



# Green and hawksbill turtle detection and abundance at foraging grounds in Bonaire, Caribbean Netherlands

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**ABSTRACT:** Abundance estimates corrected for changes in detection are needed to assess population trends. We used transect-count surveys and *N*-mixture models to estimate green turtle *Chelonia mydas* and hawksbill turtle *Eretmochelys imbricata* detection and total abundance at foraging grounds in Bonaire during 2003–2018, and we used these total abundance estimates to fit a Bayesian state–space logistic model and make abundance predictions for 2019–2030. During 2019–2022, we also recorded distance categories to estimate detection and total abundance using distance sampling and *N*-mixture models. In the present study, we focus on distance sampling to estimate observer detectability and total abundance, and to determine if total abundance increased, declined, or did not change during 2019–2022 and when compared with 2003–2018 estimates and 2019–2030 predictions. Detectability averaged 0.53 (SE = 0.02) for green turtles and 0.51 (SE = 0.06) for hawksbill turtles. Density (ind. km<sup>-2</sup>) and population size (individuals in the 4 km<sup>2</sup> survey region) averaged 72.1 (SE = 17.3) and 288 (SE = 69) for green turtles and 21.8 (SE = 4.6) and 87 (SE = 18) for hawksbill turtles. Green turtle total abundance did not change during 2019–2022 ( $p > 0.05$ ) but remained low when compared with 2003–2018 estimates and 2019–2030 predictions. Hawksbill turtle total abundance declined between 2020 and 2021 ( $z = 2.15$ ,  $p = 0.03$ ) and increased between 2021 and 2022 ( $z = -3.04$ ,  $p = 0.002$ ), but 2019–2022 estimates were similar to 2003–2018 estimates and 2019–2030 predictions. Our methodology can be used to monitor sea turtle populations at coastal foraging grounds in the Caribbean.

**KEY WORDS:** *Chelonia mydas* · *Eretmochelys imbricata* · Density · Observer detectability · Population size · Distance sampling

## 1. INTRODUCTION

Sea turtles continue facing conservation threats from natural and anthropogenic disturbances, including habitat loss and degradation from climate change, development, and contamination (Pike et al. 2015, Fuentes et al. 2016, Bjorndal et al. 2017, Wallace et al. 2017, Arcangeli et al. 2019); nest depredation by invasive species (Engeman et al. 2019); and mortality from fishing bycatch, boat collisions, and

the harvesting of eggs, juveniles, and adults for subsistence or commercial purposes (Wallace et al. 2013, Humber et al. 2014, Lagueux et al. 2014, García-Cruz et al. 2015). For example, satellite tracking of sea turtles nesting at Bonaire and Klein Bonaire in the Caribbean Netherlands revealed migration distances of 197–3135 km to foraging grounds across the Caribbean (Becking et al. 2016), including the coastal waters of countries where harvesting still occurs (Humber et al. 2014, Lagueux et al. 2014, García-

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Cruz et al. 2015). Currently, in Bonaire and Klein Bonaire most lethal incidents are related to fishing, boating, and contamination, with poaching occurring infrequently (Sea Turtle Conservation Bonaire 2021). In response to these and other threats, Sea Turtle Conservation Bonaire has been conducting a wide variety of activities, including volunteer-based community outreach and education campaigns to increase awareness and participation in conservation efforts, as well as research and monitoring to better understand sea turtle population dynamics and the importance of nesting and foraging grounds locally and regionally (Becking et al. 2016, Bjorndal et al. 2017, Christianen et al. 2019, Rivera-Milán et al. 2019, van der Zee et al. 2019, Sea Turtle Conservation Bonaire 2021).

Long-term monitoring at nesting and foraging grounds is essential to assess sea turtle population trends (Dutton et al. 2005, Chaloupka et al. 2008, Saba et al. 2012, Lagueux et al. 2014, García-Cruz et al. 2015, Mazaris et al. 2017, Ceriani et al. 2019, Rivera-Milán et al. 2019). However, when monitoring sea turtle population trends, survey-based abundance estimates need to account for incomplete counts due to imperfect detection (Mazerolle et al. 2007, Pfaller et al. 2013, Strindberg et al. 2016, Ceriani et al. 2019, Rivera-Milán et al. 2019). Motivated by this need, research statisticians have developed methods to estimate detection and abundance and assess population trends (Burnham et al. 1980, 2004, Buckland et al. 2001, 2004, 2015, Marques & Buckland 2003, 2004, Thomas et al. 2004, Kéry & Royle 2016). For example, we used transect-count surveys and *N*-mixture models to estimate green turtle *Chelonia mydas* and hawksbill turtle *Eretmochelys imbricata* detection and total abundance (density or population size) at foraging grounds off the western coast of Bonaire and the entire coast of Klein Bonaire during 2003–2018, and we used these total abundance estimates to fit a Bayesian state-space logistic model and make abundance predictions for 2019–2030 (Rivera-Milán et al. 2019).

