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# Spatial and temporal analysis of juvenile blacktip reef shark (*Carcharhinus melanopterus*) demographies identifies critical habitats

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## Abstract

Reef shark species have undergone sharp declines in recent decades, as they inhabit coastal areas, making them an easy target in fisheries (i.e., sharks are exploited globally for their fins, meat, and liver oil) and exposing them to other threats (e.g., being part of by-catch, pollution, and climate change). Reef sharks play a critical role in coral reef ecosystems, where they control populations of smaller predators and herbivorous fishes either directly via predation or indirectly via behavior, thus protecting biodiversity and preventing potential overgrazing of corals. The urgent need to conserve reef shark populations necessitates a multifaceted approach to policy at local, federal, and global levels. However, monitoring programmes to evaluate the efficiency of such policies are lacking due to the difficulty in repeatedly sampling free-ranging, wild shark populations. Over nine consecutive years, we monitored juveniles of the blacktip reef shark (*Carcharhinus melanopterus*) population around Moorea, French Polynesia, and within the largest shark sanctuary globally, to date. We investigated the roles of spatial (i.e., sampling sites) and temporal variables (i.e., sampling year, season, and month), water temperature, and interspecific competition on shark density across 10 coastal nursery areas. Juvenile *C. melanopterus* density was found to be stable over 9 years, which may highlight the effectiveness of local and likely federal policies. Two of the 10 nursery areas exhibited higher juvenile shark densities over time, which may have been related to changes in female reproductive behavior or changes in habitat type and resources. Water temperatures did not affect juvenile shark density over time as extreme temperatures proven lethal (i.e., 33°C) in juvenile *C. melanopterus* might have been tempered by daily variation. The proven efficiency of time-series datasets for reef sharks to identify critical habitats (having the highest juvenile shark densities over time) should be extended to other populations to significantly contribute to the conservation of reef shark species.

KEYWORDS
competition, dynamics, population, reef shark, temperature, time series

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Serge Planes and Isabel Smallegange share equal last authorship.

## 1 | INTRODUCTION

Reef sharks are threatened by anthropogenic activities despite emerging conservation strategies (Roff *et al*., 2016; Ward-Paige & Worm, 2017). They play a key role in coral reef ecosystems by maintaining a fear pressure on lower trophic levels, which prevents the dispersal of fish communities, limiting grazing and resource consumption on the reef (Roff *et al*., 2016). However, reef sharks suffer direct and indirect anthropogenetic threats (Heupel *et al*., 2019). Direct threats are associated to targeted fisheries, being part of by-catch, poaching of isolated reefs located in marine protected areas and indirect threats to the destruction of their habitats (Knip *et al*., 2010), to material and sound pollution (Fernández & Anastasopoulou, 2019), and removal of their prey species (Consales & Marsili, 2021; Dulvy *et al*., 2021; Heupel *et al*., 2019; Stevens, 2000). Yet despite the current conservation measures adopted by several countries worldwide to mitigate these anthropogenic effects, many reef shark species are still listed as vulnerable, near threatened, or threatened on the IUCN Red List for endangered species (MacNeil *et al*., 2020; White *et al*., 2017). Because all coral reef ecosystems are affected by human activities in one way or another, we have no baseline for what a healthy reef shark population should look like (Ferretti *et al*., 2018; Hughes *et al*., 2003; Lecchini *et al*., 2021). Moreover, geopolitical boundaries defining protected coral reef ecosystems do not necessarily have the highest shark densities (MacNeil *et al*., 2020; Ward-Paige & Worm, 2017). For example, shark densities can be 218 sharks/km$^2$ in no-entry marine reserves on the Great Barrier Reef in Australia, but 9000 sharks/km$^2$ in the uninhabited atolls of the Line Islands (Ferretti *et al*., 2018). However, because we have no reference data regarding reef shark abundances on healthy reefs, it is challenging to establish efficient conservation strategies that set targets for reef shark abundance thresholds (Ferretti *et al*., 2018).

As 32.6% of all Chondrichthyan species are currently threatened by extinction (Dulvy *et al*., 2021), it has never been more important to implement species-specific conservation strategies and protect critical shark habitats (e.g., foraging habitats and nurseries) (Flowers *et al*., 2022; García-Barón *et al*., 2021; Mariani *et al*., 2021; Robbins *et al*., 2006; Tuya *et al*., 2022). Identifying critical habitats and understanding the impact of emerging threats (e.g., anthropogenetic disturbances, rise in water temperature, and ocean acidification) likely to influence shark behavior and dispersion requires large datasets (McClatchie *et al*., 2014). Indeed, these datasets should capture species-specific behavioral traits and associated habitats together with interspecific competition and environmental variables (e.g., water temperature) influencing shark dispersion and/or mortality (Hobday & Evans, 2013; Matich *et al*., 2017). Time-series datasets for free-ranging shark species have been scarce because of the difficulties in following such species through space and time. Reef shark time-series datasets are also lacking because they have been low research priority (Nadon *et al*., 2012; Peterson *et al*., 2017). The knowledge caveats on reef shark populations together with rising extinction risks highlights the importance of understanding the critical drivers of shark population dynamics in situ (Flowers *et al*., 2022; Mariani *et al*., 2021; Robbins *et al*., 2006; Tuya *et al*., 2022) to adapt management strategies accordingly.

Reef sharks are vulnerable to environmental changes and disturbances due to their life-history traits, behavior, and physiology (Chin *et al*., 2012; Heupel *et al*., 2019). Sharks that are reef resident are found year-round at or near coral reefs, and non-resident species utilize coral reef habitats opportunistically or seasonally (Heupel *et al*., 2019; Speed *et al*., 2012). Reef residents are thus dependent on habitats that are critical to their reproduction and survival (Heupel *et al*., 2019). The slow growth, late sexual maturity, and small litter size (viviparity with four to six pups per litter) in reef resident sharks, such as Carcharhinids, make them vulnerable to any kind of disturbance and exploitation (Chin *et al*., 2012; Mourier, Mills, & Planes, 2013; Mull *et al*., 2022; Vignaud *et al*., 2014). Their vulnerability is enhanced because female sharks give birth to their pups in shallow, coastal areas that are often exposed to human activities (e.g., construction of coastal infrastructure, nutrient runoff, tourism, and fishing) (Mourier & Planes, 2013; Vignaud *et al*., 2014). Adult female reef sharks may select these shallow coastal areas because they provide ample resources for their offspring and/or because shallow waters protect their pups against larger predators (George *et al*., 2019; Mourier & Planes, 2013). However, because these nursery waters are so shallow, in addition to being impacted by anthropogenic factors, neonate and juvenile reef sharks are front-line casualties of climate change (Bouyoucos, Watson, *et al*., 2020). Specifically, sea surface temperature in coastal areas of the South Pacific is predicted to increase by 3–5°C, and marine heatwaves will occur more frequently (Bouyoucos, Watson, *et al*., 2020; Pörtner *et al*., 2022; Van Der Stocken *et al*., 2022). Marine heatwaves, periods of extreme regional warming, have increased in frequency by 50% since 1925 and in intensity by 20% since 1989 (Oliver, 2019; Smale *et al*., 2019). This increase is the result of the increase in mean sea surface temperature and not variability, and thus marine heatwaves have significant implications for marine ecosystems (Oliver, 2019). Because reef sharks, like numerous tropical species, already live close to their maximum temperatures for various metrics of performance, increasing mean water temperatures and marine heatwaves pose an array of challenges relating to physiology, ecology, and ultimately survival (Bouyoucos, Morrison, *et al*., 2020; Rummer *et al*., 2014; Schoen *et al*., 2021). Further research efforts are required to understand the effects of anthropogenic disturbances together with past and present water sea surface temperatures that might impact juvenile and adult reef shark population demography (Osgood & Baum, 2015).

