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The Fast-Greedy algorithm reveals hourly fluctuations and associated risks of shark communities in a South Pacific city

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ABSTRACT

Unprovoked shark bites are increasing globally. Regional hotspots like Nouméa show rising incidents involving bull sharks (Carcharhinus leucas) and tiger sharks (Galeocerdo cuvier), leading to the culling of these protected species. Identifying high-risk areas and times is key to balancing human safety and shark conservation. Here, we collected five years of acoustic telemetry data for both shark species in the lagoon of Nouméa. The data were categorized by species, divided into 24 hourly subsets, and modeled as bipartite graphs. The Fast-Greedy algorithm was applied to identify distinct communities of sharks and stations. Normalized mutual information was used to cluster communities and detect spatiotemporal patterns. The study revealed up to 9 hourly communities for bull sharks and 21 for tiger sharks, each grouping into 3 clusters. Several high-risk areas and times were identified. Bull sharks formed schools, and a cluster was observed in the harbor between 6:00 and 13:00, increasing bite risk on nearby beaches in the morning. Tiger sharks were more solitary and were present day and night at most stations except those in relatively turbid areas. Both species showed fission-fusion dynamics, with communities merging at dusk, indicating increased movement and a higher risk during this low-light period. A key innovation of our modeling framework was its ability to handle temporal variability in community detection algorithms applied to bipartite networks. The model identified key overlap periods of shark-human activity, highlighting the need for real-time monitoring, safety measures, and public awareness to reduce bite risk and promote coexistence.

1. Introduction

Understanding the complex balance between conservation efforts and public safety in the context of large marine predators is a critical and complex task in marine ecology. This is especially true for large shark species such as the bull shark (*Carcharhinus lucas*) and the tiger shark (*Galeocerdo cuvier*), which are not only essential to the health of marine ecosystems but also pose significant risks in human-dominated areas (Henderson et al., 2024; Huveneers et al., 2023). Often regarded as apex predators, these sharks face growing threats from human activities, including culling and other harmful risk management measures implemented in response to accidental interactions with humans. Current statistics from the International Shark Bite Profile reveal that in 2022, there were 57 unexplained shark bites worldwide, which highlights the potential danger these animals can pose in populated

areas (Huveneers et al., 2023). In the South Pacific, the capital and largest city of New Caledonia, Nouméa, a region well known for its rich marine biodiversity, has experienced a rise in the number of shark bites in recent years. From 1958 to 2020, 67 shark bites were recorded in New Caledonia, of which 13 were fatal. Tiger sharks were responsible for 20 bites, 8 of which were fatal. Bull sharks were responsible for 14 bites, including two fatalities (Maillaud et al., 2022).

Bull sharks are known for their ability to grow in both freshwater and marine environments, including coral reefs, tropical lagoons, and rivers. They are recognized as one of the most dangerous shark species (West, 2011). Tiger sharks are mostly found in tropical and warm waters and often feed on a variety of marine life (Riley et al., 2022). Their frequent visits to shallow reefs increase their interactions with humans, making them second only to great white sharks in

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terms of the number of shark bites (Whitenack et al., 2022). Like bull sharks, tiger sharks are also near threatened due to human activities and are listed on the IUCN Red List, making it illegal to hunt them globally (Whitenack et al., 2022). In response to increased shark activity and subsequent public safety concerns, New Caledonian local authorities have implemented several conservation and safety measures (Gauthier et al., 2020). These include patrolling and monitoring Nouméa bays, banning shark feeding, temporary closures of swimming areas following shark reports, shark culling following shark bites, and tracking shark movements using acoustic telemetry (Huveneers et al., 2023).

The technique of acoustic telemetry is key for studying aquatic species movements and habitat preferences using a network of receivers and transmitters (Cooke et al., 2004; Hedger et al., 2009; Alós et al., 2011; Lyu et al., 2020). Transmitters placed on the animals emit signals that provide location and environmental information, which are picked up by an array of underwater receivers (Brownscombe et al., 2019). Acoustic telemetry has been usefully employed to inform spatial management (Carrier et al., 2018), in particular, in assisting the designation and evaluation of marine protected areas (MPAs) (Carlisle et al., 2019; Espinoza et al., 2015; Knip et al., 2012). Network analysis is a powerful way to visualize and interpret complex multidimensional data. It involves the creation of networks of nodes (entities) connected by edges (relationships), allowing for the analysis of how entities interact within the network. An important application of network analysis to animal behavior is its ability to identify and measure specific features of relationships that are not captured by more common measures of behavior (Wey et al., 2008).

The combination of telemetry data and network analysis significantly enhances the study of animal behavior, especially in the aquatic environment (Lea et al., 2016; Bastille-Rousseau et al., 2018; Lilly et al., 2020; Carrier et al., 2018; Whoriskey et al., 2019; Haulsee et al., 2016; Feyer et al., 2024; Lédée et al., 2015; Aspillaga et al., 2021; Kraft et al., 2024; Martínez-López et al., 2009). Typically, these analyses have employed unipartite graphs, representing either individuals or receivers as nodes, to model the data. For instance, studies like Lilly et al. (2020) and Lédée et al. (2015) have used unipartite graphs to examine individual movement patterns and habitat preferences by representing tagged animals as nodes within a single network. In contrast, other research has employed bipartite graphs, where nodes represent both individuals and receivers, to explore the interactions between these two entities. For example, Whoriskey et al. (2019) and Kraft et al. (2024) have demonstrated the value of bipartite graph models in identifying spatial and temporal movement patterns by mapping the connections between tagged animals and receiver stations.

