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Assessing temporal and spatial patterns in habitat use of green sea turtles (*Chelonia mydas*) in Pearl Harbor, Hawaii

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Abstract

Assessing presence and habitat use of sea turtles within foraging grounds provides valuable information for managing both populations and regions. Availability of food sources and several environmental factors can influence sea turtle abundance and distribution in given regions. Distribution of green turtles (*Chelonia mydas*) in the Hawaiian Archipelago is determined by the presence of suitable foraging, breeding, and resting habitats. Hawaiian green turtles comprise a distinct subpopulation, which settle in foraging grounds around the Main Hawaiian Islands in between reproductive migrations to their main rookeries, situated on the Northwest Hawaiian Islands. Population structure of green turtles foraging aggregations found on the Main Hawaiian Islands is comprised of juvenile turtles measuring from 35cm in straight-line carapace length (SCL) to adult turtles larger than 81cm SCL. Pearl Harbor is a landlocked estuary with restricted public access situated on Oahu, one of the Main Hawaiian Islands. In this study we aimed to assess temporal and spatial patterns in habitat use of green turtles in Pearl Harbor. From March 2000 to May 2011, linear dive transects to survey for sea turtles were performed in Pearl Harbor; the Harbor and the Entrance Channel were divided into 21 specific areas. Divers recorded the number of turtles sighted per transect, qualitative sighting data on sea turtle species such as behaviour and size, and environmental predictors during the transects. Marine environment of the sampled locations was characterized to the maximum extent, using both direct observations from the time-period considered and current data. We applied a Hierarchical Generalized Additive Model with a Zero-Inflated Poisson distribution to model turtle sightings as a function of temporal and environmental predictors. We found a general increase in turtle records along the time-period examined and a non- uniform distribution of green turtles in Pearl Harbor. The increase and spatial distribution found reflect conservation efforts to the Hawaiian subpopulation and quality of habitats found in Pearl Harbor Entrance Channel. Entrance Channel locations provided resting habitat, having relatively higher macroalgae and coral cover, underwater caves, and seagrass present. The lower number of turtles detected within the harbor is probably a combination of two factors: a true absence of turtles in this region and a failure in turtle detection caused by poor visibility conditions. We found seasonality to the presence of green turtles, with a slight decrease in turtle sightings during the early months of the year. Size distribution encountered followed the patterns observed on other Hawaiian Main Islands, with a prevalence of individuals ranging from 50cm to 1.0m SCL sighted in transects. We found turtles from the three size-categories to have distinct preferences regarding depths they occupy. Smaller turtles were sighted in transects at shallower sites and larger individuals on deeper locations. Our study allowed to reconstruct green turtle past use of an historic location such as Pearl Harbor, over ten years of sampling, and identified significant resting habitat within the landscape. We hope these results will ultimately provide useful information for managing turtle populations which use Pearl Harbor and contribute to the extensive knowledge on the ecology of Hawaiian green turtles.

Keywords: Green turtle; Direct in-water observations; Distribution modelling; Behaviour; Resting; Pearl Harbor

Resumo

As tartarugas marinhas (superfamília Chelonioidea) são um grupo de 7 espécies de répteis, cujas populações se encontram ameaçadas. A sistemática sobre-exploração levou ao desaparecimento de muitas populações de tartarugas marinhas. Contudo, após intensos esforços de conservação aplicados, algumas populações encontram-se atualmente a recuperar. É fundamental determinar o uso de recursos por parte destas populações em recuperação, uma vez que as tendências populacionais observadas em tartarugas marinhas são reguladas por mecanismos ambientais como a disponibilidade de recursos. A disponibilidade de recursos como fontes de alimento e diversos fatores ambientais, influenciam a abundância de tartarugas marinhas em determinadas regiões e, como tal, a sua distribuição espácio-temporal. Fortemente correlacionados com a disponibilidade de recursos, fatores ambientais como a temperatura da água e o tipo de substrato são responsáveis pela distribuição das áreas de alimentação das tartarugas marinhas e, consequentemente, pela distribuição destes animais em determinadas regiões.

No Arquipélago do Havai, a tartaruga-verde (*Chelonia mydas*) é a espécie de tartaruga marinha mais frequentemente observada. As tartarugas verdes havaianas constituem uma subpopulação geográfica e geneticamente isolada, que foi alvo de intensas medidas de conservação, e encontra-se atualmente com estatuto de conservação Pouco Preocupante. A distribuição da tartaruga-verde no Arquipélago do Havai é determinada pela presença de áreas apropriadas para a sua alimentação, repouso e reprodução. Esta subpopulação habita águas costeiras em redor das principais ilhas havaianas entre migrações efetuadas para as suas áreas de reprodução, situadas em ilhas do noroeste do Arquipélago.

Pearl Harbor é um estuário situado em *Oahu*, uma das principais ilhas havaianas, situadas a sudeste do Arquipélago. Este local, famoso pelas piores razões durante a segunda Guerra Mundial, é um porto estratégico para a Marinha dos Estados Unidos e, como tal, é exigida uma monitorização regular dos recursos naturais presentes em *Pearl Harbor* pela *Sikes Act*. Os recursos presentes devem ser elencados num Plano de Gestão Integrada de Recursos Naturais. Este plano deve ser aprovado por agências nacionais responsáveis pela investigação, gestão e recuperação das populações de tartarugas marinhas sob a jurisdição dos Estados Unidos.

O nosso estudo tem como objetivos determinar padrões temporais e espaciais no uso de *habitat* pelas tartarugas-verdes avistadas em *Pearl Harbor* e determinar a estrutura populacional das mesmas, ao longo de 10 anos de monitorização. Para o primeiro objetivo, foram investigadas tendências anuais nos avistamentos de tartaruga em áreas distintas de *Pearl Harbor* e dados qualitativos relativos ao comportamento das tartarugas encontradas. Inerente a este objetivo, pretendemos avaliar se existe sazonalidade na presença das tartarugas nesta região, comparando o número de avistamentos entre duas estações gerais no Havai, a fresca (de Novembro a Abril) e a quente (de Maio a Outubro). Relativamente ao segundo objetivo, pretendemos determinar a estrutura populacional das tartarugas observadas, com algumas limitações, através de estimativas visuais do comprimento da carapaça das tartarugas.