In this study we investigate the hypothesis that juvenile blacktip reef shark densities change per nursery and over the years, likely in response to mean daily water temperature variability, interspecific competition with sicklefin lemon sharks (co-occurring in the same habitats), and lagged temperature and density-dependent effects. Blacktip reef sharks (*Carcharhinus melanopterus*) are a model species well suited to study the spatial and temporal distribution of a reef shark species because of its wide distribution among tropical coral reefs of the Indian and Pacific Oceans (Maisano Delser *et al*., 2019). *C. melanopterus* were monitored around Moorea Island (French Polynesia) where previous studies identified this species population as sedentary (Mourier & Planes, 2013; Vignaud *et al.*, 2014). The combination of the environmental configuration and this species' behavior made it possible to collect one of the first decade long time-series datasets for reef sharks together with abiotic and biotic variables (e.g., water temperature and interspecific competition with juvenile lemon sharks *Negaprion acutidens*). These two shark species were monitored during the summer months from October to February, providing the warmest water temperatures juveniles are exposed to around Moorea Island annually (Bouyoucos, Morrison, *et al.*, 2020). Juveniles were specifically monitored because they use an array of different habitats (i.e., mangroves, coral, or sand-covered areas) that are close to shore, thus reducing monitoring difficulties while still providing environmental variability (Matich *et al.*, 2017). The human population of the island increased from 2000 inhabitants in 1946 to about 17,000 now, resulting in exponential coastal infrastructure development around Moorea (construction of harbors, embankments, jetties in opposition to areas with an intact natural coastline) with coastal areas being highly disturbed and others left rather pristine (Madi Moussa *et al.*, 2019; Vignaud *et al.*, 2014). Habitat type together with infrastructure distribution around Moorea Island creates spatial heterogeneity which was hypothesized to have site-specific effects on juvenile shark density over time. The low dispersion rate of neonate and juvenile sharks in their birth habitats together with their sensitivity to temperature is likely to cause decreases in shark densities when daily mean water temperature increases (Bouyoucos, Morrison, *et al.*, 2020; Mourier & Planes, 2013). The co-occurrence of sicklefin lemon and blacktip reef sharks was found in previous studies to create interspecific competition dominated by sicklefin lemon sharks, which is likely to have a negative effect on the juvenile blacktip reef shark densities (Matich *et al.*, 2017). Water temperatures were also expected to be a determinant factor of juvenile blacktip reef shark survival (Bouyoucos, Morrison, *et al.*, 2020). Past water temperature measures and density-dependence in a sampling site could have influenced the survival and/or triggered the dispersion of juvenile sharks in the sampling sites, creating a lag response in juvenile blacktip reef shark density per sampling site (Ikpewe *et al.*, 2021; Lin *et al.*, 2021; Rastetter *et al.*, 2021). Finally, intraspecific competition in juvenile blacktip reef sharks can lead to juvenile shark dispersion and/or increased mortality rates (Carlson & Baremore, 2003; Grossman & Simon, 2020; Matich *et al.*, 2021). Therefore, we will (a) assess the spatial and temporal variability in the juvenile blacktip reef shark demography, (b) determine the effect of water temperature on juvenile shark densities, (c) test the effect of interspecific competition on juvenile blacktip reef shark density per sampling site and over time, and (d) account for the effect of density-dependent (juvenile *C. melanopterus* lagged CPUE per site and per sampling season) and -independent (lagged water temperature) variables on the density changes in blacktip reef sharks.

## 2 | MATERIALS AND METHODS

### 2.1 | Ethics approval

All shark capture and research protocols were approved under Arrêté no. 9524 issued by the Ministère de la Promotion des Langues, de la Culture, de la Communication et de l'Environnement of the French Polynesian government on October 30, 2015, and James Cook University's Animal Ethics Committee (A2394 and A2769). All applicable international, national, and/or institutional guidelines for the sampling of animals were followed.

### 2.2 | Reef shark sampling

Juvenile *C. melanopterus* and *N. acutidens* (sicklefin lemon sharks) were monitored around the island of Moorea (17°30′ S, 149°51′ W), which is located within the world's largest shark sanctuary French Polynesia (4,771,088 km$^2$), where shark fishing has been banned throughout the entirety of the exclusive economic zone (EEZ) since 2012 (Ward-Paige & Worm, 2017). Moorea's coastline is about 60 km long, comprising shallow mangroves, sand flats, and coral reef habitats, propitious for the development of neonatal reef sharks (Chin *et al.*, 2016; Madi Moussa *et al.*, 2019). Data were obtained from a monitoring programme led by the CRIOBE (Center for Island Research and Environmental Observatory) and Physioshark (James Cook University shark physiology research programme) across 10 different sites around Moorea (Figure 1) from 2013 to 2022 and between the months of October and February, in synchronicity with the parturition period of female blacktip reef sharks around Moorea (Porcher, 2005). The sharks that were sampled are defined as neonate sharks or YOY with the distinction lying in the degree of healing of the umbilical scar; sharks with open umbilical scars are estimated to be less than 3 weeks old (Debaere *et al.*, 2023). In this study, both neonate and YOY sharks, *C. melanopterus* and *N. acutidens*, were counted during the sampling events and are hereafter referred to as "juvenile" sharks.