During the 2019–2022 transect-count surveys, we also recorded detections into 10 m distance categories to expand the analysis tool kit and estimate detection and total abundance using distance sampling and *N*-mixture models. Here, we focus on results from the application of conventional and multiple-covariate distance sampling (Buckland et al. 2001, 2004, 2015, Marques & Buckland 2003, 2004). Conventional and multiple-covariate distance sampling are ‘robust’ methods (sensu Burnham et al. 1980, 2004, Buckland et al. 2001, 2015) that com-

bine survey-based and model-based analytical approaches for parameter estimation (e.g. see Buckland et al. 2015, Chap. 5–8). Our main objective was to use distance sampling to estimate observer detectability and total abundance of green and hawksbill turtles in western Bonaire and Klein Bonaire, and to determine if total abundance increased, declined, or did not change during 2019–2022 and when compared with the 2003–2018 survey-based estimates and the 2019–2030 model-based predictions made by Rivera-Milán et al. (2019).

## 2. MATERIALS AND METHODS

### 2.1. Transect-count surveys

The survey region covered 4 km<sup>2</sup> between 12° 18' N, 68° 23' W and 12° 01' N, 68° 15' W (Fig. 1). It was characterised by a plateau with sand, rubble, and coral bottom substrates up to a depth of about 10 m, and a drop-off with mainly coral at a depth of

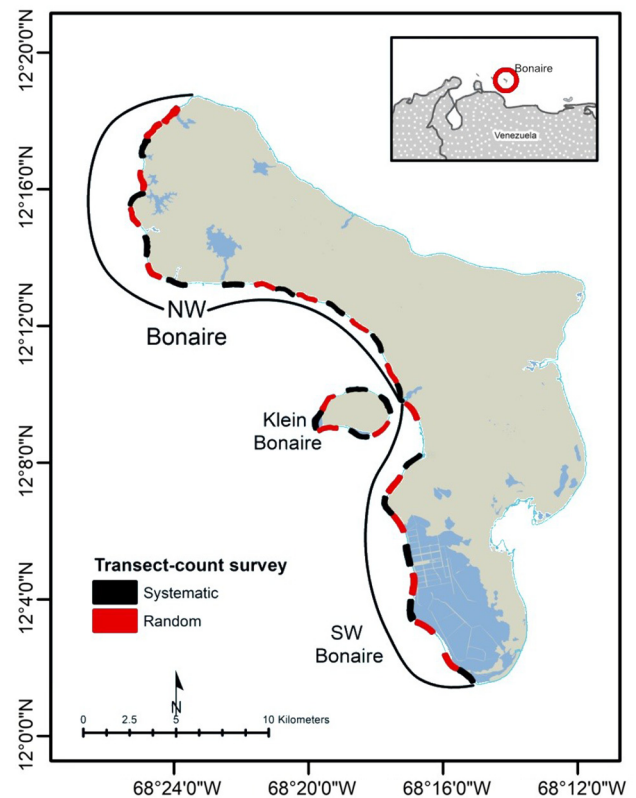


Fig. 1. Bonaire and Klein Bonaire, Caribbean Netherlands, showing the 4 km<sup>2</sup> survey region with thirty-six 1 km transects used to count green and hawksbill turtles during 2019–2022. The location of Bonaire and Klein Bonaire with respect to the northern coast of Venezuela is shown in the inset

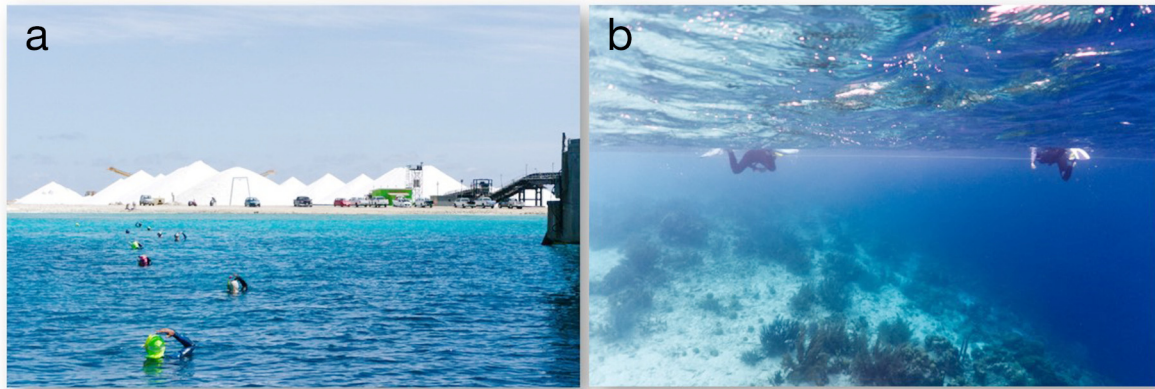


Fig. 2. (a) Observers using hand signals to start a standard transect-count survey and (b) a rope attached to their diving belts to demarcate the boundaries of 10 m distance categories