Para este estudo, *Pearl Harbor* e o Canal de Entrada de *Pearl Harbor* foram subdivididos em 21 áreas específicas. De Março de 2000 a Maio de 2011, monitorizações subaquáticas seguindo uma metodologia de transectos lineares ocorreram em *Pearl Harbor* várias vezes ao longo do ano. Os transectos foram realizados por mergulhadores, com um circuito aberto SCUBA, e conduzidos por cientistas da Marinha. Ao longo dos transectos, foram registados número e espécie das tartarugas marinhas observadas e variáveis oceanográficas como a profundidade e a visibilidade. Durante os avistamentos, os mergulhadores estimaram visualmente o comprimento da carapaça em linha reta (SCL) das tartarugas, possibilitando a inclusão de cada indivíduo numa de três classes de tamanho: indivíduos até 50cm SCL; indivíduos desde 50cm até 1.0m SCL e indivíduos com comprimento superior a 1.0m. A temperatura da superfície do mar foi recolhida remotamente para cada uma das áreas amostradas para o período de

tempo examinado, com a mais fina resolução espacial possível, tendo sido associadas temperaturas médias mensais a cada um dos transectos desde 2002 até 2011. Para uma caracterização concisa do tipo de cobertura bentónica das zonas amostradas, recorremos às observações diretas do ambiente marinho durante os transectos e também a monitorizações relativamente mais recentes dos recursos marinhos nesta região.

Para a modelação dos avistamentos de tartaruga ao longo de 10 anos de monitorização, usámos um modelo aditivo generalizado hierárquico (HGAM) com uma distribuição *Poisson* zero-inflacionada. Este foi utilizado para determinar as relações não lineares entre o número de tartarugas observadas por transecto e variáveis temporais, ano e mês, e ambientais, profundidade, visibilidade e temperatura da superfície da água. O comprimento do transecto foi usado como termo *offset*, para ter em conta o esforço de amostragem não-constante, e as 21 áreas amostradas foram designadas como efeito aleatório no modelo, permitindo assim incorporar variações não explicadas pelas outras variáveis específicas de cada área. Com as predições do modelo escolhido, foi possível construir um perfil de distribuição espacial das tartarugas em *Pearl Harbor*. Relativamente à análise dos dados qualitativos, recorremos ao teste Qui-quadrado para determinar diferenças nos comportamentos observados entre áreas amostradas, e ao teste *Kruskal-Wallis* para determinar a existência de diferenças entre as três classes de tamanho relativamente à profundidade a que foram observadas.

Entre 2000 e 2011 foi avistado um total de 680 tartarugas marinhas. Do total de avistamentos, 679 eram tartarugas-verdes e apenas uma tartaruga-de-pente (*Eretmochelys imbricata*) foi positivamente identificada. Os avistamentos de tartaruga-verde ocorreram em 121 transectos (26%), enquanto os restantes 343 transectos tiveram zero avistamentos (n=464). A frequência da presença de tartarugas em transectos variou entre os locais amostrados, tendo esta sido relativamente superior em áreas localizadas no Canal de Entrada. Dentro do porto, verificámos uma presença relativamente menor e, em algumas áreas, não foram avistadas tartarugas durante o período de tempo examinado. Relativamente aos resultados do modelo, considerando um nível de significância de 5%, todas as variáveis à exceção da profundidade influenciaram o número de avistamentos de tartaruga por transecto. Verificámos um aumento generalizado do número de tartarugas-verdes observadas ao longo do tempo, para todas as áreas combinadas. Observámos uma diminuição do número de tartarugas observadas nos primeiros meses do ano. O número de tartarugas observadas aumentou, não surpreendentemente, com o aumento da visibilidade. Relativamente à variável temperatura, observámos dois picos associados com um maior número de tartarugas avistadas, o primeiro entre os 24ºC e os 25ºC e o segundo pico aos 26.5ºC.
Relativamente aos dados qualitativos, encontrámos dois comportamentos dominantes exibidos pelas tartarugas avistadas em transectos, nadar e repousar. Através das observações diretas, verificámos que locais para repouso incluíram abrigo como caves submersas na região do canal de Entrada. Nenhuma tartaruga foi observada a alimentar-se. Indivíduos entre os 50cm e 1.0m SCL foram os mais frequentemente observados e, tartarugas superiores a 1.0m SCL foram também relativamente abundantes nos transectos efetuados. Verificámos uma segregação das tartarugas por tamanho quanto à profundidade a que foram observadas em que, a profundidades superiores, foram avistados indivíduos de maiores dimensões.

As tartarugas-verdes encontram-se distribuídas de forma não-uniforme em *Pearl Harbor*. O aumento observado no número de avistamentos de tartaruga por transecto pode ser devido à crescente tendência populacional observada na tartaruga-verde havaiana. A presença de elementos atrativos para repouso, nomeadamente elementos usados como refúgio no Canal de Entrada, pode também ter levado à mais frequente presença de tartarugas nesta zona. Duas áreas forneceram importantes locais de repouso para as tartarugas-verdes, confirmado pelas observações diretas do uso de *habitat* e um número constante de tartarugas observadas em transectos ao longo dos anos. No entanto, os métodos usados no nosso estudo

não permitem avaliar a fidelidade das tartarugas-verdes a estas áreas nem quantificar a disponibilidade de alimento e/ou abrigo em cada uma delas.
Consideramos que o baixo número de tartarugas detetadas em transectos dentro do porto pode ter duas origens. A verdadeira ausência das tartarugas nesta zona poderá ser uma das origens. A relativamente menor disponibilidade de alimento e elementos usados para repouso dentro do porto pode levar ao menor uso desta zona pelas tartarugas, que parecem usar maioritariamente algumas áreas do Canal de Entrada, onde a abundância destes recursos pode ser relativamente superior. A segunda explicação poderá estar relacionada com falsos zeros, isto é, as tartarugas estavam presentes durante as monitorizações efetuadas, mas não foram detetadas pelos mergulhadores devido às más condições de visibilidade dentro do porto.
Relativamente à sazonalidade encontrada na presença das tartarugas, o menor número de avistamentos nos primeiros meses do ano poderá estar relacionado com a migração reprodutiva da tartaruga-verde havaiana para ilhas a noroeste do Arquipélago.
A distribuição das tartarugas por tamanho observada está de acordo com o que já tinha sido encontrado em outras áreas de alimentação da tartaruga-verde havaiana, e também com o tamanho mínimo conhecido a partir do qual se dá o recrutamento de juvenis para áreas de alimentação.
O presente estudo permitiu determinar padrões temporais e espaciais de uso de *habitat* das tartarugas-verdes, ao longo de 10 anos de monitorização. Este tipo de informação é essencial para a gestão dos recursos naturais, em particular das populações de tartarugas marinhas, a uma escala local por parte da Marinha. Em última análise, os nossos resultados contribuíram para o amplo conhecimento existente acerca da ecologia da tartaruga-verde havaiana e para a sua conservação.