A standardized protocol was used from 2013 through 2022 to monitor, sample, and measure sharks (Bouyoucos *et al.*, 2018; Mourier & Planes, 2013). Blacktip reef shark and sicklefin lemon shark abundance was estimated as the number of sharks caught per sampling event (measured in time by hours and minutes). The start and end time of each sampling event was recorded, except for the sampling season 2013–2014 (i.e., due to a lack in the standardization of the sampling method in the first sampling year), during which a standardized sampling duration of 2 h and 30 min was employed. Each sampling site was visited twice per month, during which a monofilament gillnet (50.0 cm × 1.5 m, mesh-size of 5 cm) was set perpendicular to shore for about 3 h. Once a shark was netted, it was carefully removed from the net, brought ashore, and placed into a 150-L container of clean, aerated seawater. Then, a series of measurements (length, weight, healing stage of the umbilical scar) were recorded, and the dorsal fin was clipped, and tissue stored in ethanol for further genetic analysis. The entire measurement and sampling procedure lasted approximately 10 min. The monitoring programme was held annually from 2013 through 2022 between October of the current year and February of the next year, in synchronicity with the parturition period of female blacktip reef sharks around Moorea (Porcher, 2005).

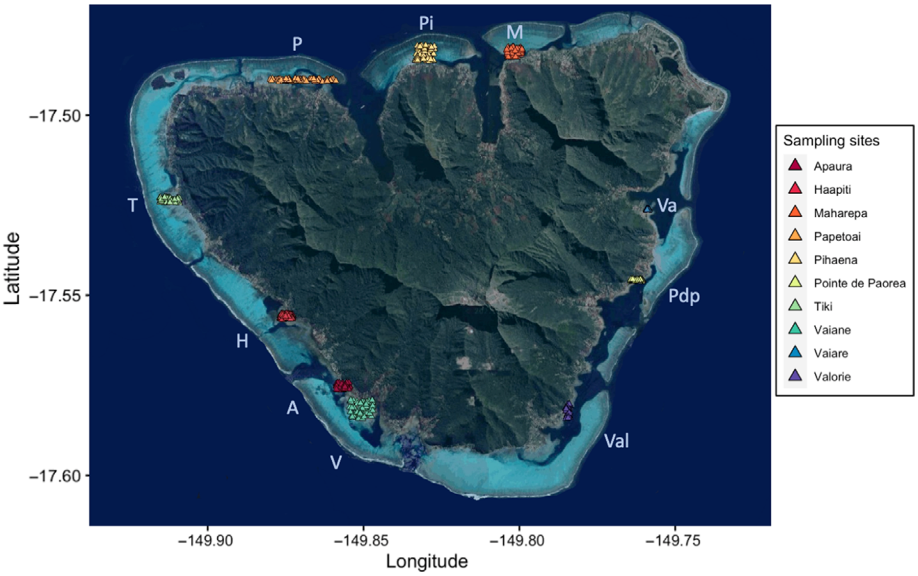

**FIGURE 1** Map of the island of Moorea, French Polynesia, showing the sampling events in each of the 10 sampling sites located in the lagoon area on each of the three coasts of the island. Every letter represents the name of one of the 10 sampling sites as follows: P, Papetoai; Pi, Pihaena; M, Maharepa; Va, Vaiare; Pdp, Pointe de Paorea; Val, Valorie; V, Vaiane; A, Apaura; H, Haapiti; T, Tiki. The sets of colored triangles in each sampling site represent the sampling events; a jitter in the GPS coordinates from each sampling event was used to represent the approximate dispersion of the juvenile and neonate sharks following Bouyoucos, Romain, *et al*., 2020. The triangles per sampling event per site do overlap depending on the surface of the sampling site.

## 2.3 | Water temperature measurements

Two temperature loggers (UA-002-64, Onset Computer and ElectricBlue) were installed per sampling area in up to 50 cm deep water and were separated by *c*. 10–20 m. The loggers recorded water temperature every 10 min (accuracy = ±0.5°C, resolution = 0.14°C at 25°C) and were installed in the sampling areas from October through the end of February for the sampling seasons three (2015–2016) to nine (2021–2022). A daily water temperature average was calculated for each sampling event (the daily water temperature fluctuation from 2013 through 2022 was of 3.1 ± 2.39°C) to capture the seasonal variability in daily mean water temperature per sampling site. The mean daily water temperature per sampling sites was then used to test for the presence of a negative effect between water temperature increase and juvenile shark density.

**TABLE 1** Structures of the full linear models used to analyse the response variable (*CPUE_Cm*: CPUE of *C. melanopterus*).

| Model no. | Full model |
|---|---|
| 1.1 | $\beta_1 + \beta_2 St + \beta_3 M + \beta 4Se + \beta 5CPUE\_Na + \beta 6T$ |
| 1.2 | $\beta 1 + \beta 2St + \beta 3M + \beta 5CPUE\_Na + \beta 6T + \beta 7J$ |
| 1.3 | $\beta 1 + \beta 2St + \beta 3M + \beta 5CPUE_{Na} + \beta 6T + \beta 7J + \beta 8B$ |
| 1.4 | $\beta 1 + \beta 2St + \beta 3M + \beta 5CPUE_{Na} + \beta 7J + \beta 8B$ |
| 1.5 | $\beta 1 + \beta 2St + \beta 3M + \beta 5CPUE_{Na} + \beta 7J + \beta 8B + \beta 9Lc$ |
| 1.6 | $\beta 1 + \beta 2St + \beta 3M + \beta 5CPUE_{Na} + \beta 7J + \beta 8B + \beta 10Lt$ |

*Note*: The explanatory variables are *St*, site; *M*, month; *Se*, season; *CPUE_Na*, CPUE *N. acutidens*; *T*, temperature; *J*, julian day; *B*, Boolean temperature measurement unit; *Lc*, lagged CPUE of *C. melanopterus*; *Lt*, lagged temperature.
Abbreviation: CPUE, catch per unit of effort.

## 2.4 | Statistical analyses

The measurement protocol (described in the previous section) did allow us to control for possible confounding effects of time of day by fishing (2.5 to a 3 h period, usually from 1700 to 2000 p.m.) and time of year (identified by month) when analysing CPUE (catch per unit effort) for *C. melanopterus* (CPUE_Cm).