15–20 m (Fig. 2). We divided the survey region into the northwest and southwest coastal sections of Bonaire (1.75 and 1.57 km<sup>2</sup>, respectively) and the entire coast of Klein Bonaire (0.68 km<sup>2</sup>). We established eighteen 1 km transects with random starts and eighteen 1 km transects systematically with a minimum separation of 250 m between the nearest transects to secure representative coverage of the survey region (Fig. 1). The area covered by a transect averaged 0.11 km<sup>2</sup> (SD = 0.04, range = 0.05–0.19).

A standard survey lasted an average of 42 min per transect (SD = 8, range = 25–72). During a standard survey, the observers (mean = 9, SD = 1, range = 5–13) were positioned at a 90° angle and maintained a fixed distance of 10 m between each other using a marine-grade polyester rope attached to their diving belts (Fig. 2). That is, their positions along the fully extended rope were used to demarcate the boundaries of 10 m distance categories at each side of the transect centreline (Fig. 2a). The observer at the transect centreline coordinated the survey (e.g. swimming direction and pace, starting and finishing time). The observers snorkelled slowly parallel to the coast, covering the reef contour from the shallow water to the drop-off (Fig. 2b). Each one of them had a watch and an underwater slate for data recording. The observers maintained visual contact with each other and used standard hand signals for communication (Fig. 2a). The first observer that detected a sea turtle recorded the species, perceived size class (small [juvenile], medium [juvenile-subadult], large [adult]; see Table 1), behaviour at detection (resting, swimming, or feeding), detection time and movement direction, and distance category (0–10, 11–20, 21–30, 31–40, 41–50, 51–60 m). The most experienced observers were positioned at the boundaries of the 0–10 and 10–20 m distance categories to maximise

detection at, and maintain high detection near, the transect centreline (Buckland et al. 2001). In addition, when surveying a broad area between the shoreline and the drop-off (Fig. 2), we included the option of having or not having a free-swimming observer detached from the rope to cover the shallow water. The free-swimming observer kept the same direction and pace as the group of observers, keeping visual contact while snorkelling at about 10 m from the outermost observer attached to the rope. At the end of each survey, the observers met to check the data and, by consensus, correct any potential errors (e.g. double counts and distance category misallocations).

## 2.2. Distance sampling

Conventional and multiple-covariate distance sampling rely on fitting a detection function  $\hat{g}(y)$ , where the probability that an observer detects a sea turtle ( $\hat{P}_d$  or detectability hereafter) declines with perpendicular distance  $y$  from the transect centreline (Buckland et al. 2001, 2004, 2015). We modelled detectability as a function of  $y$  and covariates represented by vector  $\mathbf{z}$  (i.e.  $g[y, \mathbf{z}]$ ). We estimated density as

$$\hat{D} = \frac{n}{2wL\hat{P}_a\hat{P}_d(\mathbf{z}_i)} \quad (1)$$

where  $\hat{D}$  = the number of green or hawksbill turtles km<sup>-2</sup>,  $n$  = the number of detections of each species, and  $L$  = thirty-six 1 km transects and  $\hat{P}_a$  = green or hawksbill turtle availability for detection in the surveyed area. We conducted an exploratory analysis with the grouped distance data of each species separately before right truncation using the midpoints of 6 distance categories (i.e.  $w = 60$  m). Based on results

from the exploratory analysis (e.g. the trade-off between model fit, sample size  $n$ , and coefficient of variation [CV] of the density estimator; Buckland et al. 2001), we right truncated the grouped distance data of each species at  $w = 40$  m. We estimated detectability of green and hawksbill turtles within 40 m of the transect centreline as

$$\hat{P}_d(z_i) = \frac{1}{w} \int_0^w \hat{g}(x, z_i) dx \quad (2)$$

However, green and hawksbill turtle detection probability had 2 components, detectability and availability. For example, sea turtles may become unavailable for detection by hiding and remaining motionless inside crevices or under marine vegetation in response to the approaching observers. Repeated transect-count surveys allowed us to estimate both detection components using distance sampling ( $\hat{P}_d$ ) and  $N$ -mixture models ( $\hat{P}_{da}$ ). That is,  $\hat{P}_a = \hat{P}_{da}/\hat{P}_d$  (Rivera-Milán et al. 2019). During 2019–2022, availability within 40 m of the transect centreline averaged 0.58 (SE = 0.14) for the green turtle and 0.43 (SE = 0.13) for the hawksbill turtle. In separate analyses for each species and year, we included availability estimates and bootstrapped SEs as multipliers in the density estimator (Buckland et al. 2001, Thomas et al. 2010, Thomas & Marques 2012). Survey effort accounted for the length (1 km) and the number of visits per transect (1 in 2019 and 2021 and 3 in 2020 and 2022; Buckland et al. 2001).