Palavras-chave: Tartaruga-verde; Áreas de repouso; Comportamento; Modelação; Observações diretas; *Pearl Harbor*

Table of Contents

1. Introduction 1
2. Methods 5
   2.1. Study site 5
   2.2. Study design 5
   2.3. Characterization of the sampled locations 8
   2.4. Data collected 8
      2.4.1. Turtle sampling 8
      2.4.2. Environmental covariates 8
   2.5. Statistical analysis 10
3. Results 12
   3.1. Environmental setting 12
   3.2. Turtle species found 14
   3.3. Turtle sampling presence 14
   3.4. Turtle sightings modeling 15
      3.4.1. Annual trends 16
      3.4.2. Seasonal patterns and environmental associations 17
      3.4.3. Model predictions 18
   3.2. Qualitative observations: behaviour and size-class distribution 20
4. Discussion 23
   4.1. Spatio-temporal distribution of green turtles 23
      4.1.1. Annual trends, habitat associations and behaviours 23
      4.1.2. Sources of zero observations 25
      4.1.3. Seasonal patterns and environmental associations 26
   4.2. Size-class distribution and depth preferences 27
   4.3. Suggestions for future improvement and final considerations 28
5. References 29
6. Supplementary Material 35

Table Index

Table 2.1 - Temporal and environmental covariates collected during survey transects (2000-2011) and remotely (2002-2011)........ 9

Table 3.1 - **Description of the benthic habitats where survey transects occurred at Pearl Harbor, 2000-2011**. CCA = Crustose Coralline Algae. Percentages in each cell represent an average of the percent cover of the mosaics inside each location. Mosaics in Source column refer to orthomosaic images built in Wells et al. 2020b). Photographs were processed by the scientists and used to produce a continuous high-resolution orthomosaic scaled image of each location. On each orthomosaic, 100 points were gridded, benthic cover types underlying the gridded points were identified and percent cover of all surface types was obtained (Wells et al. 2020b). NA – Information is not available. 13

Table 3.2 - Number of survey transects performed in each month and year in Pearl Harbor, 2000-2011 14

Table 3.3 - **ZIP-HGAM model results for sea turtle sightings in Pearl Harbor, 2000-2011.** The model covariates and values for effective degrees of freedom (edf), Chi-square ($X2$) and p-values are shown. Model presented a deviance explained of 78.6%. Shaded rows correspond to variables or interaction terms statistically significant considering 5% as the significance level. 16

Table 3.4 - **Summary table of green turtle behaviours by sampling location and region in Pearl Harbor, 2000-2011**. Additional observations concerning resting features and particular observations are listed. Total number of turtles observed per location (n) is shown. {-} means no behaviours were observed given the fact no turtles were observed. 20

Figure Index

Figure 2.1 – **a)** Satellite image of the Hawaiian Archipelago with Oahu, one of the Main Hawaiian Islands, illustrated; **b)** Satellite image of the island of Oahu, showing the location of the study: Pearl Harbor.. 6

Figure 2.2. - Satellite image of Pearl Harbor, Oahu, with the numbered locations where survey transects occurred between 2000 and 2011. 7

Figure 3.1 - Frequency distribution of sea turtles sighted per transect in Pearl Harbor, 2000-2011..... 15

Figure 3.2 – **Proportion of transects where at least one turtle was sighted per sampling location, in Pearl Harbor, 2000-2011**. Numbers above frequency bars represent total transects performed per locations during the time-period examined. Entrance Channel Locations: 1-5 and 17-21. Locations inside the harbor: 6-16.. 15

Figure 3.3 - **Response curve for variable Year of ZIP-HGAM.** Shaded areas show 95% confidence intervals. 17

Figure 3.4 - **Response curves for the significant interaction terms between Year and Area of ZIP-HGAM.** Shaded areas show 95% confidence intervals. 17

Figure 3.5 - **Response curves for significant variables - Month, SST and Visibility - and non-significant variables – Depth - of ZIP-HGAM, given a significance level of 5%.** Shaded areas show 95% confidence intervals and bottom vertical lines represent observations. 18

Figure 3.6 - a) **Observed distribution** (Average number of turtles sighted per transect per location, in Pearl Harbor, 2000-2011), b) **Predicted distribution of turtles based on the ZIP-HGAM** (Number of turtles expected to be sighted per transect). Predictions used average values of environmental predictors, depth, SST and visibility, and transect length, incorporated as offset term the model. 19

Figure 3.7 - Frequency distribution of the behaviours turtles were performing when first sighted (n = 680).. 20

Figure 3.8 - **Frequency distribution of the behaviours green turtles were observed performing, per location where higher turtle presence was found**. Location 19: n=211; Location 2: n=77; Location 21: n=148.. 21

Figure 3.9 - Size-class distribution found of the green turtles sighted in Pearl Harbor, 2000-2011, based on in-water direct observations (n=630) 21

Figure 3.10 - **Kruskal-Wallis comparing the three turtle size categories across transect depth (m) in which individuals were recorded.** <0.5 represents the smallest size class, with individuals up to 50cm in Straight-Line Carapace Length; 0.5-1 represents medium size class with turtles ranging from 50cm to 1.0m SCL; >1 represents large size class, with individuals estimated to be above 1.0m in SCL. $PHolm - corrected$ represent Holm adjusted p-values used in the Dunn's pairwise comparisons. .. 22

Annex Figure and Table Indexes

Annex Figure 6.1 - Spatial variability of sea surface temperature monthly means, remotely extracted and averaged for the time-period examined, 2002-2011, in Pearl Harbor 35

Annex Figure 6.2 - Spatial variability of the average underwater visibility, in meters, estimated in transect surveys per location, Pearl Harbor, 2000-2011.. 35

Annex Figure 6.3 - Spatial variability of the average depth, in meters, of transect surveys per location, Pearl Harbor, 2000-2011 36

Annex Figure 6.4 - **Sampling effort per location in Pearl Harbor, 2000-2011**, expressed in a) Total transects performed per location, b) Average transect length, in kilometers, of all transects performed per location... 37

Annex Figure 6.5 - Mann-Whitney test comparing mean monthly sea surface temperatures found for two general seasons in Hawaii, from 2002-2011 in Pearl Harbor... 38

Annex Table 6.1 - Spearman correlation coefficient calculated between covariates incorporated in the ZIP-HGAM optimal model 38

Annex Table 6.2 - **Comparison between models results for the number of turtles sighted per transect in Pearl Harbor, 2000-2011.** Distribution of families considered during the statistical analysis are presented in the first column. Temporal and environmental variables, Akaike's Information Criterion (AIC) and explained deviance values of each model considered are shown. Interaction terms between sampling area and year were incorporated in all models but are not shown 39

Annex Table 6.3 - **Summary data: total transects performed per location per year**. {-} represents no turtle surveys were performed in the given location in that year. The first part of the table presents transects performed within locations. The second part, separated by a shaded row, presents transects that crossed locations, as indicated by location names that are separated by hyphens. 40