Linear regression models, assuming an independent and identically distributed normal distribution of the residuals, were used to relate CPUE_Cm to the categorical factors site *St* (with levels Vaiare, Apaura, Haapiti, Maharepa, Papetoai, Pihaena, Pointe de paorea, Tiki, Vaiane, and Valorie); month *M* (with levels October, November, December, January, February); season *Se* (1 [October until February 2013/14], 2 [October until February 2014/15], 3 [October until February 2015/16], 4 [October until February 2016/17], 5 [October until February 2017/18], 6 [October until February 2018/19], 7 [October until February 2019/20], 8 [October until February 2020/21], 9 [October until February 2021/22]); the continuous variables *CPUE_Na* (CPUE of juvenile *N. acutidens*); and temperature *T* (Model 1.1, Table 1). The regression coefficients of each of the respective explanatory variables were labeled $\beta 2, \beta 3, \beta 4, \beta 5, \text{and} \, \beta 6$ Table 1. Because of the seasonality of the sampling event, which represents nested data over time (in accordance with the parturition period of the blacktip reef shark population of Moorea from October to February), we analysed another model, within which we incorporated the continuous temporal variable Julian day *J* (starting as a linear time variable on date October 21, 2013 which was indicated as $t = 0$) which was used to replace the seasons (*Se*). A linear regression was used to predict CPUE_Cm with the Julian day *J* variable from 2013 through 2022, with $\beta 7$ being its regression coefficient (Model 1.2, Table 1). As the temperature variable had missing data from 2013 through 2015, we surmised that this could influence the outcome of the model. Therefore, we included a Boolean variable *B* that denoted whether temperature had been measured ($B = 1$) ($B = 0$) to assess if shark dynamics differed between periods that we measured temperature and periods where we had not. The regression coefficient of the Boolean variable was $\beta 8$ (Model 1.3, Table 1). Temperature was then removed from Model 1.3. to test if it affected shark dynamics, (Model 1.4, Table 1).

As we found that the effect of temperature in Model 1.3 was non-significant (see results, Table 2), Model 1.4 was defined as the final model. The residuals and the prediction for Model 1.4 were plotted over linear time, and for each of the 10 sampling sites around the island of Moorea, to visually assess our assumption that there was no autocorrelation in the data.

Visual inspection of histograms (Figure 2) suggested a negative binomial distribution and zero-inflated *C. melanopterus* CPUE. Indeed, *C. melanopterus* CPUE integrates 43.9% of zeros, due to sampling events where no juvenile shark was sampled.

**TABLE 2** Summary table of the results of the six models implemented in this study giving the adjusted $R^2$, the *p*-value, the median residuals, and the AIC.

| Model statistics | Model 1.1 | Model 1.2 | Model 1.3 | Model 1.4 | Model 1.5 | Model 1.6 |
|---|---|---|---|---|---|---|
| $R^2$ (adjusted) | 0.147 | 0.147 | 0.118 | 0.119 | 0.129 | 0.125 |
| *p*-Value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| Median residuals | −0.0074 | −0.0074 | −0.0085 | −0.0084 | −0.0079 | −0.0083 |
| AIC | −1511.076 | −1511.128 | −2823.628 | −2825.284 | −2475.856 | −1397.335 |

*Note*: The detail of the results for each variable of all models, except Model 1.4, are available in Table S1.

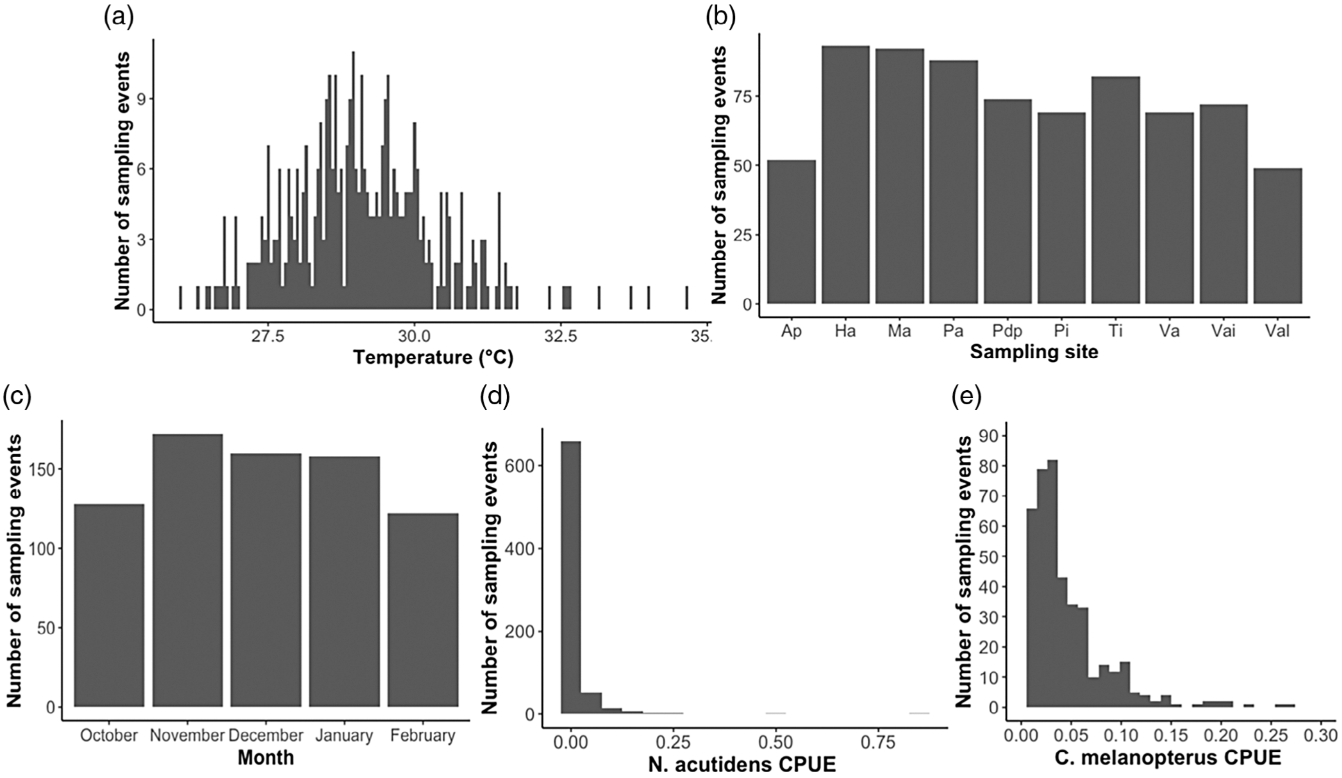

**FIGURE 2** Histograms of the numerical and categorical variables used in this study: (a) displays the average daily temperature from each sampling event; (b) shows the number of sampling events per sampling site (sampling sites are labeled as follows: "Ap," Apaura; "Ha," Haapiti; "Ma," Maharepa; "Pa," Papetoai; "Pdp," Pointe de Paorea; "Pi," Pihaena; "Ti," Tiki; "Va," Vaiane; "Vai," Vaiare; "Val," Valorie; (c) shows the number of sampling events per month; (d) shows the *Negaprion acutidens* CPUE (catch per unit of effort) repartition per sampling event, and (e) shows the *Carcharhinus melanopterus* CPUE repartition per sampling event.