For each species separately, we evaluated the fit of uniform, half-normal and hazard-rate key functions with and without cosine and polynomial series expansions using Pearson's  $\chi^2$  test ( $p < 0.05$ ; Buckland et al. 2001). We used Akaike's information criterion corrected for small sample sizes (AIC<sub>c</sub>) for model selection (Burnham & Anderson 2002). The half-normal and hazard-rate key functions with and without series expansions were used to assess the effects of covariates on detectability. We describe the covariates and expected effects on detectability in Table 1. In addition, we post-stratified the grouped distance data of each species by year, accounting for survey effort per stratum, and used the 2-tailed  $z$ -test ( $p < 0.05$ ; Buckland et al. 2001) to determine if total abundance increased, declined, or did not change during 2019–2022 and when compared with the 2003–2018 survey-based estimates and the 2019–2030 model-based predictions made by Rivera-Milán et al. (2019).

The basic assumptions of distance sampling were (1) the certain detection of individuals at the transect centreline, (2) detection at an initial location before responsive movement, (3) correct distance category

allocation, and (4) a representative survey scheme to justify abundance inferences from the surveyed area to the survey region (i.e. estimated population size  $\hat{N} = \hat{D} \times A$ , where  $A = 4$  km<sup>2</sup>). Regarding the first assumption, we consider it unlikely that, with the clear water conditions typical of Bonaire and Klein Bonaire (Fig. 2b), experienced observers positioned at the boundaries of the 0–10 and 10–20 m distance categories missed individuals that were available for detection at the transect centreline (i.e.  $g[0] = 1$ ). With respect to the second and third assumptions, the use of wide distance categories by observers snorkelling slowly at a 90° angle likely lessened any bias from undetected responsive movement and incorrect distance category allocation. Lastly, regarding the fourth assumption, we established thirty-six 1 km transects independently of green and hawksbill turtle distributions, and the random-systematic scheme provided representative coverage of foraging grounds in the 4 km<sup>2</sup> survey region. For the analyses, we used programs DISTANCE 7.4 release 2 (Thomas et al. 2010) and R ver. 4.2.0. (R Core Team 2022) with package DISTANCE ver. 1.0.5. (Miller et al. 2019). Results are presented as means and bootstrapped SEs with lognormal 95% confidence intervals (CIs) for total abundance estimates.

### 3. RESULTS

#### 3.1. Green turtle

During 2019–2022, we had 703 green turtle detections. Based on model fit ( $\chi^2 = 0.08$ ,  $df = 1$ ,  $p = 0.78$ ) and the precision of the density estimator (mean CV = 0.24, SE = 0.04), we selected the half-normal key function with 1 cosine series expansion for the green turtle grouped distance data (Fig. 3a). The half-normal key function with 1 cosine series expansion and free-swimming observer defined as a 2-level categorical covariate provided the best fit to the data (Table 2, Fig. 3b). However, the free-swimming observer covariate had a weak effect on detectability (i.e. beta coefficient  $\beta = 0.00005$ , SE = 0.11 for level 0 = absence; Fig. 3b). As a result, detectability averaged 0.51 (SE = 0.04) when a free swimmer was absent and 0.56 (SE = 0.05) when present. Overall, detectability (mean = 0.53, SE = 0.02) and availability (mean = 0.58, SE = 0.14) accounted for 7 and 64% of the variation in total abundance estimation. Encounter rate ( $n/L$ ) averaged 0.002 (SE = 0.0003) and accounted for 29% of the variation in total abundance estimation.

Table 1. Descriptions and expected effects of detectability covariates included in the multiple-covariate distance sampling analysis of green and hawksbill turtle transect-count surveys in western Bonaire and Klein Bonaire during 2019–2022