Annex Table 6.4 **– Number of total transects performed in each location, number of transects with sea turtles sighted, and summary statistics of the counts per transect.** The first part of the table presents transects performed within locations. The second part, separated by a shaded row, presents transects that crossed locations, as indicated by location names that are separated by hyphens........... 41

Annex Table 6.5 - **Number of turtles expected to be sighted in transects per location, based on the optimal ZIP-HGAM**. Predictions used average values of environmental predictors, depth, SST and visibility, and transect length, incorporated as offset term the model. 42

List of Acronyms

AIC : Akaike's Information Criterion 10
CCA : Crustose Coralline Algae 13
DPS : Distinct Population Segment 2
ESA : Endangered Species Act 2
FFS : French Frigate Shoals 2
GAM : Generalized Additive Model 10
GLM : Generalized Linear Model 10
HGAM : Hierarchical Generalized Additive Model 10
INRMP : Integrated Natural Resources Management Plan 5
murSST : Multi-scale, Ultra-high Resolution Sea Surface Temperature 9
NFESC : Naval Facilities Engineering Services Center 5
NMFS : National Marine Fisheries Service 5
PHEC : Pearl Harbor Entrance Channel 5
SCL : Straight-Line Carapace Length 2
SST : Sea Surface Temperature 9
U.S. Air Force : United States Air Force 3
U.S. Navy : United States Navy 3
USFWS : United States Fish and Wildlife Service 5
ZIP : Zero-Inflated Poisson 10

Assessing temporal and spatial patterns in habitat use of green sea turtles (*Chelonia mydas*) in Pearl Harbor, Hawaii

1. Introduction

Sea turtles (superfamily Chelonioidea) are a group of long-lived marine reptiles and all its seven species are of conservation concern (Spotila 2004). Historic and systematic over-exploitation depleted many populations. Nonetheless, some populations have been subject to continuous monitoring and conservation efforts and have been recovering (Chaloupka et al. 2008a; Piacenza et al. 2016). Turtle population conservation status and trends are regulated by environmental mechanisms such as resource availability (Board & National Research Council 2010). Knowledge on resource use is therefore essential to the conservation of increasing sea turtle populations (Bjorndal et al. 2019).

Resources vary spatially and temporally, being unpredictable. Sea turtle movements are resource driven and, for some species, tend to compensate for resource instability (Brill et al. 1995; Shimada et al. 2016). When resources are available, sea turtles can develop affinities for specific areas and use them continuously to forage and/or rest, displaying strong site fidelity (Broderick et al. 2007; López-Castro et al. 2010). By exhibiting a preference for resources, distribution of animals in the landscape is often not uniform, and individuals can assemble in suitable habitats. Their distribution would most likely be a function of the spatial patterns of their habitats (Boyce & McDonald 1999).

The availability of resources such as food items has been hypothesized to determine animals' preference for certain habitats (Morrison et al. 2012), consequently determining their distribution. Abundance of prey species influence the diversity of sea turtles diet, affecting their foraging strategies and causing them to vary along their geographical distribution (López-Mendilaharsu et al. 2005; Santos et al. 2015). Environmental features such as structural complexity of habitats and water temperature are highly correlated with the availability of resources, consequently explaining variations in sea turtles' spatial distribution in given regions. Benthic structure and cover type have been found to be significant predictors of sea turtle abundance (Rincon-Diaz et al. 2011; Williams et al. 2017), thus a characterization of benthic habitats within foraging grounds is essential to examine relationships between habitat type and sea turtle presence. Sea surface temperature also impacts turtle distribution (Hawkes et al. 2007; Becker et al. 2019). All sea turtles life stages can be affected temporally and geographically by changes to climatic processes (Witt et al. 2010; Hamann et al. 2013), which include the increase of water temperature. Variations in turtles diet according to sea surface temperature have already occurred (Esteban et al. 2020), and the use of water temperature data at finer spatial and temporal scale has been highlighted as a method to better understand its role as a driver in sea turtles diet (Esteban et al. 2020). Knowledge on habitat use shifts on a local scale is therefore required to gain insights on the potential effects of climate change on sea turtles foraging grounds.

Size-class distribution can explain variations in sea turtles' foraging strategies and spatial distribution within foraging grounds (Esteban et al. 2020). Size-partitioning of sea turtles within their feeding areas have been described for green turtles (*Chelonia mydas*) (Heithaus et al. 2005; Hamann et al. 2006; Bresette et al. 2010; López-Castro et al. 2010). Bresette et al. (2010) found size-class differences according to bathymetry, with juvenile green turtles using shallower locations whereas larger individuals were sighted foraging in deeper waters, revealing distinct habitat requirements according to turtle size. Since fine-scale variations in the landscape such as depth might affect both sea turtle size-distribution and presence (Becker et al. 2019), it is important to assess these two features across varying depth in foraging grounds.

The knowledge of habitat requirements for foraging and resting is critical for the improvement of management plans of sea turtle populations (Russell & Balazs 2009; Parker et al. 2009). The characteristics of optimal feeding habitat differ among sea turtle species, with most species being found on neritic foraging grounds (Plotkin 2002; Jones & Seminoff 2013). Within their resident feeding pastures, sea turtles spend most of their time shifting between actively foraging and resting (Balazs 1980). Resting is essentially characterized as an inactive state of turtles. In coastal shallow waters, sea turtles commonly rest in coral reef and hard bottom habitats and/or sand bottom areas (Hazel et al. 2009; Walcott et al. 2014; Summers et al. 2017), usually in locations which can provide refuge, are free from strong currents and are of low-disturbance (Balazs 1980). Cleaning behaviour commonly occurs within resting areas, and can occur either as self-cleaning or sea turtles being cleaned by fishes (Heithaus et al. 2002; Schofield et al. 2006).

In the Hawaiian Archipelago, green turtles are the most frequently observed sea turtle (Balazs 1980; Chaloupka et al. 2008b). Sightings and strandings of hawksbill turtles (*Eretmochelys imbricata*) in Hawaiian waters are relatively uncommon (Parker et al. 2009), nonetheless, the small population is increasing (National Marine Fisheries Service and US Fish and Wildlife Service 2013). Other species have been documented in the region, however they are considered rare visitors or were only sighted in deep oceanic waters – loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*) and olive ridley turtles *(Lepidochelys olivacea*) (Balazs 1980; Chaloupka et al. 2008b).