Juvenile blacktip reef sharks may experience intraspecific competition, which could result in autocorrelation in juvenile shark densities over time. This property can be implemented in regression models by adding variables that represent the response variable at a previous time instant, so-called lagged variables. Model 1.5 (Table 1) incorporates a lagged *C. melanopterus* CPUE (*Lc*) to test for the effect of density dependence over time in the sampling sites. *Lc* (regression coefficient $\beta_9$) was built by inserting the value of the previous sampling event for each site and per season in the next sampling event (see Equation 1):

$$Lc_t(St,Se) = \mathrm{CPUE}_{\mathrm{Cm}\,t-1}(St,Se) \tag{1}$$

where *St* is the site and *Se* is the season for each CPUE value per sampling event *t*.

Model 1.6 (Table 1) integrates a lagged water temperature (*Lt*) per site and per season to evaluate the effect of previous site temperature on *C. melanopterus* CPUE. Lt (regression coefficient $\beta_{10}$) was built as the temperature from the previous event was admitted for the next sampling event per site and per season, and written as follows:

$$Lt_t(St,Se) = T_{t-1}(St,Se) \tag{2}$$

where *St* is the site and *Se* is the season for each temperature (*T*) measurement (average per day) per sampling event.

Visual inspection of scatterplots of model residuals against fitted values to assess homogeneity and model residuals against explanatory variables to assess independence was used for model validation. For the final model, to test for differences in *C. melanopterus* CPUE among sampling sites in the linear regression model, the function “glht” from the “multcomp” package was used to perform the Tukey post-hoc test for comparisons of means. The same procedure was implemented for the variable month, and all analyses were performed using R version 4.3.0 (R Core Team, 2023).

## 3 | RESULTS

The CPUE per hour of fishing ranged from 0 to 0.267 for *C. melanopterus*, and from 0 to 0.833 for *N. acutidens* (Figure 2). The water temperature in the sampling sites ranged from 26.02 to 34.63°C (Figure 2). The sampling took place from October 21, 2013, to February 27, 2022, in the 10 sampling sites around Moorea (Figure 1). The sampling took place during nine sampling seasons that corresponded to the parturition period started beginning October and ending late February (Table 2).

The overall $R^2$ of the final model (Model 1.4) is below the $R^2$ of the other models because removing the temperature data removed missing data, especially from 2013 through beginning 2015 (Table 3). Temperature was nonsignificant despite that it, each season, always increased between October and February (Figure 3).

**TABLE 3** Detail of the summary statistics of the linear regression Model 1.4 (details of the other models are available in Table S1).

| Variable | Estimate | *p*-Value |
|---|---|---|
| (Intercept) | 0.0119 | 0.317 |
| Month November | 0.0005 | 0.898 |
| Month December | −0.0003 | 0.936 |
| Month January | −0.0156 | <0.001* |
| Month February | −0.0199 | <0.001* |
| Julian Day | −0.000002 | 0.242 |
| Site Haapiti | 0.0357 | <0.001* |
| Site Maharepa | 0.0289 | <0.001* |
| Site Papetoai | 0.0276 | <0.001* |
| Site Pihaena | 0.0085 | 0.19119 |
| Site Pointe de Paorea | 0.0268 | <0.001* |
| Site Tiki | 0.0203 | <0.001* |
| Site Vaiane | 0.0102 | 0.12565 |
| Site Vaiare | 0.0342 | <0.001* |
| Site Valorie | 0.0169 | 0.02* |
| CPUE_Na | 0.0808 | 0.01* |

*Note*: The first column indicates the variables integrated in the model (the months, the site, the *N. acutidens* CPUE [CPUE_Na], Julian day), the second the estimate and the last column the *p*-value (“*” indicates *a* < 0.05 significant value).
Abbreviation: CPUE, catch per unit of effort.

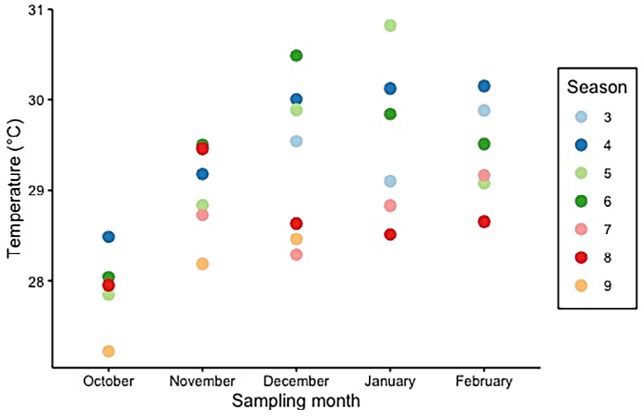

**FIGURE 3** Mean water temperature averaged over all sites around the island of Moorea for each month and per sampling season. Each color represents a different sampling season; missing water temperature data were omitted for some months in some sampling seasons. Water temperature loggers were installed at the end of the third sampling season until the final season in 2022; thus no water temperature data are available for seasons 1 and 2.

Model 1.1, like Models 1.2, 1.3 (Table S1), and 1.4, indicated that the variable month significantly affected CPUE (CPUE was highest in October = November = December>January = February, Figure 3); the months January and February were the months with the most significant effect on CPUE_Cm (Table 3: January, coefficient = −0.0156, *p*-value < 0.001; February, coefficient = −0.0198, *p*-value < 0.001). The months January and February were not significantly different (general linear hypothesis test [GLHT], $t_{(1,739)} = -0.0044$,

$t_{(1,739)} = -1.028$, $p = 0.842$, Figure 4), neither were the months October and November (GLHT, Estimate [E] = –0.0005, $t_{(1,739)} = 0.128$, $p = 0.999$, Figure 4), November and December (GLHT, Estimate [E] = –0.0009, $t_{(1,739)} = -0.225$, $p = 0.999$, Figure 4). The months December and January were significantly different (GLHT, Estimate [E] = –0.0152, $t_{(1,739)} = -3.831$, $p = 0.0013$, Figure 4) as well as the months November, January (GLHT, Estimate [E] = –0.0161, $t_{(1,739)} = -4.119$, $p < 0.001$, Figure 4) and the months October, January (GLHT, Estimate [E] = –0.0156, $t_{(1,739)} = -3.651$, $p = 0.003$, Figure 4). The months October, February (GLHT, Estimate [E] = –0.0199, $t_{(1,739)} = -4.389$, $p < 0.001$, Figure 4) and November, February (GLHT, Estimate [E] = –0.0205, $t_{(1,739)} = -4.864$, $p < 0.001$, Figure 4) and December, February (GLHT, Estimate [E] = –0.0196, $t_{(1,739)} = -4.593$, $p < 0.001$, Figure 4) were significantly different from each other.

