Guiana in 2013. White star = tagging site.



Figure 5. Graphs show daily maximum depth (m) between time at release (triangle pointing down) and time of tag pop-off (triangle pointing up), and maps show reconstructed movement of three Goliath Grouper tagged in French Guiana in 2013 (top three rows), as well as the above information for the unattached tag (bottom row). Dark and light grey ellipses indicate the 50% and 95% confidence intervals. The geolocation data recorded for two other tagged fish were corrupted and so not used to reconstruct movement.

The satellite tag on Fish1 popped up 16 km from the tagging site (Figure 5). Fish1 stayed at shallow depths (<10 m), except for a brief time when the fish was at a depth of 15 m during the first two days after tagging. The movement was in a north-west direction (Figure 5). Fish2 stayed within a 10 m depth, but occasionally descended to a depth of 25 m. Movement was toward the south-east (Figure 5). The satellite tag deployed on Fish3 popped-up on 20 October 2013, after a 41-day delay. The data recorded showed a movement of 1150 km toward Trinidad and Tobago (Figure 5). Fish4's tag popped up in the mangroves near the River Approuague Estuary, 14 km away from the tagging site (Figure 5). The data were corrupted, which limited the number of records; the maximum depth in these limited records was 8 m.

Fish5 was the only individual tagged at the Battures du Connétable. This fish moved to the northwest off Suriname, 360 km away from where it was tagged. Fish5 spent 80% of its time within a 10 m depth, but reached a maximum depth of 25 m (Figure 5). However, because of the poor condition of Fish5 upon release, following its capture at 20 m depth, the depth profile recorded suggested that this fish encountered buoyancy-regulation issues post-tagging—it is plausible that the fish did not survive for long. Thus, we assume that this fish moved passively with the current.

Acoustic recordings during September and October 2011 provided three hours and 34 min. of sound recordings; however, we discontinued the monitoring at the end of October because of navigation dangers at night. In these recordings, we detected no Goliath Grouper sounds (i.e., frequencies of <60 Hz).

The commercial fisher undertook 762 fishing trips between 1990 and 2011 (mean = 34 fishing trips per year). In these 22 years of fishing, 78% of fishing trips were on rocky sites (seven different locations), 15% in estuaries (10 different locations) and 4% were not identified. Between 1990 and 1999, 39 \pm 19 (mean \pm SD) fishing trips were undertaken per year, then this number dropped to 15 ± 9 SD fishing trips after 2000 (Figure 6). The number of Goliath Grouper caught per year ranged from a minimum of 0 in 2000 to a maximum of 267 in 1993, with a mean of 47 ± 74 SD individuals captured per year. The number of Goliath Grouper caught per fishing trip ranged from 0 to 24 individuals, with a mean of 1.5 ± 2.8 SD individuals. Across the 22-year fishing record, the CPUE varied in three periods. From 1990 to 1994, the CPUE was maximal, with 3.5 ± 0.8 individuals caught per fishing trip. From 1995 to 2004, the CPUE decreased to 0.5 ± 0.3 SD individuals caught per fishing trip, and after 2005, the CPUE increased again, with 1.4 ± 0.8 SD individuals caught per fishing trip, representing a value $2.5 \times$ less than the number of captures in the early 1990s (Figure 6). None of the 70 local recreational and commercial fishers that were questioned about landing reproductively active Goliath Grouper stated to have landed any female fish with eggs.



Figure 6. Number of fishing trips per year (white bars) and average number of Goliath Grouper caught per fishing trip (black line) by a commercial fisher off French Guiana between 1990 and 2011.

4. Discussion

4.1. Spawning Activity in French Guiana

Rocky habitats are frequently used by Goliath Groupers for spawning, and the Île du Grand Connétable marine reserve was identified as a potential Goliath Grouper reproduction site due to the high abundance of Goliath Grouper regularly observed around October [13,37]. A substantial proportion of fish caught during our survey were larger than the reported size at maturity in other locations [21], but none of the captured fish showed external signs of active reproduction, i.e., the tight genital openings lacked any of the redness and the males were not expressing milt (e.g., [11,39]).