Despite these advancements, a common limitation has been the static representation of these networks, which often aggregate telemetry data into a single unipartite or bipartite graph (Carrier et al., 2018; Haulsee et al., 2016; Martínez-López et al., 2009). This approach can obscure temporal variations in animal behavior, as the resulting networks often reflect average or cumulative movement patterns rather than dynamic changes over time. However, a persistent methodological challenge lies in accounting for the temporal dynamics of animal associations. Network structures derived from telemetry data are sensitive to the temporal resolution of analysis, with the choice of time window greatly influencing observed co-occurrence patterns and modular structures (Yin and Rudolf, 2023; Jacoby and Freeman, 2016; Jacoby et al., 2012; Baker et al., 2023; Pasquaretta et al., 2020; Papastamatiou et al., 2020; Finn et al., 2014; Garcia et al., 2015; Bruneel et al., 2020). To address these challenges, several techniques from dynamic network analysis have emerged, including snapshot-based community detection, modularity tracking across time, and tensor decomposition methods (He et al., 2017; Caravelli et al., 2013; Aviyente, 2021; Al-Sharoa et al., 2017). These techniques allow researchers to monitor evolving group structures, but they are rarely adapted to ecological

telemetry settings—particularly when it comes to preserving the full structure of interactions between individuals and spatial locations.

In movement ecology, most studies reduce telemetry data to unipartite projections-e.g., co-occurrence networks that link animals based on shared space use or location-location graphs based on shared visits (Whoriskey et al., 2019; Aspillaga et al., 2021; Mourier et al., 2011). These unipartite approaches oversimplify the underlying relational structure by collapsing bipartite information (e.g., which animals visited which locations at what times) into single-mode networks. As a result, the rich, two-mode structure of telemetry data is lost. To our knowledge, no published study has used dynamic bipartite graphs to represent both individuals and locations across time slices while analyzing temporal community stability in animal movement data. This represents a major gap in the field, particularly for systems—such as marine environments— and issues—such as the risk of shark bites where temporal variation in spatial structure is crucial information for both the conservation of threatened species and the design of public safety measures.

Our study addresses this gap by developing a novel framework that constructs hourly bipartite networks linking individual sharks to acoustic receivers (locations), preserves the full two-mode structure of the data, and analyzes how these structures evolve across time. Additionally, this research aims to enhance our understanding of how bull and tiger sharks move around the lagoon of Nouméa, paying particular attention to the time they spend in areas of high human activity, such as harbors, beaches, coral islets, and bays. This information is key to identify areas and times of enhanced risk of bite.

To achieve these objectives, we collected data on the movement patterns of 30 sharks and the duration of their stay in specific locations using 44 hydrophones deployed from November 2018 to November 2023. We divided the large dataset of 753,621 detections by species and hourly time slots to track animal movement throughout the day. We then modeled the resulting datasets using bipartite graphs linking sharks to the stations they visited, with weighted edges representing the number of visits per hour. Next, we applied the Fast-Greedy community detection algorithm to each hourly bipartite graph (Finn et al., 2014; Haulsee et al., 2016) and then used Normalized Mutual Information (NMI) to evaluate the similarity of resulting community structures across the diel cycle (Zhong et al., 2024; Amelio and Pizzuti, 2015; Chen et al., 2015; Jerdee et al., 2023). Hours with similar community configurations were clustered, and communities from aggregated clusters were reassessed to identify temporally stable communities. This framework - through the integration of dynamic bipartite network construction, modularity-based community detection, and community similarity clustering via Normalized Mutual Information (NMI) - offers a significant alternative to existing models. Applied to acoustic telemetry data in Nouméa, it revealed periods of increased connectivity between sharks and specific locations, providing valuable insights into temporal variations in shark space use and the risk of shark bites. This knowledge can further contribute to the development of informed public safety measures.

2. Materials and methods

2.1. Study area and tagged sharks

Our study site Nouméa, the capital of New Caledonia, is characterized by an extensive lagoon of about 20 km wide, including inshore bays and beaches, lagoon patch reefs and islets, and a large barrier reef. Situated in Grande Terre's densely populated southern province, Nouméa is home to about two-thirds of the island's human population, contrasting sharply with the more sparsely populated northern province (D'agata et al., 2016; Juhel et al., 2019). This concentration of human activity in highly favorable habitats for sharks poses important challenges for conservation and public safety issues. In order to study shark movements, 44 VR2 W acoustic receivers (Vemco Ltd., Halifax,

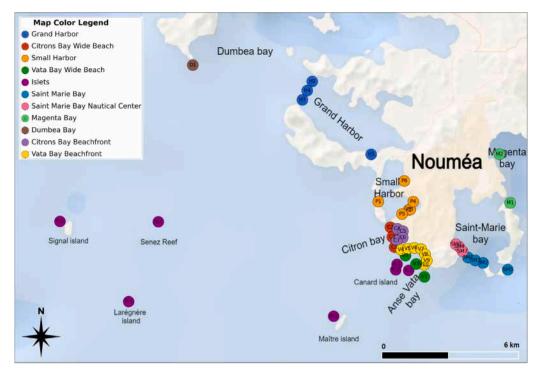


Fig. 1. Geographical distribution of acoustic receivers deployed in diverse areas of Nouméa, New Caledonia. Each dot on the map represents the location of a receiver, and its color corresponds to areas indicated in the map's color bar. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Canada) were deployed in the lagoon of Nouméa. Four receivers were installed in November 2018 in the Grand Harbor area, including at the industrial fishing wharf (station H1). In January 2019, an additional 20 receivers were deployed at various strategic locations: one at the exit of Dumbéa Bay, one in Small Harbor, four across different islets (Canard, Maître, Larégnère, and Signal), one at Senez Reef, six along Wide Beach (three in Citrons Bay and three in Anse Vata Bay), four in St. Marie's Bay, one at the St. Marie's Nautical Center, and two in Magenta Bay. In July 2019, another 20 receivers were deployed, five within Small Harbor marinas, two on Canard Islet, and several receivers along beach areas, including four in Citrons Bay, seven in Anse Vata Bay, and two in the Sainte-Marie's Bay Nautical Center (SM6 and SM7), where children learn sailing (Fig. 1).