Covariate	Type	Description	Expected effect
Size class	Categorical, 2 levels (0 = small, 1 = medium-large)	Perceived size class: small (<50 cm, juvenile-subadult), medium (50–70 cm, juvenile-subadult), large (>70 cm, adult)	Small less detectable than medium-large
Behaviour	Categorical, 2 levels (0 = resting, 1 = feeding-swimming)	Behaviour at detection: resting (not moving), feeding or swimming (moving)	Resting less detectable than feeding-swimming
Month	Categorical, 2 levels (0 = Jan–Mar, 1 = Apr–Jul)	Temporal changes in detectability	Uncertain about direction and magnitude of effect
Year	Categorical, 4 levels (0 = 2019, 1 = 2020, 2 = 2021, 3 = 2022)	Temporal changes in detectability	Uncertain about direction and magnitude of effect
Coastal section	Categorical, 3 levels (0 = NW Bonaire, 1 = SW Bonaire, 2 = Klein Bonaire)	Spatial changes in detectability	Uncertain about direction and magnitude of effect
Bottom substrate	Categorical, 2 levels (0 = sand 1 = rubble-coral)	Spatial changes in detectability	More detectable in sand than rubble-coral
Bottom substrate	Continuous, km <sup>2</sup> ; range = 0–0.07 sand, 0.02–0.08 coral, 0.02–0.10 rubble	Transect centreline to 60 m on each side, measured at start, middle, and end	More detectable in sand than rubble-coral
Transect area	Continuous, km <sup>2</sup> ; range = 0.05–0.19	Shoreline to drop-off, measured at transect start, middle, and end	Detectability decreasing with area
Starting time	Continuous, hr:min; range per survey = 08:31–14:30	Observers ready to start count (e.g. see Fig. 2a)	Uncertain about direction and magnitude of effect
Duration time	Continuous, min; range per survey = 25–72	Time elapsed between survey start and end	Uncertain about direction and magnitude of effect
No. of observers	Continuous, range per survey = 5–13	Observers positioned at 10 m distance categories (e.g. see Fig. 2a,b)	Detectability increasing with observers
Experience index	Continuous, range of mean per survey = 1.6–3	0 = low (first time), 1 = medium (more than once but infrequent), 2 = high (many times, frequent)	Detectability increasing with experience
Free-swimming observer	Categorical, 2 levels (0 = absent, 1 = present)	Detached from the rope to cover shallow water in broad areas	Detectability higher with presence than absence
No. of boats	Continuous, range per survey = 0–67	Boats at or near the transect	Detectability decreasing with boats (disturbance)
No. of divers	Continuous, range per survey = 0–31	Divers at or near the transect	Detectability decreasing with divers (disturbance)

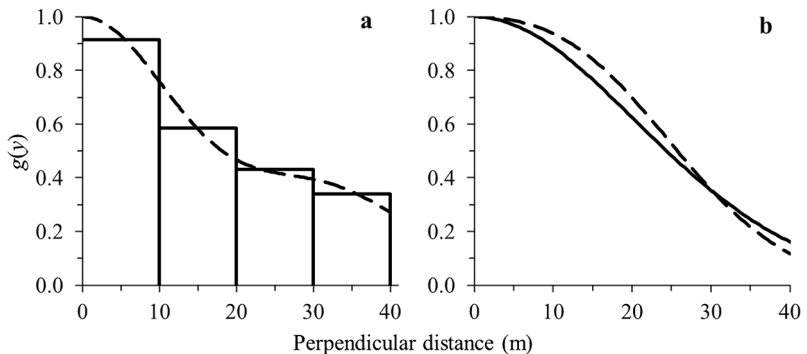


Fig. 3. (a) Observer detectability based on the half-normal key function with 1 cosine series expansion and (b) the effect of free-swimming observer defined as a 2-level categorical covariate (dashed line for presence and solid line for absence) for green turtles in western Bonaire and Klein Bonaire during the 2019–2022 transect-count surveys. Distance data right truncated at  $w = 40$  m

Table 2. Small-sample size Akaike’s information criterion values and differences for the top 5 ranked distance sampling detectability models of green and hawksbill turtles in western Bonaire and Klein Bonaire during the 2019–2022 transect-count surveys. Distance data right truncated at  $w = 40$  m. For additional information about model formulation, see Buckland et al. (2001, 2004, 2015) and Marques & Buckland (2003, 2004). For additional information about covariates, see Table 1

Key function	Series	Covariates	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Parameters
<b>Green turtle</b>					
Half-normal <sup>a</sup>	1 cosine	Free swimmer <sup>b</sup>	1622.41	0.00	3
Half-normal	1 cosine	Month	1630.45	8.05	3
Half-normal	1 cosine	Behaviour	1642.81	20.40	3
Half-normal	1 cosine	Year	1669.05	46.65	5
Half-normal	1 cosine	Size	1695.84	73.43	3
<b>Hawksbill turtle</b>					
Half-normal <sup>c</sup>	None	Month <sup>d</sup>	110.30	0.00	2
Half-normal	None	Free swimmer	114.95	4.64	2
Half-normal	None	Year	120.17	9.86	4
Half-normal	None	Rubble	125.29	14.99	2
Half-normal	None	Behaviour	126.97	16.67	2

<sup>a</sup>AIC<sub>c</sub> = 1793.13 for the half-normal key function with 1 cosine series expansion and without covariates (Fig. 3a)  
<sup>b</sup>For graphic representation, see Fig. 3b  
<sup>c</sup>AIC<sub>c</sub> = 128.87 for the half-normal key function without series expansion and without covariates (Fig. 4a)  
<sup>d</sup>For graphic representation, see Fig. 4b