Green turtles have a circumglobal distribution, inhabiting neritic foraging areas in tropical and subtropical regions (Seminoff et al. 2003). *C. mydas* has a long history of human exploitation leading to a few extinct stocks. However, the Hawaiian population has experienced one of the most consistent monitoring efforts compared to other worldwide populations (Balazs & Chaloupka 2004; Balazs et al. 2015). This once depleted population has been showing an increasing recovery trend over the years (Balazs et al. 2015), due to the protection of the turtles and their foraging and nesting habitats by the Endangered Species Act (ESA) (Humburg & Balazs 2015; Valdivia et al. 2019). The ESA has the purpose to protect and recover threatened species and habitats upon which they depend (Humburg & Balazs 2015). Hawaiian green turtles belong to a genetically discrete population (Dutton et al. 2008), comprising a Distinct Population Segment (DPS). A DPS is defined as a vertebrate fish or wildlife population or group of populations that are considered discrete from other populations of the species (US Fish and Wildlife Service 1996). DPSs are listed and protected under the Endangered Species Act. Green turtles are classified globally as Endangered (IUCN 2004), though the Hawaiian subpopulation conservation status is Least Concern (IUCN 2018).

The subpopulation can be found throughout the Hawaiian Archipelago. The primary nesting locations of the Hawaiian green turtles are situated on a northwestern atoll of the Hawaiian island chain, French Frigate Shoals (FFS), which accounts for more than 90% of turtles nesting in the Archipelago (Balazs & Chaloupka 2004). After the hatchlings emerge from the nest and enter the water at FFS, they are thought to reside in the pelagic environment in the north central Pacific region. Successively, juveniles recruit to Hawaiian foraging grounds, at approximately 35cm in straight line carapace length (SCL) (Balazs & Chaloupka 2004). Distribution of adults, subadults and juveniles above 35cm SCL in Hawaii seem to overlap, and it is mostly determined by the presence of sites with suitable breeding, foraging, and resting habitats (Balazs 1980). Green turtles settle into foraging grounds around the main Hawaiian Islands, showing strong fidelity to preferred foraging areas (Balazs 1976; Keuper-Bennett & Bennett 2000; Balazs et al. 2017).

After their recruitment to the neritic environment, green turtles primarily forage on marine algae and seagrasses (Bjorndal et al. 1997; López-Mendilaharsu et al. 2005; McDermid et al. 2007). In their neritic diet, green turtles have also been found to include a wide variety of marine invertebrates such as sponges

(Porifera), sea pens (Anthozoa), sea hares (Gastropoda), small crustaceans (Malacostraca), tube worms (Annelida), small tunicates (Thaliacea) and hydrozoans (Cnidaria) (Jones & Seminoff 2013). The Hawaiian subpopulation predominantly consumes benthic algae, however, its diet seems to vary between foraging grounds (Arthur & Balazs 2008). Similar to other marine turtle populations worldwide, diet selection in this species seem to be a balance between local abundance and selective feeding (Bjorndal 1980). Within their resident foraging grounds, Hawaiian green turtles have been documented to actively forage at night (Balazs et al. 1987, 2002; Brill et al. 1995), while resting activity occurs during both day and nighttime (Balazs et al. 1987, 2002). In Hawaiian coastal areas, green turtles rest on the base of corals, sand and silt channels and vertical holes. The use of ponds at Hawaiian bays and warmer water areas within the landscape as resting habitat have also been noticed (Balazs et al. 1987; Harrington et al. 2002). Although residing in the same areas, Balazs (1980) found juveniles and subadults using resting habitats located at shallower depths, when compared with adult individuals (Balazs 1980).

At-sea monitoring is used to characterize habitat use and spatial distribution of sea turtles. Free diving, with or without capturing the turtles, circumnavigation by dive boat, records on turtles' behaviour, photo-identification and characterization of benthic habitat have been important in obtaining behavioral underwater data and allow to assess sea turtle distribution, site fidelity and population structure within regions (López-Castro et al. 2010; Williams et al. 2017; Becker et al. 2019). Time-depth recorders and video-time-depth recorders are also widely utilized, providing information on turtles' interaction with the environment (Seminoff et al. 2006). Animal-borne imaging allows researchers to experience what the animal sees and hears in the wild. By integrating environmental data, these devices have been useful in understanding sea turtles' localized habitat use (Heithaus et al. 2002). Satellite telemetry and later analysis identifying home ranges and quantifying habitat availability have been shown to be crucial in assessing habitat use and turtle distribution (Balazs et al. 2017).

Pearl Harbor is a landlocked estuary controlled by the United States Navy (U.S. Navy) and United States Air Force (U.S. Air Force) located on Oahu, one of the Main Hawaiian Islands. The harbor is a unique location with current and historic significance for Polynesian culture (Kirch 1997), the American public, and the military. Since the start of its use as a military base, Pearl Harbor environment has been altered significantly. During the 20th century, the construction of the Naval Base led to the deepening of previously shallow areas. Military ship traffic and the disposal of wastes into the harbor affected the water quality as well as the marine resources (Grovhoug 1992). Once extremely degraded, the environmental conditions of the harbor have improved by the end of the 20th century, revealing a remarkable resilience to previous stresses (Coles et al. 1999). Monitoring the state of natural resources consequently became mandatory in military bases in the U.S. by the Sikes Act of 1960 (16 USC §§ 670s-670o), including Pearl Harbor. It has been documented that marine communities can benefit greatly from restricted public access (King 2007; Smith & Marx 2016). Knowing the distribution and habitat use of a species provides important information for managing natural resources at a naval base such as Pearl Harbor.

The U.S. Navy has been applying an in-water dive survey methodology to assess the presence of sea turtles. This method allowed divers to directly observe and record the behaviour of sea turtles, without capturing them, as well as environmental variables. Underwater direct observations are highly important, as they capture aspects of animal's behavior that are difficult to obtain from remote sensing data, animal-borne imaging or video-time-depth recorders (Schofield et al. 2006). Unmarked populations are widely used in ecological studies and provide valuable data on habitat associations. Capturing animals can be stressful, difficult and, if resources are limited, these might be better spent on improving other aspects of the study such as design. The use of trained divers in this study – scientists from the U.S. Navy – provided cost-effective data.

This work had two overall objectives related to sea turtle ecology around Pearl Harbor, one regarding spatio-temporal distribution of turtle sightings, and a second related to the biology of turtles observed. The first objective of this study was to assess sea turtle spatio-temporal distribution in Pearl Harbor, comparing the features of different sites, annual trends in turtle sightings per location, seasonal patterns and qualitative sighting data regarding turtle behaviour. Since the Hawaiian green turtle subpopulation has been showing an increasing population trend for decades (Balazs & Chaloupka 2004), our first hypothesis is that turtle records will increase over the years. The second hypothesis is that spatial distribution of sea turtles in Pearl Harbor is influenced by the presence of food sources - such as macroalgae and seagrass - and resting sites - such as coral reef structure habitats – and, consequently, turtles will not be equally distributed in the region. A third hypothesis is related with sea turtle seasonal distribution in Pearl Harbor. As the observed nesting activity of the Hawaiian green turtle at FFS begins in April and extends until October (Balazs 1980; Niethammer et al. 1997), we hypothesized the cool season – from November to April – to have a superior number of turtles sighted in Pearl Harbor. Finally, a second objective related to the biology of the turtles observed was to determine population structure concerning size-class distribution of turtles, within limitations, based on in-water observations. We expect both juvenile, from 35cm SCL, and mature individuals to be present in the study region.