A total of 31 sharks were internally fitted with V16 acoustic coded transmitters (68×16 mm; frequency: 69 kHz; high power output; VEMCO Ltd., Halifax, Canada), with transmission delay times randomly ranging from 30 to 90 s (one minute average). Sharks were captured at several locations around Nouméa using circle hooks attached to a floating drum line baited with large pieces of fish (mostly skipjack and albacore tuna collected from local fisheries waste). The animals were processed immediately after capture in a tonic immobility state alongside a small runabout, where their total length in centimeters and sex were recorded, and then released. The studied sharks comprised 19 bull sharks, with a sex distribution of 5 males and 14 females, and 11 tiger sharks, with 1 male and 10 females (Table 1). One bull shark was excluded from the analysis due to its absence from the detection records.

2.2. Acoustic telemetry detections data set

Data were collected from November 2018 to November 2023. The battery life of the hydrophones lasted for one year, so the data were downloaded in November of each year and the batteries replaced. Raw acoustic data were filtered to remove potential false detections using the FDA Analyzer Tool from the VUE software (VEMCO Ltd., Halifax, Canada). The dataset was split by species and then divided into 24

hourly subsets, with each subset representing detections from a specific species and an hour of the day (steps 1 and 2 in Fig. 2).

2.3. Graph construction

We analyzed the 24 datasets for each species by first linking sharks to the stations they visited. The network analyses produced a series of 24-hourly bipartite graphs where nodes represented two distinct entities: sharks and stations. An undirected edge connected each shark to the stations it visited, with edge weights representing the number of visits to each station. This weighting served as an indicator of the relative use of each station by individual sharks (step 3 in Fig. 2). This structure aimed at capturing the interactions and associations between species and their environments.

2.4. Community detection

In network science, a community refers to a set of nodes with stronger interconnections than with nodes outside the community (Wasserman and Faust, 1994). To provide an interpretation of station and shark groupings, we therefore applied the Fast-Greedy community detection algorithm to each hourly bipartite graph (step 4 in Fig. 2). This algorithm is part of the Social Network Analysis (SNA) family. It uses a greedy optimization method, initially treating each vertex (node) as an individual community and then iteratively merging pairs of vertices (or communities) that produce the largest increase in modularity (Clauset et al., 2004; Newman, 2010). This metric quantifies the strength of a network's division into modules. The Fast-Greedy algorithm is suitable for our analysis due to its effectiveness in optimizing modularity and its compatibility with bipartite structures. To ensure the quality of our community detection results, we also tested two additional algorithms: the Label Propagation algorithm, in which nodes adopt the most frequent neighboring label (Cordasco and Gargano, 2011), and the Multilevel algorithm, which uses a hierarchical approach to optimize modularity (Blondel et al., 2008). All analyses were performed in Python using NetworkX (NetworkX community, 2024).

Table 1
The 30 studied sharks with information on their IDs [(T for Tiger, B for Bull), Unique Identifier, and Sex (F for Female, M for Male)], species, sex, size, and tagging date.

(F for Female,	, M for Male)], species, se	x, size, and tagging d	ate.	
ID	Specie	Sex	Size (cm)	Tagging date
B01F	Bull shark	Female	255	27/11/2018
B02F	Bull shark	Female	271	28/11/2018
B03F	Bull shark	Female	282	30/11/2018
B04F	Bull shark	Female	312	08/03/2019
B05F	Bull shark	Female	275	05/11/2019
B06F	Bull shark	Female	294	06/11/2019
B07F	Bull shark	Female	275	10/12/2019
B08F	Bull shark	Female	305	21/01/2020
B09M	Bull shark	Male	237	07/07/2020
B10M	Bull shark	Male	237	15/09/2020
B11F	Bull shark	Female	302	15/10/2020
B12F	Bull shark	Female	306	15/10/2020
B13F	Bull shark	Female	294	15/10/2020
B14M	Bull shark	Male	271	15/10/2020
B15F	Bull shark	Female	285	15/10/2020
B16F	Bull shark	Female	302	15/10/2020
B17M	Bull shark	Male	170	19/11/2020
B18M	Bull shark	Male	259	25/03/2021
B19F	Bull shark	Female	215	28/04/2021
T01F	Tiger shark	Female	205	19/11/2020
T02F	Tiger shark	Female	220	19/11/2020
T03M	Tiger shark	Male	160	12/03/2021
T04F	Tiger shark	Female	168	27/04/2021
T05F	Tiger shark	Female	157	28/04/2021
T06F	Tiger shark	Female	245	28/04/2021
T07F	Tiger shark	Female	370	27/07/2021
T08F	Tiger shark	Female	300	27/07/2021
T09F	Tiger shark	Female	280	16/03/2022
T10F	Tiger shark	Female	337	29/06/2022
T11F	Tiger shark	Female	348	29/06/2022

2.5. Normalized mutual information

To quantify the temporal similarity of detected communities across the 24 bipartite graphs for each species, we calculated Normalized Mutual Information (NMI; step 5 in Fig. 2) between community partitions in bipartite graphs i and j, where i, j are the 24 h of the day. NMI is a measure used to evaluate network partitioning performed by community detection algorithms. It is often used due to its comprehensive meaning and its ability to compare two partitions even when they contain a different number of clusters (Amelio and Pizzuti, 2015; Lancichinetti et al., 2009). NMI is an information-theory approach used to measure the shared information between two data distributions (Cover and Thomas, 2005; Mahmoudi and Jemielniak, 2024), defined as:

$$\mathrm{NMI}(X,Y) = \frac{2 \cdot MI(X,Y)}{H(X) + H(Y)}$$

where MI(X,Y) is the mutual information between X and Y, and H(X), H(Y) the entropy of X and Y respectively. The mutual information MI is a measure of the amount of information that one random variable contains about another one. Considering two random variables X and Y, the MI value can be calculated as follows:

$$MI(X,Y) = \sum_{x \in X} \sum_{y \in Y} p(x,y) \log \left(\frac{p(x,y)}{p(x)p(y)} \right)$$

where p(x, y) is the joint probability distribution function, p(x), p(y) are the marginal probability distribution functions of x and y respectively. The entropy H is a fundamental concept in information theory that measures the uncertainty or randomness of a random variable. It can be calculated as follows:

$$H(X) = -\sum_{x \in X} p(x) \log p(x)$$

where $p(x_i)$ is the probability of outcome x_i .