Similarly, the acoustic recorders did not pick up any of the low-frequency sounds produced by Goliath Grouper aggregations prior to and during spawning activity between September and October at Îlets de Rémire. Ref. [28] used a similar method of passive acoustic recordings with underwater hydrophones and showed that Goliath Grouper in the Gulf of Mexico were prolific producers of single-pulse low frequency sounds at aggregation sites. While the habitat in Îlets de Rémire appears suitable for spawning aggregations, i.e., rocky substratum, relatively shallow depths, and close to juvenile rearing habitat [40], the sampling showed that, on average, Goliath Grouper were smaller at Îlets de Rémire relative to the other two sites and only 36% were larger than the reported size at maturity in other locations [21]. To strengthen our findings, acoustic surveys should be repeated and conducted all year around to cover all possible periods of the year.

It remains unknown whether or not Goliath Grouper spawning aggregations, which typically occur on wrecks and artificial reefs as well as natural rocky habitats [16], occur further offshore than our sampling area. Rocky areas were not located in offshore waters examined using acoustic surveys in areas between Cayenne and the Oyapock Estuary in 2011 and 2012 in the south-east of French Guiana [43], but as previously mentioned, there is little information on the seabed characteristics off French Guiana's coastline. Additionally of note is that the substratum in the western part of French Guiana's coastal waters is mud, which is not a suitable spawning habitat for Goliath Grouper. In this western stretch of coastline, trawling surveys are possible, and only one Goliath Grouper was captured during scientific trawling surveys of the continental shelf of French Guiana performed between 1975 and 2006 (data from the Institut français de recherche pour l'exploitation de la mer [44], ascertaining the lack of the presence of Goliath Grouper in this area during the sampling period. Combining the information from the interviewed recreational and professional fishers in French Guiana, demonstrating that Goliath Grouper with eggs have never been captured, and from our results (no captures of fish ready to spawn), these findings suggest that the probability of Goliath Grouper spawning sites off French Guiana is low.

4.2. Evidence of Spawning-Related Movements

Goliath Grouper can show high home-site fidelity, while being capable of extensive migrations to aggregation sites prior to spawning [45], and this was observed in our study whereby the pop-up location for three of these fish was relatively near to their location of tagging. No Goliath Grouper in our study were found to initiate a large eastward movement, which was likely due to the strong Guiana Current, which moves north-westerly from Brazil [46–48]. Fish4, whose tag was located 14 km south of the marine reserve, in the mangrove of the Approuague Estuary, was considered as a likely move, otherwise the Guiana current would have transported the tag in a north-western direction [46]. Fish1's tag was located 16 km away from the tagging site, between the marine reserve and Îlets de Rémire, with a precision of >500 m. We consider this a true reflection of Fish1's movements, because the tag could not have been transported by the Guiana Current over such a distance between its release and its arrival at the surface. Fish2's tag popped up 2 km away from the marine reserve but with a low location precision (± 1.5 km), and so it is not possible to confirm this as a true movement. That said, Fish2 reached depths of 20 and 25 m regularly whilst tagged, and such depths are accessible only at the Battures du Connétable or further

offshore [29]. Without knowing specifically where Fish2 went, we can affirm that Fish2 left the marine reserve to go further north-west, where the French Guiana continental shelf is deeper. Mangroves and deeper habitats represent feeding habitats for Goliath Grouper [17,33], and therefore the purpose of Fish2's short movements could have been to feed.