Green turtle density (ind. km<sup>-2</sup>) and population size (individuals in the 4 km<sup>2</sup> survey region) averaged 72.1 (SE = 17.3, 95% CI = 45.3, 114.5) and 288 (SE = 69, 95% CI = 181, 458) during 2019–2022 (Table 3). Total abundance did not differ during 2019–2022 (2-tailed z-test range = 1.16–1.56, p-value range = 0.12–0.25; Table 3), and did not differ but remained low when compared with the 2003–2018 survey-based estimates (e.g. population size mean = 555, SE = 149, 95% CI = 337–943;  $z = 1.63$ ,  $p = 0.10$ ) and the 2019–2030 model-based predictions (e.g. population size mean = 430, Markov chain Monte Carlo SD = 179, 95% Bayesian confidence interval [BCI] = 177–821;  $z = 0.74$ ,  $p = 0.46$ ) made by Rivera-Milán et al. (2019; see their Table 5, Figs. 2 & 3). Distance sampling and  $N$ -mixture models generated similar total abundance estimates for the green turtle. For example, based on  $N$ -mixture models, density averaged 80.8 (SE = 17.3, 95% CI = 53.0–121.5) and population size averaged 323 (SE = 69, 95% CI = 212–486) during 2019–2022.

### 3.2. Hawksbill turtle

During 2019–2022, we had 56 hawksbill turtle detections. Based on model fit ( $\chi^2 = 0.29$ ,  $df = 2$ ,  $p = 0.87$ ) and the precision of the density estimator (mean CV = 0.46, SE = 0.04), we selected the half-normal key function without series expansion for the hawksbill turtle grouped distance data (Fig. 4a). The half-normal key function without series expansion and month defined as a 2-level categorical covariate provided the best fit to the data (Table 2, Fig. 4b). Covariate month had a moderate effect on detectability (i.e.  $\beta = -0.70$ , SE = 0.40 for level 0 = January–March; Fig. 4b). As a result, detectability averaged 0.42 (SE = 0.06) in January–March and 0.73 (SE = 0.10) in April–July. Overall, detectability (mean = 0.51, SE = 0.06) and availability (mean = 0.43, SE = 0.13) accounted for 11 and 54% of the variation in total abundance estimation. Encounter rate averaged 0.0002 (SE = 0.00004) and accounted for 34% of the variation in

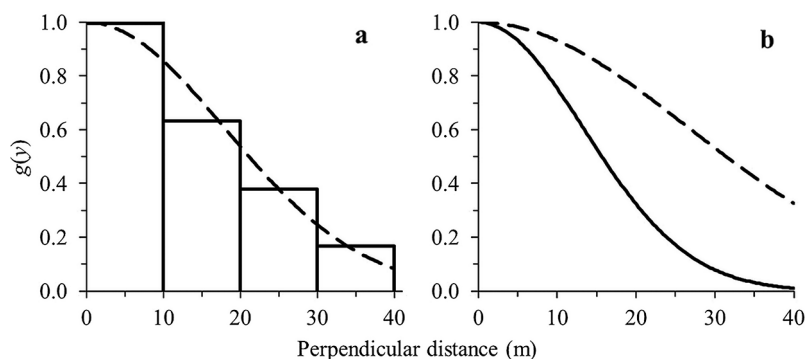
total abundance estimation.

Hawksbill turtle density (ind. km<sup>-2</sup>) and population size (individuals in the 4 km<sup>2</sup> survey region) averaged 21.8 (SE = 4.6, 95% CI = 14.5–32.8) and 87 (SE = 18, 95% CI = 58–130.0). Total abundance declined between 2020 and 2021 ( $z = 2.15$ ,  $p = 0.03$ ) and

Table 3. Distance sampling estimates of density (ind. km<sup>-2</sup>) and population size (individuals in the 4 km<sup>2</sup> survey region) with bootstrapped standard errors and 95% confidence intervals for green and hawksbill turtles in western Bonaire and Klein Bonaire during the 2019–2022 transect-count surveys. Distance data right truncated at  $w = 40$  m and post-stratified by year, with the half-normal key function with 1 cosine series expansion used for the green turtle (Fig. 3a) and the half-normal key function without series expansion used for the hawksbill turtle (Fig. 4a)

Year	$\hat{D}$	SE	95% CI	$\hat{N}$	SE	95% CI
<b>Green turtle</b>						
2019	82.8	26.8	44.5–153.5	331	107	178–614
2020	80.3	12.8	59.0–109.3	321	51	236–437
2021	50.3	14.3	29.2–86.7	201	57	117–347
2022	74.8	15.5	50.0–111.7	299	62	200–447
<b>Hawksbill turtle</b>						
2019	10.0	7.0	3.0–34.5	40	28	12–138
2020	32.0	11.0	16.7–61.5	128	44	67–246
2021	7.0	3.8	2.7–18.7	28	15	11–75
2022	38.0	9.5	23.5–61.5	152	38	94–246