The normalized mutual information (NMI) takes values in the range [0, 1]. Value 1 indicates maximum mutual information share between X and Y, implying both represent the same communities. Value 0

indicates no information sharing between X and Y. The NMI matrix, which quantifies the similarity between community structures, can therefore be treated as a correlation matrix in the context of clustering. Thus, in order to explore the similarity between the shark communities detected in 24 hourly bipartite graphs per species, we performed hierarchical clustering as implemented in the Python's scipy.cluster.hierarchy module (SciPy community, 2024). To achieve this, we first computed the pairwise distances from the NMI values, specifically using 1-NMI as the distance metric. Then, we used the weighted method to transform the distance matrix into a linkage matrix. This method computes the average distance between clusters, making it effective for this type of community comparison. The resulting dendrogram was then used to visualize the hierarchical relationships and clustering patterns of the community detection outcomes across different graphs, based on their similarities in NMI. A heatmap was also generated to provide a detailed view of pairwise NMI values. This method of generating dendrograms based on NMI values has been widely used in the literature. For example, Fortunato (2009) provided a thorough review of community detection methods, discussing the utility of NMI as a measure of similarity for hierarchical clustering of detected communities across networks. By adopting these established methods, our approach offers a robust framework for analyzing variations in shark and station communities across 24 hourly bipartite graphs. After establishing the dendrogram and identifying clusters of temporally analogous hours, we consolidated all bipartite graphs inside the same cluster into a singular bipartite graph. This aggregation preserved the structure of sharkstation interactions but over longer time windows defined by NMI clustering similarity. We then reapplied the Fast-Greedy community detection algorithm to these aggregated graphs (step 6 in Fig. 2). This step allowed us to identify temporally stable community structures by smoothing out short-term fluctuations and reinforcing persistent interaction patterns. This process facilitated the analysis of space-use and community dynamics across different times of the day, aiming to reduce noise from short-term fluctuations and highlight consistent interaction patterns.

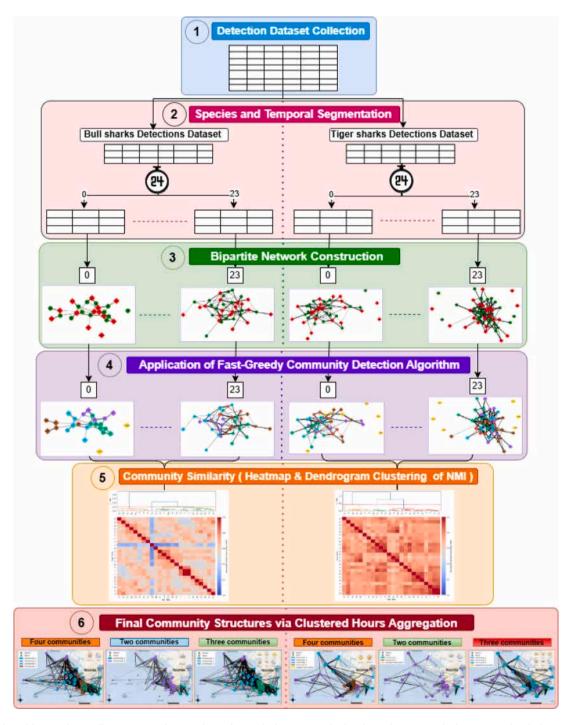


Fig. 2. Methodological framework: (1) collecting acoustic detection dataset for two shark species; (2) dividing dataset by species and splitting into 24 hourly datasets; (3) constructing hourly bipartite graphs; (4) applying the Fast-Greedy community detection algorithm to identify hourly community structures; (5) using Normalized Mutual Information (NMI), heatmaps and dendrograms clustering to compare hourly communities and identify temporal changes in community structure; (6) aggregating similar hourly networks based on temporal clustering and reapplying Fast-Greedy community detection algorithm to detect stable community patterns.

3. Results

3.1. Acoustic telemetry detections

A total of 753,620 detections were recorded over five years, with bull sharks accounting for the majority (644,636 detections) compared to tiger sharks (108,984 detections). Among bull sharks, females (n=14) contributed 480,145 detections, while males (n=5) contributed 164,491 detections. For tiger sharks, females (n=10) contributed

103,180 detections, whereas the sole male tiger shark contributed 5804 detections. Detection counts ranged widely, with bull sharks showing greater variability and higher totals than tiger sharks, and females in both species generally displaying higher per-individual averages compared to males. Bull shark females had individual detection counts ranging from 1491 to 175,877 (median = 17,446), while males ranged from 18,271 to 69,849 (median = 25,598). Similarly, tiger shark females ranged from 130 to 84,695 (median = 2116) detections per individual, whereas the single male had a relatively low total.

3.2. Key connections in shark movement patterns using bipartite graphs

In our analysis of 24 hourly bipartite graphs for each species, we observed strong variability in the number of sharks visiting each station, the number of stations visited by each shark, and the number of visits by station for a given hour slot across 5 years, based on data from all sharks combined (Supplementary Material, Figures A.1 to A.3 for bull sharks and Figures A.4 to A.6 for tiger sharks).