2. Methods

2.1. Study site

The Hawaiian Archipelago is situated in a remote region of the north-central Pacific. It comprises eight large inhabited and geologically young islands on the southeast of the Archipelago, Main Hawaiian Islands, and smaller volcanic islands, atolls, and reefs on the northwest (Figure 2.1). Oahu was formed by two volcanoes - the Waianae on the west and the Koolau on the east (Carlquist 1970). Between and to the south of them there is a broad coastal plain, where Pearl Harbor is located. Pearl Harbor is a landlocked estuary divided into three main lochs, which are the fragments of drowned river valleys (Stearns 1985). These lochs are joined together by a main entrance channel, Pearl Harbor Entrance Channel (PHEC), which connects the harbor with the open sea. Pearl Harbor is the largest estuary in the Archipelago, covering an area of approximately 21 km^2 and has around 58km of total shoreline length (Coles et al. 1999).

This location is also a critical and strategic port for the U.S. Navy, which accommodate all types of warships. The military controls most of the harbor waters and much of the harbor shoreline and, consequently, land use is mainly limited to operational and industrial activities (Grovhoug 1992). Since Pearl Harbor, PHEC and much of the adjacent land is owned and controlled by the U.S. Navy and U.S. Air Force, natural resources present are required by the Sikes Act to be summarized regularly, in an Integrated Natural Resources Management Plan (INRMP). This management plan have to be approved by the National Marine Fisheries Service (NMFS) and the United States Fish and Wildlife Service (USFWS), national agencies responsible for the investigation, management and recovery of marine turtle populations under the jurisdiction of the United States (National Marine Fisheries Service and US Fish and Wildlife Service 1998).

2.2. Study design

For this study, Pearl Harbor and Pearl Harbor Entrance Channel were subdivided into specific areas. Permanent distinctive structures, such as headlands or channel markers, and GPS coordinates allowed the correct identification of each sampling area. Starting from west of the entrance channel and moving clockwise around the harbor, each area was assigned a number. A map with the numbered sampling areas (Figure 2.2) was created using the software QGIS version 3.8.1 (QGIS Development Team 2019). Sampling locations were redesigned as polygon features on QGIS, adapted from an U.S. Navy initial draft. The map created only serves the purpose to illustrate the division of locations where survey transects were performed and does not allow for an accurate estimation of total area covered in surveys.

From March 2000 to May 2011, underwater surveys following a line-transect methodology occurred in Pearl Harbor at times spread throughout the year. Some measurements required for distance sampling though were not collected, such as distance of the turtles to the track line (Buckland et al. 2001). Divers performed line transects with an open circuit compressed air SCUBA, conducted by scientists from the NFESC (Naval Facilities Engineering Services Center). Divers tried to achieve a constant swimming rate, though the actual speed varied between sampling locations due to variations in sea currents. Swim rates and distances were periodically confirmed with GPS measurements and timed swims over fixed distances between permanent buoys. Transects inside Pearl Harbor and in the entrance channel followed an isobath that was parallel to the shoreline or the sides of the channel. Only a few transects crossed the channel or open areas where vessels frequently pass, which would be unsafe for the divers and could obstruct vessel traffic. Several transects could occur in a day but, if it they were performed in the same area, they were performed at different depths.

a) b)

Figure 2.1 – **a)** Satellite image of the Hawaiian Archipelago with Oahu, one of the Main Hawaiian Islands, illustrated; **b)** Satellite image of the island of Oahu, showing the location of the study: Pearl Harbor.

Figure 2.2. - Satellite image of Pearl Harbor, Oahu, with the numbered locations where survey transects occurred between 2000 and 2011.

2.3. Characterization of the sampled locations

Direct observations from the time-period examined in this study and recent Navy assessment reports on marine environment allowed for a concise characterization of benthic cover type of some of the locations where survey transects occurred. This characterization was only possible for locations recently sampled, namely in the Entrance Channel, thus information for other sampling locations was not available. Based on the characterization, the relationship between habitat types, turtle sightings and respective behaviour observed will be examined in detail. Locations on the Entrance Channel were further identified by the side of the channel they belong to. The presence or absence of seagrass and turtle caves in each location were also listed. Turtle caves are potential sites sea turtles might use to rest. Cavities and ledges can be used as turtle resting habitats and, generally, are recognized as so due to the actual observation of resting turtles or the noticeable abrasion on the limestone caused by their shells (Wells et al. 2020b).

Some of the locations sampled hold relevant features worth mentioning, as these might affect turtle presence. Location 1, outside Pearl Harbor, includes an underwater training range, hence, military personnel train for salvage, underwater demolition, and underwater explosives in this area. Locations 6 and 10, belonging to the West Loch Channel, inside Pearl Harbor, had several freshwater springs observed during our surveys. Locations 7 and 8, also situated on the West Loch Channel, are the location of a wreckage from World War II. Location 19, in the entrance channel, begins where an outfall pipe of a Wastewater Treatment plant emerges from the seafloor and this pipe extends to the southeast of the area. Extensive seagrass beds have been observed adjacent to Location 19.

2.4. Data collected

2.4.1. Turtle sampling

In each survey, number and species of sea turtles sighted along the transect were recorded. For each turtle observed, divers collected qualitative observations regarding their behaviour, such as foraging, swimming, resting and/or cleaning. Resting turtles were characterized as remain stationary in a given area. Cleaning activity encompassed the grooming of solitary turtles by cleaner fishes, turtles rubbing themselves on, for example, rocks, or turtles performing cleaning stations. Cleaning stations are formed by assemblages of turtles stacked on top of each other, waiting to be cleaned by fishes.

Straight-line carapace length was visually estimated for turtles sighted along transects and classified into three possible categories: small, comprising turtles with an estimated SCL measuring less than 0.5m (<0.5m SCL); medium, comprising individuals with an estimated SCL ranging from 50cm to 1.0m (0.5-1.0m SCL) and large, which holds turtles with an estimated SCL above 1.0m (>1.0m SCL).