Fig. 4. (a) Observer detectability based on the half-normal key function without series expansion (dashed line) and (b) the effect of month defined as a 2-level categorical covariate (dashed line for April–July and solid line for January–March) for hawksbill turtles in western Bonaire and Klein Bonaire during the 2019–2022 transect-count surveys. Distance data right truncated at  $w = 40$  m



increased between 2021 and 2022 ( $z = -3.04$ ,  $p = 0.002$ ), but the 2019–2022 estimates were similar to the 2003–2018 survey-based estimates (e.g. population size mean = 70, SE = 13, 95 % CI = 49–107) and the 2019–2030 model-based predictions (e.g. population size mean = 95, SD = 47, 95 % BCI = 34–214) made by Rivera-Milán et al. (2019; see their Table 5, Figs. 2 & 3). Distance sampling and  $N$ -mixture models generated similar total abundance estimates for the hawksbill turtle. For example, based on  $N$ -mixture models, population size averaged 86 (SE = 19, 95 % CI = 57–131) during 2019–2022.

#### 4. DISCUSSION

Conventional and multiple-covariate distance sampling provided useful alternatives for estimating detectability and total abundance of green and hawksbill turtles and monitoring the 2 species at foraging grounds in western Bonaire and Klein Bonaire during 2019–2022. For example, conventional distance sampling allowed post-stratification of the grouped distance data of each species by year to estimate detectability globally and total abundance per stratum (Buckland et al. 2001). The use of a global detectability function after post-stratification by year was particularly useful for the hawksbill turtle, which had a sample size of 56 detections during 2019–2022. Buckland et al. (2001) recommended a minimum sample size of 60–80 detections for reliable modelling of the detectability function in transect-count surveys. However, the sample size required depends on data quality to meet basic method assumptions (e.g.  $g[0] = 1$ ) and maintain desirable modelling properties (e.g. the so-called ‘shape criterion’, which states that the model should have a ‘shoulder’ reflecting high detectability near the transect centreline; Buckland et al. 2001, 2015). The sample sizes and grouped distance data of the green and hawksbill

turtles were adequate for modelling their detectability functions globally after post-stratification by year using the half-normal key function with 1 cosine series expansion (Fig. 3a) and the half-normal key function without series expansion (Fig. 4a). For the green turtle ( $n = 703$ ), detectability averaged 0.92 (SD = 0.085, range = 0.76–1.00) within 0–10 m and 0.60 (SD = 0.10, range = 0.47–0.76) within 10–20 m of the transect centreline (Fig. 3a). For the hawksbill turtle ( $n = 56$ ), detectability averaged 0.95 (SD = 0.05, range = 0.86–1.00) within 0–10 m and 0.70 (SD = 0.11, range = 0.55–0.86) within 10–20 m of the transect centreline (Fig. 4a).

Multiple-covariate distance sampling allowed us to explore the effects of categorical and continuous covariates on detectability (Table 1). Contrary to what we expected with respect to the effects of covariates such as perceived size class, bottom substrate, and observer experience (Table 1), free-swimming observer and month were the only ones supported by the data (Table 2, Figs. 3b & 4b). However, free-swimming observer had a weak effect on the detectability of green turtles (Fig. 3b) and month had a moderate effect on the detectability of hawksbill turtles (Fig. 4b). As a result, the proportion of total abundance variance that came from detectability was small (7–11 %) in comparison with encounter rate (29–34 %) and availability (54–64 %). Although the effect on detectability was weak, we suggest that the presence of a free-swimming observer allowed the other observers to better concentrate on detecting green turtles at or near the boundaries of the 10 m distance categories in which they were positioned along the rope. Free-swimming observer was the second-ranking covariate for hawksbill turtles, although  $\Delta\text{AIC}_c = 4.64$  (Table 2), suggesting considerably less support from the data (Burnham & Anderson 2002). Regarding the moderate effect of month, it is possible that the detectability of hawksbill turtles increased between January–March and April–July

because of the onset of the nesting season (April–December) and an increase in the presence and availability of large females in the 4 km<sup>2</sup> survey region. Month was the second-ranking covariate for green turtles, although  $\Delta AIC_c = 8.05$  (Table 2), suggesting much less support from the data (Burnham & Anderson 2002). For the other covariates (Tables 1 & 2),  $\Delta AIC_c \geq 9.86$ , suggesting essentially no support from the data (Burnham & Anderson 2002). For future analyses, we can divide survey effort per 1 km transect into ten 100 m segments and use more advanced model-based methods to explore the effects of covariates on transect-level abundance, detectability, availability, and encounter probabilities in repeated transect-count surveys (e.g. see Buckland et al. 2015 and Kéry & Royle 2016, Chap. 6–9).