Bull sharks exhibited dense, persistent spatial networks throughout the day, with high activity levels centered on a core set of inshore stations - fishing wharf (H1), Grand Harbor exits (H3, H4), and Small Harbor exit (P1) - which consistently showed high degrees and edge weights, with some links exceeding 10,000 visits. Peaks in connectivity occurred in early morning (0 h-6 h) and late afternoon (16 h-19 h), indicating diel shifts in mobility. Among 19 tracked individuals, B04F, B02F, B03F, and B06F contributed most to network structure and spatial coverage. In contrast, tiger sharks showed sparser, more fragmented and temporally variable patterns, with lower degrees per individual and per station, and frequent periods of disconnection, likely due to inactivity or use of areas outside the array. Their activity was concentrated around offshore and mid-shelf sites - Signal Island (IS1), Larégnère Island (IS3), Senez Reef (IS2), and Sainte-Marie Bay (SM3) - which formed distinct hubs between 4 h-10 h and 18 h-23 h. Most tiger shark edges had low weights (1-500 visits), though some exceeded 2000, suggesting key aggregation zones. T10F, T05F, T06F, and T02F showed the broadest station use and highest detection frequencies, while others remained unconnected for extended periods.

3.3. Shark community detection at hourly resolution

The application of the Fast-Greedy community detection algorithm over the 24 hourly bipartite graphs achieved the highest modularity scores, outperforming alternative methods (Supplementary Material, Table B.1). Given its superior performance, we used this algorithm for the remainder of our analyses. It revealed notable differences in the number of detected communities for bull sharks (Fig. 3(a)) and tiger sharks (Fig. 3(b)).

For bull sharks, the number of detected communities ranged from 2 to 9 (Fig. 3(a)). The highest community counts occurred during daylight hours and were associated with an increase in isolated communities (up to 6 per hour). Interestingly, these isolated communities always consisted of single stations, never single sharks, suggesting that this species tends to move in groups that are more mobile at night. The main isolated stations were located at Anse Vata, Citrons Bay, and Small Harbor. Bull sharks also formed between two and four multiset communities - each involving at least one shark and one station with three such communities observed during most hours. The analysis of tiger sharks revealed a higher number of detected communities, ranging from 11 to 21 (Fig. 3(b)). As with bull sharks, the highest community counts corresponded to the greatest number of isolated communities, ranging from 7 to 17 per hour. In contrast to bull sharks, however, isolated communities occurred both during the day and at night and included not only single stations but also single sharks, suggesting that this species is relatively solitary. The main isolated stations were located at Grand Harbor, Small Harbor, Anse Vata, and Magenta. Multiset communities ranged from two to five per hour, with three communities observed during most hours.

3.4. Spatiotemporal structure of shark communities

The Fast Greedy algorithm, combined with Normalized Mutual Information and clustering techniques, identified three temporally stable community structures at specific time intervals for each species (Figs. 4 & 5; Supplementary Material, Figures B.2, B.3, B.4, B.5, B.6 and B.7). The number of communities within each interval ranged from two to four, regardless of species.

For bull sharks, the first interval clustered 15 h (1, 2, 3, 6, 7, 8, 9, 10, 11, 12, 13, 16, 18, 19, and 22 h), representing the baseline spatial structure of their communities during most hours of the day and night (Fig. 4C). Three distinct communities were observed, with a clear spatial and sex-based structuring. The first community included four males mostly visiting Anse Vata and Citrons Bays, nearby coastal islets (Canard and Maître), and the Nautical Center of Sainte-Marie (green community in Fig. 4C). The second consisted of two females around Dumbéa Bay, Grand Harbor, and oceanic Signal Islet (purple community in Fig. 4C). The third and largest community was composed of eleven females and one male located at the Grand Harbor fishing wharf, the marinas of Small Harbor and frequently visiting oceanic Laregnère islet and Senez reef (cyan community in Fig. 4C). The second interval clustered a single time slot, 17 h, corresponding to dusk (Fig. 4B). At this time, only two communities were observed. The first and smaller community included just two males localized in Sainte Marie Bay (green community in Fig. 4B). The second encompassed all other bull sharks and stations (purple community in Fig. 4B), suggesting a disruption of the baseline structure at dusk, associated with broad shark movements and strong connectivity between the harbor, the beaches, and the lagoon islets. The third interval clustered 8 h (0, 4, 5, 14, 15, 20, 21, and 23 h), spanning mostly nighttime from 8 PM to 5 AM but also including the middle afternoon (2 PM to 3 PM). Four communities were observed. These were similar to those observed during the baseline structure (Fig. 4C), except that the baseline male community (green in Fig. 4C) occasionally split into two subgroups: one with two males linked to Anse Vata Bay, Maître Islet, the Nautical Center of Sainte-Marie, and Magenta Bay (green community in Fig. 4A); and another with two males visiting Citrons Bay, Anse Vata Bay, Small Harbor, and Canard Islet (brown community in Fig. 4A). Tiger sharks also exhibited three time intervals with relatively stable community structures: a baseline structure with three communities spanning most hours, a distinct shift associated with broad shark movements around dusk, and a fragmentation of the baseline structure into four communities during a third interval. The baseline community structure was observed for 13 h (0, 2, 4, 5, 6, 7, 10, 11, 15, 19, 20, 22, and 23 h), covering the entire day and night except most hours in the afternoon (red cluster in Fig. 5). It included three communities. The first was restricted to three stations in Sainte-Marie Bay and was linked to a single female (T01F) (green community in Fig. 5C). The second included five females visiting all islets (except Canard Islet) and some stations at Ricaudy Reef near Anse Vata Bay (purple community in Fig. 5C). The third visited more coastal stations encompassing Dumbéa Bay, the exit of Grand Harbor, Citrons Bay, Canard Islet, Anse Vata Bay, the Nautical Center of Sainte-Marie Bay, and Magenta Bay, with four females and one male (cyan community in Fig. 5C). The second time interval clustered four hours (3, 17, 18, and 21 h), including dusk (green cluster in Fig. 5). Two communities were observed. The first remained unchanged, restricted to a single female at Sainte-Marie Bay (green community in Fig. 5C). The second included all other sharks and stations, except a few isolated stations in the harbor, again suggesting baseline structure disruption and broad shark movement at dusk (purple community in Fig. 5B). The third time interval clustered 7 h (1, 8, 9, 12, 13, 14, and 16 h), covering mostly the afternoon but also some hours at night and in the morning. At these times, the baseline tiger shark community structures fragmented into four communities. While the first (green) and second (purple) communities remained consistent with the baseline structure, the third community split into two. One sub-community (brown in Fig. 5A) consisted of one male and one female visiting Anse Vata, Citrons Bay, the Nautical Center of Sainte-Marie Bay, and Magenta Bay. The other sub-community (cyan in Fig. 5A) involved three females visiting the exit of Grand Harbor, Dumbéa, and Sainte-Marie Bays.