Distinguishing features of the turtles sighted such as patterns of coloration, bite marks, patterns of barnacle growth and others were also recorded when possible. If a turtle could be positively identified and was sighted more than once in the same transect visit, it was only recorded as a single sighting. If the turtle could not be positively identified, then each sighting in each species and size category was recorded. Factors that could reduce the potential for miscounting turtles were accounted, such as the regular rates at which divers moved. The potential for re-sighting a turtle and counting it as a new turtle was thus low.

2.4.2. Environmental covariates

In situ environmental data was collected while performing transects. Underwater visibility in meters was recorded by the divers, with a visual estimation of distances underwater. The duration in minutes of each survey and depth in meters were also recorded, using dive computers of SCUBA equipment. This allowed divers to stay at the same depth during the transect. Transect length was calculated from knowing the length of time in minutes the diver took to perform the transect. An average swim rate of 1km/30min was used. Underwater visibility and depth, both in meters, were used as environmental predictors potentially affecting the number of sea turtles sighted per transect in Pearl Harbor.

Concerning the covariates obtained remotely, sea surface temperature (SST) was included in our set of covariates to test which environmental predictors impact turtle sightings in Pearl Harbor. Sea surface temperature monthly means were extracted from the Multi-scale, Ultra-high Resolution Sea Surface Temperature (murSST) 1-km data set, Version 4.1, produced at the NASA Jet Propulsion Laboratory (JPL) (NOAA NMFS SWFSC ERD & NOAA NESDIS CoastWatch WCRN 2021). This data set was accessed on the ERDDAP version 2.11 website (Simons 2020) and downloaded in a .xlsx Microsoft Excel file format. Water temperature values were extracted from June 2002 until May 2011 at the finest available pixel resolution (0.01 degrees or approximately 1.11km). Monthly sea surface temperature means were obtained for each Pearl Harbor sampling location based on its coordinates and dimensions. The size of the areas defined in this study was variable. Locations sampled in the entrance channel were found to generally vary from 1 to 2km in dimensions, both length and width (Figure *2.2*.). When locations exceeded 1km in extension and, consequently, were between two ranges of dataset coordinates, an average between the two temperature values was computed. Inside the harbor, some locations were found to be much lower than 1km in dimensions, both length and width (Figure *2.2*.), thus values at the finest resolution possible were applied.

The environmental variables collected for each location were averaged for the duration of the sampling period considered (2000-2011). This will allow a potential examination of the spatial variability of underwater visibility, sea surface temperature and depth in Pearl Harbor. For a clearer visualization, choropleth maps were produced with the "sf" package (Pebesma 2018) and are presented in the Supplementary Material (Annex Figure 6.1, Temperature; Annex Figure 6.2, Visibility; Annex Figure 6.3, Depth). Summary characteristics of the explanatory variables used as predictors for sea turtle distribution are presented in Table 2.1.

Table 2.1 - Temporal and environmental covariates collected during survey transects (2000-2011) and remotely (2002-2011)

Predictor Acronym	Description	Data Type	Mean and Range	Data Source
Year	Year	Numerical	[2000-2011]	-
Month	Month of the year	Numerical	[1-12]	-
Visibility	Underwater Visibility in meters	Numerical	15 [0.75 - 40.0]	Field Observation
Depth	Depth in meters	Numerical	14 [3.0 – 36.6]	Field Observation
SST	Sea Surface Temperature in Celsius degrees	Numerical	25.9 [23.2 – 27.4]	murSST from URL: https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41mday/
StripLength	Length of the transect performed in kilometers	Numerical	1 [0.23 – 3.23]	Calculated from knowing the duration in minutes. A swim rate of 1km/30min was used
Myarea	Sampling location	Categorical	-	-

2.5. Statistical analysis

When modeling ecological count data, many data sets have a large proportion of transects with zero counts. If the mean is low, that might not represent a real problem but, if the mean of the observations is large, then this might represent over dispersion: the data presents larger variability than that can be coped with standard distributional models. Zero-inflation must be accounted to prevent ambiguous ecological conclusions due to the incorrect estimation of functional relationships between covariates (Virgili et al. 2017). Generalized linear models (GLM) with standard distributions are inadequate for this type of data (Dénes et al. 2015). Generalized additive models (GAM) are semi parametric extensions of GLMs and allow for the functional relationships between the explanatory variables and the response variable to be described by smooth curves. A hierarchical generalized additive model (HGAM) is an extension to the standard GAM, which allows the modeling of nonlinear functional relationships between the predictors and the response to vary between groups by integrating interaction terms (Pedersen et al. 2019). HGAMs allow investigation of not only how functional relationships vary between groups, but also if a relationship holds across the mentioned groups (Pedersen et al. 2019).

We used a HGAM to model relationships between sea turtle sightings from ten years of line transect surveys and both *in situ* and remote environmental data. A Zero-Inflated Poisson (ZIP) distribution, with an identity link function, was used to model the nonlinear HGAM relationships between the response variable and the covariate. The link function most commonly used with Poisson distribution is log, however, with the ZIP distribution, only the identity link function is currently supported (Wood 2017). ZIP distribution used with GAM is appropriate for data in which the zero-inflation rate is simply dependent on the Poisson mean (Wood 2017). This distribution holds two parameters, which control the zero-inflation rate, and they were internally estimated in model fitting. ZIP GAMs have been recently considered when estimating animal populations' distributions based on environmental predictors when the proportion of zero counts is high (Virgili et al. 2017). The initial selection of explanatory variables to incorporate in the model was based on the Spearman correlation coefficient between combinations of covariates (Annex Table 6.1). If there were collinear covariates, presenting correlation coefficients with absolute value higher than 0.7, than the least important variable, in terms of its biological theoretical relationship, was excluded from the model.

The response variable considered was the number of turtles sighted per transect. It was modeled as a function of six smooth terms: year, an interaction term between year and sampling location, month, underwater visibility, sea surface temperature, depth and sampling location. We incorporated transect length as an offset term. Offset terms are commonly used for correcting the number of given events, usually incorporated in models with the Poisson distribution, to account for non-constant sampling effort (Mannocci et al. 2014; Virgili et al. 2017). The interaction term between year and sampling location produced location-specific smoothers, permitting examination of annual turtle sightings trend for each location. In the interaction term mentioned, we allowed each location-specific smoother to have its own smoothing parameter, hence, the only information shared between locations is through the global smoother year and the random effect for group-level intercepts (Pedersen et al. 2019).