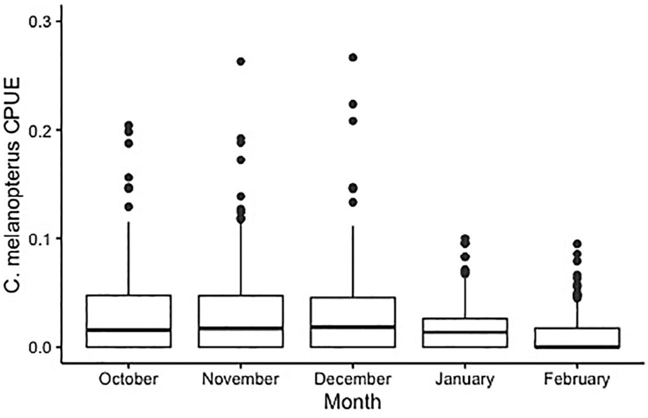

**FIGURE 4** Boxplot of the *Carcharhinus melanopterus* CPUE (catch per unit of effort) per month. The black dots represent the outliers per month.

The variable year in Model 1.1 was nonsignificant (Table 3: year, *p*-value = 0.0946) and, when replaced with the linear time variable (Figure 5), linear time was significant in Model 1.3 ($p = 0.054$, Table 3) but not in the final model, Model 1.4 (linear time, *p*-value = 0.7453, Figure 5; Table 3), indicating that CPUE_Cm did not significantly increase or decrease over time (Julian day, Figure 5).

The sampling sites that have the lowest *C. melanopterus* CPUE are Apaura (mean CPUE_Cm = 0.0049 ± SD = 0.013) < Pihaena (0.0118 ± 0.0199) < Vaiane (0.0176 ± 0.0349) < Valorie (0.0192 ± 0.0248) and the sites with the highest *C. melanopterus* CPUE are the sites Tiki (0.0257 ± 0.0319) < Pointe de Paorea (0.0283 ± 0.0419) < Maharepa (0.0302 ± 0.0449) < Papetoai (0.0309 ± 0.0368) < Vaiare (0.0361 ± 0.0458) < Haapiti (0.0398 ± 0.0425) (Figure 6).

The *C. melanopterus* CPUE from 2013 through 2022 is significantly different in the sites Vaiare and Haapiti from the sites Apaura (GLHT [Haapiti/Apaura], Estimate [E] = 0.0356, $t_{(1,739)} = 5.782$, $p < 0.01$ and GLHT[Vaiare/Apaura], Estimate [E] = 0.0342, $t_{(1,739)} = 5.265$, $p < 0.01$, Figure 6), Pihaena (GLHT[Haapiti/Pihaena], Estimate [E] = –0.0271, $t_{(1,739)} = -4.821$, $p < 0.01$ and GLHT[Vaiare/Pihaena], Estimate [E] = 0.0256, $t_{(1,739)} = 4.295$, $p < 0.01$, Figure 6) and Vaiane (GLHT [Haapiti/Vaiane], Estimate [E] = –0.0255, $t_{(1,739)} = -4.291$, $p < 0.01$ and GLHT[Vaiare/Vaiane], Estimate [E] = 0.0241, $t_{(1,739)} = 3.826$, $p < 0.01$, Figure 6). The *C. melanopterus* CPUE of the sampling sites Papetoai and Maharepa was significantly higher than that of the sites

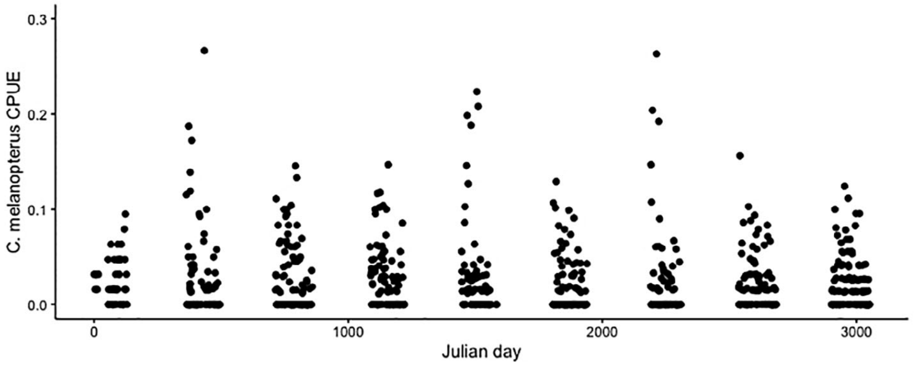

**FIGURE 5** Plot of *Carcharhinus melanopterus* CPUE (catch per unit of effort) values over Julian day.

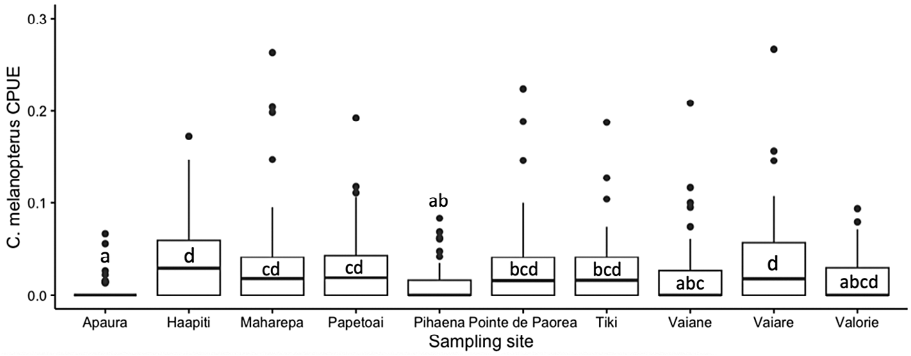

**FIGURE 6** Boxplot of the *Carcharhinus melanopterus* CPUE (catch per unit of effort) for each of the 10 sampling sites around the island of Moorea. The black dots represent the CPUE outliers. The diagrams display the mean, the lower and upper quartiles, the percentile range, and the outliers (black dots); the letters provide a gradient in the CPUE levels from the lowest sampling site with the lowest CPUE (letter "a") to the sites with the highest CPUE (letter "d").