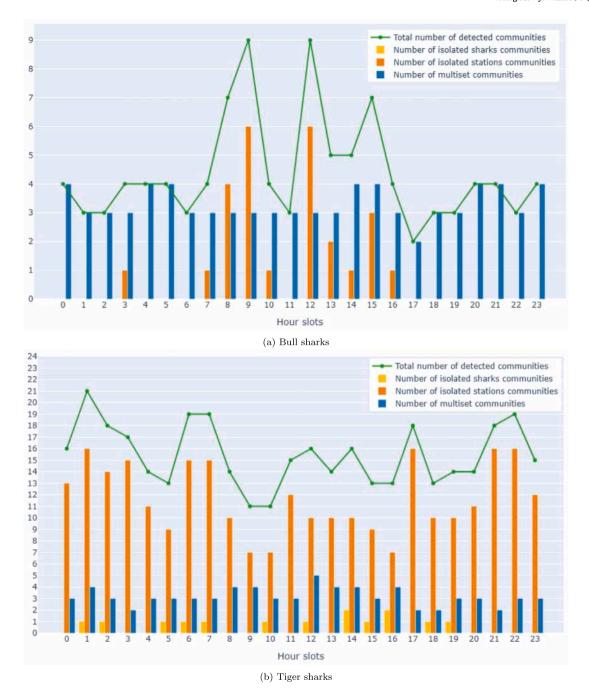


Fig. 3. Number of communities (sharks and stations) detected by the Fast-Greedy algorithm across 24 hourly bipartite graphs. The green line shows the variation in the total number of detected communities. Blue bars indicate communities that include both sharks and stations. Yellow and orange bars represent isolated communities, highlighting instances of isolated sharks or stations, respectively (i.e., no visit made or detected). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Unprovoked shark bites are increasing globally, sparking crises in many countries, including the archipelago of New Caledonia in the South Pacific (McPhee, 2014). A shark crisis typically rests on three pillars. First, an incident involving a shark bite triggers an immediate economic crisis, with businesses in the tourism industry impacted by client cancellations due to fears around swimming and water activities (Dudley and Cliff, 2010). In response to this economic impact, authorities often decide to implement culling campaigns, significantly reducing populations of these animals, which are often both threatened and legally protected, thus leading to an environmental crisis (Dudley and Cliff, 2010; Gallagher and Hammerschlag, 2011). This constitutes

the second pillar of the shark crisis. The third pillar involves societal tension, marked by strong divides between advocates for shark conservation and those supporting population control measures (Simpfendorfer et al., 2021). In response to such crises, science seeks to shed light on the situation, aiming to inform decision-makers and help diffuse public tensions (Shiffman et al., 2021).

A tropical lagoon is a wild natural environment where the risk of injury is never entirely absent (McPhee, 2014). Regarding sharks, it is known that unprovoked bites can occur anywhere and at any time, although such dramatic incidents are extremely rare compared to other natural risks, such as drowning or injuries from jellyfish, stingrays, or stonefish (Maslin et al., 2000). The objective, therefore, is not to identify specific locations or times where water activities in

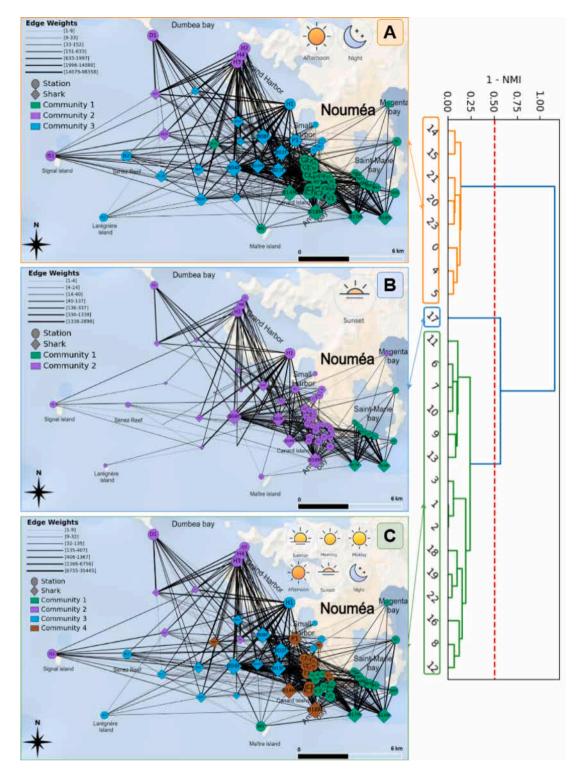


Fig. 4. Stable community structures of bull sharks detected using the Fast-Greedy algorithm applied to temporally aggregated bipartite graphs. Panels show representative two-, three-, and four-community configurations based on NMI clustering of hourly networks. Communities are color-coded to reflect spatial and individual groupings across stations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the lagoon are entirely risk-free, as zero risk does not exist in natural environments. Rather, scientists aim to identify areas and times where the risk is relatively higher, due to heightened shark activity in these zones and times that coincide with a high density of human presence (Lagabrielle et al., 2018). In Nouméa, risk-prone human activities occur during daylight hours (6 am–6 pm) in four key areas: the beaches at Citrons and Anse Vata bays, which are popular among swimmers and windsurfers (New Caledonia Tourism, 2022); the lagoon islets, used

by swimmers and snorkelers; the nautical center, attended by children learning to sail; and the main harbor, sometimes used by swimmers, divers, and those engaged in other water activities such as sailing, kayaking, and paddleboarding. These areas are recognized as popular recreational sites, indicating a high level of human presence and potential for interactions with sharks. In the absence of more detailed data, we evaluated the risk of shark bites by comparing the times and areas of shark activity – revealed by our network analysis – with the