Fish3's tag popped up near Trinidad and Tobago, i.e., 1150 km away from the tagging site. If a true migration, then this would be the longest-ever reported migration of a Goliath Grouper. For example, movement distances up to 436 km have been observed between home ranges and spawning grounds in Florida [45]. One alternative possibility is that a fishing vessel originating from Trinidad and Tobago or Venezuela caught this fish near to French Guiana and the storage of the fish delayed its availability to the satellite, but without the reconstructed pathway, this remains unverified, but seems unlikely because Venezuelan fishers do not target Goliath Grouper, but rather *Cynoscion acoupa* [49]. Relatively shortdistance movements of Goliath Grouper were also reported in a separate, but related, study [50], in which only 2 out of 85 tagged (Floy Tag & Mfg., Inc.) Goliath Grouper moved a significant distance (88 km) to the west of the tagging site. The large distance apparently moved to the west by Fish3 could indicate a migration between July and August, which corresponds with the Goliath Grouper spawning period (June to October) reported for Belize and the US [16,24,26,51]. However, as our observations are based on a limited number of individuals, further tracking work is essential to confirm this possible spawning migration.

Geolocation analysis performed on the data from the unattached Tag6 highlighted the potential inaccuracy of the geolocation analysis, and in our study, this is likely due to the high turbidity of the coastal waters of French Guiana, which decreases the light transmission and thus the reliability of the light level records [52–54]. Tracking fish in highly turbid environments necessitates more discriminatory methodologies [55], and the interpretation of tracking data from demersal species is even more complex. However, depth [56], tidal [54] and salinity data [57] can help in geolocating a tagged fish, but the geolocation estimations can still be biased. For example, in this study, we attempted to combine depth and light level data to improve geolocation estimates, but our results suggested that this combination of variables was insufficient to geolocate Goliath Groupers accurately. Therefore, estimations of movement trajectories in this study were not reliable, and we consider that only tag pop-up location and depth data were reliably recorded for inference.

4.3. Proposal of Goliath Grouper Life Cycle in French Guiana

Larvae of Goliath Grouper are planktonic [16] and carried by oceanic currents up to around 15 days after hatching [58]. Afterwards, fish larvae progressively acquire swimming capacities and can settle at locations far from their spawning sites. In lieu of any evidence of spawning activity in French Guiana, we postulate that Goliath Grouper in French Guiana's coastal waters are maintained by the transport of larvae via the north-westerly moving 'North Brazilian Current' [30] from northern Brazilian spawning sites. Indeed, Goliath Grouper larvae are transported by marine currents during the first 30 to 80 days of their life cycle (60 days on average) until they settle and develop in a benthic environment [20]. The only known spawning sites close to our sampling sites are off the Para state in northern Brazil, approximately 900 km to the south-east of French Guiana [59]. From this spawning site, the speed for a larva to reach French Guiana has been estimated from current speeds [60] as 15 km per day, meaning that drifting Goliath Grouper larvae would reach the French Guiana coastal waters in 60 days, i.e., during the peak of settlement. Furthermore, genetic analysis of Goliath Grouper individuals from French Guiana and multiple locations in northern Brazil highlighted a genetic link between these populations [61], supporting the postulated population connectivity between locations. The transport of larvae by the North Brazilian Current has also been proposed to explain the maintenance of the shrimp population (*Farfantepenaeus subtilis*) in French Guiana [62], as well as spiny lobster (*Panulirus* spp.) throughout the Caribbean [63].

Furthermore, the pattern of historical captures of a commercial fisher presented in Figure 6 suggests a link between French Guiana and northern Brazil Goliath Grouper populations. Indeed, catches taken in French Guiana waters during three periods, early 1990s, 1995–2004 and 2005–2011, show a pattern related to conservation of the species' spawning aggregations in Brazil. The drop in Goliath Grouper captures of the commercial fisher occurred four years after the widespread decline of Goliath Grouper in the late 1980s [2]. During this period, countries around the Gulf of Mexico banned the fishing of Goliath Grouper. In Brazil, regulations for the protection of goliath grouper populations started in 2002 [5,6]. Three years after the protection of the species in Brazil, the capture of Goliath Grouper in French Guiana increased again, which suggests that the populations of Brazil and French Guiana are connected. Protection of Goliath Grouper in Brazil would then have likely had a positive impact on the exploited population in French Guiana. French Guiana would then represent a sink population and Brazil the source.