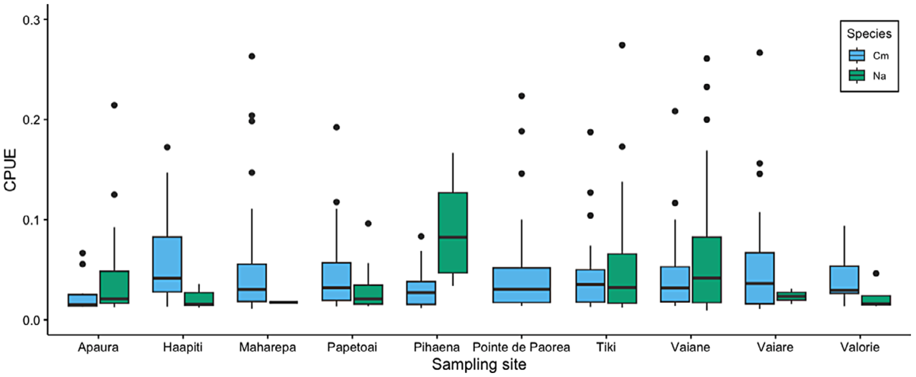

**FIGURE 7** Plot of the *Carcharhinus melanopterus* CPUE (catch per unit of effort) and the *Negaprion acutidens* CPUE for each sampling sites from 2013 through 2022. The diagrams display the mean, the lower and upper quartiles, the percentile range, and the outliers (black dots), the species "Cm" is the acronym for *C. melanopterus* and "Na" for *N. acutidens*.

Apaura (GLHT[Papetoai/Apaura], Estimate [E] = 0.0276, $t_{(1,739)} = 4.437$, $p < 0.01$ and GLHT[Maharepa/Apaura], Estimate [E] = 0.0289, $t_{(1,739)} = 4.672$, $p < 0.01$, Figure 6) and Pihaena (GLHT[Papetoai/Pihaena], Estimate [E] = −0.0191, $t_{(1,739)} = -3.349$, $p = 0.0288$ and GLHT[Maharepa/Pihaena], Estimate [E] = −0.0203, $t_{(1,739)} = -3.609$, $p = 0.0119$, Figure 6). The CPUE (of *C. melanopterus*) of the sampling sites Pointe de Paorea and Tiki is higher than the one of Apaura (GLHT[Pointe de Paorea/Apaura], Estimate [E] = 0.0268, $t_{(1,739)} = 4.154$, $p < 0.01$ and GLHT[Tiki/Apaura], Estimate [E] = 0.0203, $t_{(1,739)} = 3.237$, $p = 0.0401$, Figure 6).

In Model 1.4 we found a slightly positive significant relationship of the *N. acutidens* CPUE with the *C. melanopterus* CPUE (Table 3, $E = 0.081$, $p$-value $= 0.01$) (Figure 7).

The residuals plotted with the predictions of Model 1.4 over Julian day and for each of the 10 sampling sites revealed no autocorrelation, justifying our assumption (Tables 2 and 3). Model 1.4 had the low median residuals (−0.0083, Table 2) and the lowest AIC (−2825.284, Table 2) revealing the best fit with the *C. melanopterus* CPUE data.

In Model 1.4, the months January and February together with the sites Haapiti, Maharepa, Papetoai, Tiki, Vaiare, Valorie, and the CPUE of *N. acutidens* had a positive significant relationship with *C. melanopterus* CPUE (Table 3).

## 4 | DISCUSSION

Reef shark abundance has declined remarkably over the past decades across all coral reefs (MacNeil *et al.*, 2020; Sherman *et al.*, 2023; White *et al.*, 2017). Assessing reef shark population abundance at recovery, increase, or decline is often greatly challenging because we lack spatial and temporal monitoring data on their population dynamics (Latour & Gartland, 2020). In this study, a unique database provided time series of a juvenile reef shark population monitoring program spanning 9 years and 10 sampling sites around Moorea Island (French Polynesia). It was hypothesized that the density of the juvenile blacktip reef shark population would vary across time and space because of environmental heterogeneity due to habitat types and heterogeneous infrastructure development around Moorea Island. Moreover, water temperature and interspecific competition were expected to be explanatory variables of density variations across time and space as previous studies portrayed juvenile sharks as thermally sensitive and susceptible to competition with sicklefin lemon sharks. The lag response of juvenile shark density to water temperature and density-dependence per site was also expected. Interannual and interseasonal (among the sampling seasons stretching from October through the end of February of each year) stability was found in the juvenile blacktip reef shark population of the island of Moorea. Furthermore, the water temperature did not influence the *C. melanopterus* CPUE around the island, whereas considerable variability in the *C. melanopterus* CPUE was uncovered between the months (October to February) and between the 10 sampling sites. A slight positive correlation with juvenile sicklefin lemon sharks was uncovered as well as no lag response in juvenile blacktip reef shark density variability due to temperature neither to density-dependence per sampling site.

We found no evidence for an increase or decline in CPUE among years or sampling seasons (from October through the end of February) between 2013 and 2022, although a decrease inside the seasons (between months) was uncovered. Moorea is part of the largest shark sanctuary on a global scale, and in French Polynesia all shark species are protected. Nonetheless, it is likely that sharks are being poached in remote and uninhabited islands and atolls of French Polynesia (42 of the 118 coral islands are still uninhabited; Lecchini *et al.*, 2021) as maintaining a surveillance of such a large sanctuary is likely to present flaws. The presence of human populations increases surveillance, restricting poaching activities as sharks have economical (sharks are a lucrative source of tourism with several dedicated shark observation areas inside and outside the lagoon) (Esposito *et al.*, 2022; Rieucau *et al.*, 2018) and cultural values (Skubel *et al.*, 2019). Interannual *C. melanopterus* CPUE stability was thus achieved through the annual reproduction of the well-founded perennial and sedentary adult female blacktip reef shark community (Mourier & Planes, 2013; Porcher, 2005), which is not exposed to any kind of exploitation near Moorea Island. The absence of industrial exploitation and poaching together with the low dispersion behavior of adult blacktip reef sharks in fragmented environments might reflect the 9-year timespan juvenile *C. melanopterus* CPUE stability. The monthly variability (per sampling season) in juvenile shark densities might coincide with the high mortality rates among juvenile blacktip reef sharks. Indeed, body condition (a proxy for the overall health condition in sharks) was found to decrease with shark age, from birth to 4 weeks of age (Debaere *et al*., 2023). During the first weeks of their lives juvenile sharks utilize the lipid reserves transmitted by their mothers and stored in their liver to subsist until they transition to the independent foraging capacity (Weideli *et al*., 2019). The juvenile shark density decrease per month (from October, where many neonate sharks are caught, to February where older sharks are caught) likely shows the mortality among annual recruits that were not able to transition to an independent foraging capacity.