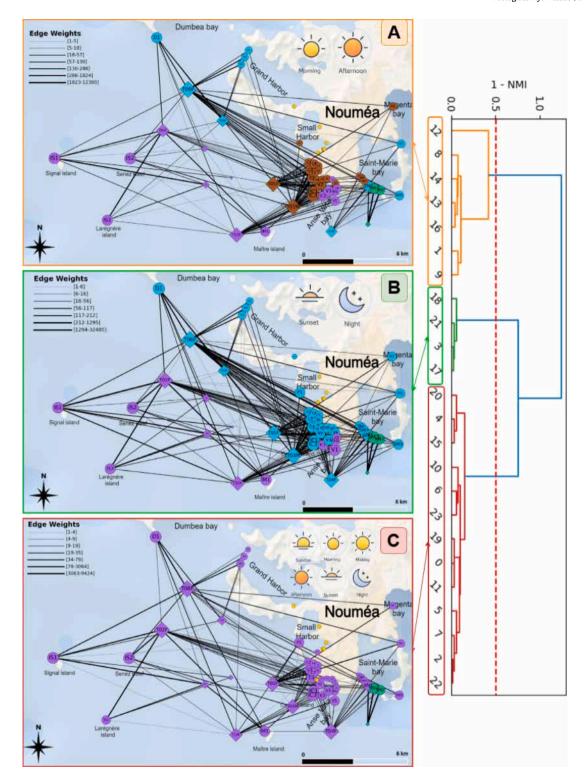


Fig. 5. Stable community structures of tiger sharks detected using the Fast-Greedy algorithm applied to temporally aggregated bipartite graphs. Panels show representative two-, three-, and four-community configurations based on NMI clustering of hourly networks. Communities are color-coded to reflect spatial and individual groupings across stations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

known times and areas of human activity. However, we acknowledge that future research would greatly benefit from incorporating direct measurements of human presence to provide a more refined assessment of interaction risks.

Our application of normalized mutual information (NMI) clustering to the communities detected using the Fast-Greedy algorithm across 24 hourly bipartite graphs revealed three distinct, temporally stable

spatial patterns in the movements of both bull and tiger sharks. Some of these communities may present a particular risk to lagoon users. Both bull sharks and tiger sharks exhibited a baseline structure with three communities present during most hours of the day and night. The two species also displayed a fusion–fission community dynamic. Fusion events were observed at dusk for both species, while fission events occurred mostly at night and in the middle of the afternoon for bull sharks

and primarily in the afternoon for tiger sharks. Fission–fusion dynamics have already been reported for reef shark communities in the central Pacific (Papastamatiou et al., 2020). Reports also exist for several taxa, including avian and mammalian species (Kerth et al., 2011; Silk et al., 2014). Our study therefore indicates that such dynamics also occur for large sharks. These species, especially tiger sharks, are known to travel large distances spanning hundreds to thousands of km (McPhee, 2014), although some sedentary behaviors have been observed at some locations (Dudley and Cliff, 2010). It seems therefore remarkable that not only many individuals from both shark species remained around the city of Nouméa for years, but also that they formed temporally stable fission–fusion groups over diel timescales.

The baseline structure included a very large community of – mostly female - bull sharks, with peak activity between 6 am and 1 pm, around the main harbor, marinas, fishing wharf, and extending into the reefs and islets of the lagoon. This community forms around the industrial fishing vessels moored at the fishing wharf (station H1). Morning, therefore, appears to be a particularly risky time for water activities in the main harbor, and to a lesser extent in the bays and islets of Nouméa. Female bull sharks often inhabit shallow (<20 m deep), warm (26 °C-33 °C) coastal and estuarine waters characterized by minimal water movement (Rider et al., 2021; Bethea et al., 2014). They exhibit strong site fidelity to structured, human-influenced coastal habitats, such as harbors and marinas (Smoothey et al., 2019; Daly et al., 2013, 2014). They are known to be attracted by human activities such as fishing or food disposal (Niella et al., 2021). The harbor of Nouméa therefore appears not only as favorable coastal habitat for bull sharks but also as an area where the fishing fleet likely attracts and retains these dangerous animals near the beaches. A similar situation is known at Recife, Brazil (Hazin and Afonso, 2013).

A second baseline structure involved a community of male bull sharks mostly visiting Anse Vata and Citrons Bay beaches, the coastal Canard and Maître islets, and the nautical center. This community split into two subcommunities at night and in the middle of the afternoon. In Australia, male bull sharks often remain in nearshore waters during the afternoon, particularly when water temperatures exceed 20 °C, following rainfall, and when swell heights range between 1.8 and 2.8 m (Smoothey et al., 2019). They exhibit localized movements into beach areas coinciding with periods of adequate rainfall and sea temperature conditions, potentially increasing human-shark interactions (Werry et al., 2018). Many elasmobranch species (sharks, skates, and rays) display aggressive behavior during mating with male biting females (Crooks et al., 2013). Mating scars have been observed in several shark species, including blacktip reef sharks (Chin et al., 2015) and bull sharks (Jenson, 1976). However, whether male aggressiveness during mating contributes to a heightened risk of unprovoked shark bites on humans remains unknown.