5. Conclusions and Recommendations

The lack of evidence in our study of spawning activity could suggest that the survey design and/or the study period were not appropriate to detect reproduction. Alternatively, spawning does not take place along the coast of French Guiana, but rather, mature individuals migrate in from elsewhere to form spawning aggregations that then move to some other location to spawn. Although the majority of Goliath Grouper that migrate to spawn return to their home range, some individuals appear to remain at spawning sites [45]. Given the direction of the Northern Brazil and Guiana Currents towards the north-west, and the propensity for (few) tagged individuals to be relocated to the west of the French Guiana sites, it could be possible that Goliath Grouper migrate westwards to spawning areas in the wider Caribbean. If mature individuals migrate to Caribbean.

Knowledge of spawning activity and locations is essential for the management of species, particularly for long-lived species which are vulnerable to exploitation. Our study, the first on Goliath Grouper reproductive behaviour along French Guiana's coast, was unable to acquire evidence of reproduction, but rather that Goliath Grouper, possibly originating from northern Brazil, use the highly productive waters to feed and subsequently spawn elsewhere. If confirmed, then French Guiana represents a sink population for Brazil and the management of the species should be considered at the international rather than a national level owing to the theoretical consequences of stressors at each location and subsequent impacts on population regulation (Figure 7). For example, impacts on the northern Brazilian population, such as overfishing or loss of habitat, would reduce the number of reproductive individuals and thus the number of larvae transported to French Guiana's coastal waters. The consequence would therefore be a decline in the French Guiana fishery stock for Goliath Grouper, as was observed prior to the fishing ban in Brazil in 2002. Equally, overfishing of the Goliath Grouper in French Guiana could reduce the number of individuals reaching sexual maturity and spawning at sites in the Caribbean (Figure 7). If some Goliath Grouper stocks are mixed but managed separately, then regulations might be ineffective [64]. If migration of Goliath Grouper from French Guiana is confirmed in the future, then a common management policy should be considered between Brazil, French Guiana and the Caribbean.

To better understand the life cycle of Goliath Grouper in French Guiana and their connectivity with other populations, further research is recommended. This could include the determination of sex and maturity stage of live fish using ultrasound, which has emerged in recent years as an appropriate tool (e.g., [65], so as to identify potential prespawners and post-spawners. Additionally, tracking and telemetry studies across multiple locations in French Guiana and the Caribbean would help determine whether mature fish migrate from French Guiana to spawn and whether they return post-spawning. Finally,

genetic analysis of Goliath Grouper inhabiting French Guiana's coastal waters and those of nearby areas, i.e., northern Brazil and Trinidad and Tobago, should be performed to assess the possible linkages between these locations.



Figure 7. Theoretical consequences of habitat loss and overexploitation on South American populations of Goliath Grouper if all populations are linked.

Author Contributions: Conceptualization, C.A. and C.C.K.; methodology, project administration, software, formal analysis, investigation, data curation, writing—original draft preparation, C.A.; writing—review and editing, C.C.K. and J.E.M.; supervision, C.C.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Direction de l'Environnement, de l'Aménagement et du Logement (DEAL), for supporting the research and the Office National de la Chasse et de la Faune Sauvage (ONCFS) for the administrative and financial management of the grouper project (Convention 2009/56).

Institutional Review Board Statement: The authors certify that all animals were humanely and ethically treated following international standards (French Guiana has no official IACUC protocols).

Acknowledgments: This study was completed in partial fulfilment of the doctoral degree in Marine Biology at the University of French West Indies and French Guiana. I thank the Grand Connetable reserve agents A. Alcide and A. Hauselmann for providing access to the field and the marine reserve in their research vessel, the Association des plaisanciers et pêcheurs de Guyane (APPG), especially E. Ribas, for their involvement and support in the grouper project. Although not involved in co-authoring this paper, R. Berzins and L. Lampert were heavily involved in the project, and I thank them for their precious advice and time. I also thank Eric Hansen (Office Français pour la Biodiversité) and Luis Lampert (IFREMER) for providing local information. Finally, I thank G.H. Copp (CEFAS) for editing this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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