Green turtles were more abundant than hawksbill turtles in the 4 km<sup>2</sup> survey region (see Rivera-Milán et al. 2019, their Table 5, and Table 3 of the present study), and total abundance estimates were more precise for the former than the latter due to sample size differences ( $n = 703$  vs. 56 detections), higher variation in the estimates of availability (mean CV = 0.24 vs. 0.30), and encounter rate (mean CV = 0.10 vs. 0.24). Green turtle total abundance did not differ during 2019–2022 (Table 3) and did not differ but remained low when compared with the 2003–2018 survey-based estimates and the 2019–2030 model-based predictions made by Rivera-Milán et al. (2019). Hawksbill turtle total abundance declined between 2020–2021 and increased between 2021 and 2022 (Table 3) but the 2019–2022 estimates were similar to the 2003–2018 estimates and the 2019–2030 predictions (Rivera-Milán et al. 2019). More question-driven research and monitoring are needed to better understand the biotic and abiotic factors behind the total abundance differences between green and hawksbill turtles and their annual fluctuations and long-term trends in the survey region; for example, using satellite images and tracking resident individuals of both species to obtain accurate location and bottom substrate data and also to determine their movement patterns and foraging preferences in the survey region (see Cuevas et al. 2007, Christiansen et al. 2019).

Our density estimates (Table 3) were within the range of density estimates reported by other researchers (León & Diez 1999, Diez & van Dam 2002, Cuevas et al. 2007, Strindberg et al. 2016, Welsh & Mansfield 2022). For example, our green turtle density estimates were similar to those

reported by Welsh & Mansfield (2022) for the Eastern Quicksands at the southernmost tip of Florida Keys in the USA but were lower than those reported by Strindberg et al. (2016) for Glover's Reef Atoll in Belize, where the hawksbill turtle had the highest density. Welsh & Mansfield (2022) and Strindberg et al. (2016) also used transect-count surveys, but the former used mark-recapture distance sampling and density surface modelling and the latter used conventional distance sampling (Buckland et al. 2015). Strindberg et al.'s (2016) hawksbill turtle density estimates were similar to our green turtle density estimates. In addition, our hawksbill density estimates were similar to those reported by León & Diez (1999) for the Dominican Republic, Diez & van Dam (2002) for Mona and Monito islands in Puerto Rico, and Cuevas et al. (2007) for the Yucatan Peninsula in Mexico. However, León & Diez (1999), Diez & van Dam (2002), and Cuevas et al. (2007) did not account for imperfect detection and may have underestimated density from incomplete counts (Buckland et al. 2001, 2004, 2015, Mazerolle et al. 2007, Kéry & Royle 2016, Strindberg et al. 2016, Rivera-Milán et al. 2019). Underlining the importance of accounting for detection when estimating total abundance, hawksbill turtles in western Bonaire and Klein Bonaire (Fig. 4b) were less detectable in January–March (mean = 0.42, SE = 0.06) than in April–July (mean = 0.73, SE = 0.10). However, green turtle detectability did not change much between January–March (mean = 0.52, SE = 0.04) and April–July (mean = 0.55, SE = 0.05).

Lastly, based on our results (e.g. similar total abundance estimates using *N*-mixture models, which do not rely on distance measurements), we suggest that any violations of distance sampling basic assumptions were negligible, and that reliable detection and total abundance estimates were obtained for monitoring green and hawksbill turtle population trends at foraging grounds in western Bonaire and Klein Bonaire. Total abundance estimates, based on distance sampling and *N*-mixture models, can also be used to model the population dynamics of both species, accounting for observation error (e.g. due to imperfect detection) and process variance (e.g. due to an incomplete understanding of foraging ecology), as well as uncertainty from annual mortality rates (e.g. due to anthropogenic disturbances; Rivera-Milán et al. 2019). The methodology implemented here has been used elsewhere (Strindberg et al. 2016) and can be useful for monitoring sea turtle population trends at coastal foraging grounds in the Caribbean.



**Acknowledgements.** We thank the STCB volunteers and interns for their dedication and assistance with fieldwork. Special thanks to the Field Specialist Gielmon 'Funchi' Egbreghts. Our gratitude to the Dutch Ministry of Agriculture, Nature, and Food Quality, and to World Wildlife Fund-Netherlands, Stichting DierenLot, and all the donors that have supported STCB's activities since 1991.

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*Editorial responsibility: Paolo Casale,  
Pisa, Italy*

*Reviewed by: R. Welsh and 2 anonymous referees*

*Submitted: August 2, 2022*

*Accepted: May 8, 2023*

*Proofs received from author(s): June 23, 2023*