A disruption of community structure was observed at dusk, with a fusion of most sharks and stations into a single community for both species. Dusk therefore appears as a transitional period characterized by greater shark movement and connectivity among stations. For bull sharks specifically, this indicates that the large group of females in the harbor merged with other communities and exhibited increased activity at the beaches and in the lagoon. Given that the baseline structure of tiger sharks included three communities with individuals visiting most stations at the beaches, islets and nautical center throughout most of the day and night, dusk appears simply as a time of increased activityand therefore, elevated risk. Tiger sharks display broader movement patterns than bull sharks, spending more time offshore and using nearshore habitats only transiently (Lipscombe et al., 2020; Niella et al., 2021). However, elasmobranchs exhibit increased foraging activity and horizontal movements (e.g., distance traveled, activity space) at dawn and dusk (review by Hammerschlag et al., 2016). Although shark safety guidelines often recommend avoiding the water during these crepuscular periods, data on human-shark incidents indicate that bites can occur at any time of day, with fewer incidents at dawn and dusk (Scala et al.,

2020). However, it remains unclear whether this pattern simply reflects lower human presence in the water during low-light hours.

These insights gained into shark behavior and risk zones were made possible through the application of one of the best community detection algorithms based on modularity. Among the algorithms evaluated, including the Label Propagation algorithm, and the Multilevel algorithm, the Fast-Greedy algorithm provided the highest modularity scores and revealed the best community structures (Finn et al., 2014; Casselberry et al., 2019). Its ability to identify isolated communities where nodes exhibited no links further enhanced our understanding of spatial and temporal patterns. However, our study still faces several limitations that must be acknowledged. One major limitation is in the relatively small number of individuals studied and the imbalance between sexesfor instance, our data included 14 female and 5 male bull sharks, and 10 female and only one male tiger shark. This may affect the generalizability of our findings, especially for male populations, which were underrepresented in our sample. Furthermore, the deployment of tags on sharks was conducted at various times, which may have affected the consistency and comparability of data across different periods and conditions. Another methodological limitation is the aggregation of data across all days at the same hours, which does not account for potential seasonal variations.

Despite these limitations, our study represents a significant advancement in the field of animal movement ecology, and particularly in shark ecology. Our modeling framework integrates several components, including dynamic bipartite network construction, modularitybased community detection, and community similarity clustering using Normalized Mutual Information (NMI). While previous studies have primarily relied on static or unipartite representations, our approach combines high temporal resolution with the preservation of the twomode structure inherent in telemetry data, allowing for a more nuanced investigation of dynamic species-habitat associations. Although each component of our framework has been applied independently in other contexts, their combined use in this form has not, to the best of our knowledge, been implemented within the field of animal movement ecology. Beyond providing ecological insights, our framework represents a scalable methodology for analyzing temporally structured movement data in other ecological and behavioral systems where dynamic spatial relationships are of interest. Looking ahead, to improve our methodology, address the limitations of our work, and enhance the robustness of our findings, it would be beneficial to explore advanced deep learning techniques such as graph neural networks (Zhou et al., 2020). These models could classify shark movements more accurately by accounting for the complexity of interactions within the marine environment, including species, sex, seasons and other ecological variables. Such advanced models may not only refine our understanding of shark behaviors but also improve the predictive accuracy of risk, thereby contributing to more effective and informed conservation and public safety strategies.

5. Conclusion

In this study, we delved into the complex movement patterns of bull and tiger sharks in the lagoon of Nouméa, highlighting their proximity to human-populated areas through advanced acoustic telemetry and graph-based modeling techniques. Our findings offer a detailed view of shark activity patterns, revealing distinct temporal and spatial behaviors across species and sexes. This nuanced understanding is essential for devising targeted strategies that enhance public safety while safeguarding conservation efforts. Specifically, we developed a novel framework that preserves the full three-mode structure of movement data (individual-location-time) and identifies temporally stable communities of sharks and locations. This was achieved by collecting five years of acoustic telemetry data, applying the Fast-Greedy community detection algorithm over 24 hourly bipartite graphs and clustering the community structures using Normalized Mutual Information (NMI).

For both species, our framework revealed several temporally stable community structures, including a baseline structure occurring at most hours of the day and night, and a fission-fusion dynamic where communities merged at dusk, suggesting higher movement activity during this low-light transitional period. Our approach highlighted critical periods of overlap between shark and human presence, underscoring the importance of hourly temporal resolution in identifying sharklocation communities when formulating management and conservation strategies. Key human-shark interaction areas such as beaches, islets and sailing schools would require prioritized risk mitigation measures, including enhanced real-time monitoring systems, time-specific safety protocols, and public awareness campaigns to educate residents and visitors on shark behavior and safety precautions. This work not only contributes to our understanding of the spatiotemporal dynamics of bull and tiger sharks, including sex-specific behavioral ecology, but also supports the development of informed, science-based management policies that ensure both human safety and the conservation of threatened marine predators. By balancing these needs, we can support sustainable human-wildlife coexistence in marine environments.

CRediT authorship contribution statement

Ibtissam Chafia: Writing – original draft, Software, Methodology, Conceptualization. Jihad Zahir: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. Christophe Lett: Writing – review & editing, Supervision, Methodology. Tarik Agouti: Writing – review & editing, Supervision, Methodology. Hajar Mousannif: Supervision. Laurent Vigliola: Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecoinf.2025.103263.

Data availability

The data used for this article is archived in the public repository Zenodo https://doi.org/10.5281/zenodo.15250000. The New Caledonian legislation regarding sensitive environmental data does not permit unrestricted public access. Accordingly, access to the data will require a Data Use Agreement (DUA), which will be systematically granted for reproducibility purposes. The analysis code is available on a public GitHub repository https://github.com/IbtissamCHAFIA/24-Hourly-Bipartite-Graphs.git.

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