We did not find a relationship between daily average and lagged (previous site-specific sampling event) water temperature and *C. melanopterus* CPUE despite the proven sensitivity of sharks to high water temperatures. Indeed, neonate blacktip reef sharks avoid areas with a water temperature of 31°C and higher and show high post-exercise mortality after acclimated to 33°C for 4 weeks (Bouyoucos, Morrison, *et al*., 2020). Although our sampling season from October to February encompasses some of the warmest months in the tropical Pacific, we did not observe water temperatures above 31°C in October, observed only one such instance in November, 12 instances in December, 15 instances in January, and 3 instances in February. We thus surmise that juvenile blacktip reef shark density could drop the most in the months December and January. The nonsignificant effect of thermally dynamic coastal areas on juvenile blacktip reef shark densities may be caused by thermally insensitive physiological performances in this shark species (Bouyoucos *et al*., 2022), which is in contradiction with previously conducted thermal tolerance experiments (Bouyoucos, Watson, *et al*., 2020). Another cause might be the nursery-bound behavior displayed by juvenile *C. melanopterus* sharks that show sedentary behaviors during the first months of their life (Bouyoucos, Romain, *et al*., 2020), preventing them from reaching less thermally threatening areas. Moreover, the daily extremes in water temperature might be tempered by daily variation allowing juvenile sharks to recover. Indeed, stress-induced mortality in experimental conditions was measured in juvenile sharks acclimated to 33°C for 4 weeks. In Moorea lagoon, in situ sampled sharks were exposed to diurnal water temperature fluctuations (3.1 ± 2.39°C; caused by wind stress, tides, diurnal solar heating and cooling, waves, freshwater inflow from the river system) inducing density-driven water circulation in the lagoon (Hench *et al*., 2008) likely minimizing the exposure of juvenile sharks to 33°C waters. Instead of causing acute death and decrease in juvenile *C. melanopterus* CPUE, measured extreme water temperature events (above 31°C) might increase their stress levels forcing juvenile sharks to live at their maximal temperature tolerance level. Over time, such high-water temperature might decrease the ability of juvenile blacktip reef sharks to function by decreasing their ability to forage, grow (Weideli *et al*., 2019), and/or escape predators (Trujillo *et al*., 2022). Ongoing climate change will increase the frequency and duration of marine heatwaves that could result in water temperatures at or exceeding 31°C (Pörtner *et al*., 2022), which could therefore decrease juvenile blacktip reef shark survival and recruitment success to the adult shark population of Moorea.

*C. melanopterus* CPUE was higher in some of the sampling sites. The sites Haapiti and Vaiare had higher *C. melanopterus* CPUE from 2013 through 2023. Maternal reproductive behavior could be the origin of such disparities among the site-specific juvenile reef shark densities (Mourier & Planes, 2013). Previous research suggested that this species of sharks might be philopatric with female sharks coming back annually for parturition at the same sites (Mourier & Planes, 2013). Some sites might favor such behavior by having decreased anthropogenic disturbance during the parturition period, thus encouraging female sharks to use these areas. Natal philopatry, the return of female individuals for parturition in the areas in which they were born, might emphasize the density disparity among sites, and juvenile female shark survival might lead to the settlement of its future offspring in that same site. Adult female *N. acutidens* parturition bi-annually around the Island of Moorea (Mourier, Buray, *et al*., 2013) and might alter the parturition behavior of *C. melanopterus* females by preventing them to give birth in some coastal areas. Indeed, *N. acutidens* were found to be part of apex predators on coral reefs along other species such as *Galeocerdo cuvier*, *Sphyrna mokarran*, *Carcharhinus obscurus*, and *Carcharhinus albimarginatus* because of their larger size and higher trophic niche, possibly allowing them to exert a top-down control on mesopredator reef sharks such as *C. melanopterus* (Frisch *et al*., 2016). Apart from the adult interspecific competition for habitats, juvenile sharks likely display a different behavior than their elders. We found a significant trend that both juvenile *N. acutidens* CPUE and *C. melanopterus* CPUE increased jointly. The significance of this finding, an interspecific positive trend in density, is in accordance with previous research that identified interspecific competition resulting in niche partitioning promoting the coexistence between the two species around Moorea Island (Frisch *et al*., 2016). The correlation was limited, likely because *N. acutidens* juvenile sharks preferred mangrove- and silt-dominated areas (e.g., Apaura, Pihaena, Tiki, Vaiane), whereas *C. melanopterus* favor sand flats with coral heads (e.g., Haapiti, Maharepa, Papetoai, Pointe de Paorea, Vaiare, Valorie). The non-exclusivity in habitat partitioning observed around Moorea might originate from sufficient resources (decreased density in the habitats, sufficient food sources) present in the sampling areas that might decrease intraspecific competition (Shiffman *et al*., 2019). The disparities in sampling areas in juvenile *C. melanopterus* densities are likely a combination of habitat type and its resources, adult female reef shark reproduction behavior, and adult and juvenile interspecific competition for habitats and niche partitioning for resources.

In summary, we provide the first long-term study for *C. melanopterus*, a widely distributed tropical species of reef sharks. Two main sites were consistently identified as having the highest densities of juvenile blacktip reef sharks, underscoring the importance of prioritizing conservation strategies for *C. melanopterus* in critical habitats. Further research is required to determine the origins (e.g., female sharks repeatedly giving birth in some nurseries, interspecific competition, or habitat type and quality) of such density disparities. The interannual stability in *C. melanopterus* density along the past and at present nonexistent effect of water temperature are encouraging regarding the elasmobranch global anthropogenic disturbances-related decline. French Polynesia, along with other high-capacity nations such as the United States, Australia, or New Zealand, is actively managing its coastal shark species (Cardeñosa *et al*., 2022). The current shark management resources available to prevent shark poaching for the dried fin trade in high-capacity nation waters are encouraging but still limited (Cardeñosa *et al*., 2022). Indeed, datasets of time series of reef shark densities are urgently required on a global scale to improve and verify the efficiency of existing strategies and establish new management strategies.

## AUTHOR CONTRIBUTIONS

Conceptualization: Isabel Smallegange, Serge Planes, Kim B. Eustache, Jodie L. Rummer. Methodology: Kim B. Eustache, Emiel van Loon, Serge Planes, Jodie L. Rummer. Investigation: Kim B. Eustache, Emiel van Loon, Isabel Smallegange. Visualization: Kim B. Eustache, Emiel van Loon, Isabel Smallegange. Supervision: Kim B. Eustache, Emiel van Loon, Isabel Smallegange. Writing—original draft: Kim B. Eustache. Writing—review and editing: Kim B. Eustache, Emiel van Loon, Isabel Smallegange, Serge Planes, Jodie L. Rummer.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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