A backwards stepwise procedure based on Akaike's Information Criterion (AIC) was applied to select covariates and interaction terms incorporated in the optimal model. Variables used in a model yielding a lower AIC were selected. A comparison between models with different families of distributions was also performed, based on multiple criteria such as AIC, deviance explained and sensible predicted distribution maps, allowing us to determine the best fit to our data. For the first criteria, similar to variables selection, the HGAM that yielded the lowest AIC was selected. Deviance explained values of each model were examined, considering that a high explained deviance can indicate a better predictive ability (Mannocci et al. 2014; Virgili et al. 2017). Further, it was necessary to also evaluate predictive ability by comparing it with the observed raw distribution. Based on the ZIP HGAM, we predicted spatial distribution profiles of turtles in Pearl Harbor with choropleth maps. For each location sampled it was assigned an abundance prediction, expressed in number of turtles expected to be sighted per transect in those locations. Profiles were constructed using average values for the environmental predictors incorporated in the model. For the comparison with the model predictions mentioned, the average number of turtles sighted per transect for the sampling period (2000-2011) was computed and graphically illustrated for each location in a choropleth map.

We used non-parametric Chi-square statistics and Kruskal-Wallis tests with consecutively pairwise comparison Dunn tests for comparative analysis of the qualitative sighting data. Differences in the behaviours' observed frequency between sampling locations with the highest turtle presence found were assessed with a Chi-square test. Differences between the three size-categories of turtles across depth were assessed with a Kruskal-Wallis test, since the assumptions of its parametric counterpart test, Analysis of Variance, were not met. We considered the results to be statistically significant for a p-value lower than 0.05. We do not take statistical significance as a dogma, and hence the relevance of the effect sizes is discussed.

Statistical analysis was implemented using R Statistical Software, version 3.6.2 (R Core Team 2019). The "mgcv" package (Wood 2017) was used for fitting all models considered to our data, determine their goodness-of-fit, and obtaining model predictions. Package "gratia" (Simpson 2018) was used for illustrating HGAM smoother plots. Choropleth maps for illustrating HGAM based spatial predictions were created with packages "ggplot2" and "sf" (Pebesma 2018), connecting R environment with the map produced on QGIS. For the qualitative sighting data, "ggstatsplot" package (Patil 2018) was used for the application of Kruskal-Wallis test and a clearer visualization of its result.

3. Results

3.1. Environmental setting

The bathymetry in Pearl Harbor has a general physical structure composed of sloping limestone shelf along the shoreline, which terminate in vertical dredge cuts. Dredge cuts are cuts made in the substrate by dredging equipment. Dredging is a common construction procedure in harbors, with the objective of keeping the channels navigable. The dredge cuts made then extend to the channel floor, having a wall habitat composed of limestone fossil reef excavated to near vertical faces, which form the channel walls. The bottom type of the channel floor varies from primarily hard substrate at the seaward entrance to soft sediment with occasional rocks or gravel in the inner harbor (Wells et al. 2016, 2020b). The benthic structure of Pearl Harbor is largely influenced by the underlying physical structure. Since the presence of hard substrate is necessary for coral establishment and growth, the highest coral cover and the highest coral biodiversity occur in the entrance channel zones, particularly on the eastern side (Wells et al. 2016, 2020b). Within the harbor, coral cover and coral biodiversity are much lower, resulting from the bottom type being primarily soft sediment. At these sites, most corals occur in solitary colonies on the edge of the dredge cuts, on the surface of boulders and manmade structures or are absent (Wells et al. 2018, 2020b; Wells 2020). Seagrass is present in some regions of the harbor, generally in patches on soft sediment of the harbor floor, with the majority occurring also in the entrance channel or in undisturbed areas inside the harbor (Wells et al. 2018, 2020b). Concerning the presence of algae, macroalgae and turf algae, it covers a notable portion of the nearshore areas of the entrance channel (Table 3.1). Macroalgae cover is mostly limited to the east side of the entrance channel and turf algae occurs equally through the entrance channel (Wells et al. 2020b).

Regarding non-coral invertebrates, a variety of sponges, annelids, hydroids (Cnidaria), sea cucumbers and sea urchins (Echinodermata) are found in Pearl Harbor. Sponges (Demospongiae) are very well represented, occurring ubiquitously throughout locations both in the entrance channel and inside Pearl Harbor (Wells et al. 2020b). Sponges have been observed on vertical man-made structures and on the surface of the harbor floor. Sea urchins (Echoinoidea) are relatively abundant in Pearl Harbor. Echoinoidea diversity is higher in entrance channel areas but are not so frequently found and are less diverse in locations within the harbor. Sea cucumbers (Holothuroidea) are also well represented. Inside the harbor, *Opheaodesoma spectabilis* (Conspicuous sea cucumber) is frequently found in most locations, whereas in the entrance channel it is rare. These individuals have been mostly found inhabiting the harbor floor (Wells 2020). Polychaetes, which are commonly found associated with hard substrates in harbors, are found covering man-made structures in Pearl Harbor waters (Wells 2020). There is a higher diversity of polychaetes in locations inside the harbor, particularly sessile worms such as feather duster worms are well represented, whereas in the entrance channel there is only one relatively common species, *Loimia medusa*. Diversity of hydroids (Hydrozoa) is relatively low, although *Pennaria disticha* (Christmas tree hydroid) is commonly sighted throughout Pearl Harbor (Wells et al. 2020b). Bivalves and gastropods can be encountered on pier pilings in a few zones of the harbor, although they are relatively rare (Wells et al. 2020b).

Table 3.1 - **Description of the benthic habitats where survey transects occurred at Pearl Harbor, 2000-2011**. CCA = Crustose Coralline Algae. Percentages in each cell represent an average of the percent cover of the mosaics inside each location. Mosaics in Source column refer to orthomosaic images built in Wells et al. 2020b). Photographs were processed by the scientists and used to produce a continuous high-resolution orthomosaic scaled image of each location. On each orthomosaic, 100 points were gridded, benthic cover types underlying the gridded points were identified and percent cover of all surface types was obtained (Wells et al. 2020b). NA – Information is not available.

Region		Location	Type of Cover						Presence of Seagrass	Presence of Caves	Source
			Coral	CCA	Macroalgae	Turf algae	Dead Coral	Uncolonized			
Pearl Harbor Entrance Channel		1	2%	0%	0%	21%	1%	76%	No	NA	Mosaics 37, 41, and 45 in (Wells et al. 2020b)
	West side of Entrance Channel	2	9%	0%	3%	12%	3%	73%	No	Yes	Mosaics 15,16,18, 21, 23, 28-32 in (Wells et al. 2020b)
			34.2 – 72.8%	0%	0%	0%	4.2 – 5.4%	26.5 – 64.5%	No	NA	10x10m grid in (Wells et al. 2020a)
		21	3%	0%	5%	2%	3%	88%	No	Yes	Mosaics 17 and 20 in (Wells et al. 2020b)
		3	1%	1%	4%	4%	1%	86%	Yes	Yes	Mosaics 3-6 and 8-14 in (Wells et al. 2020b)
		4	0%	1%	0%	54%	0%	45%	Yes	Yes	Mosaics 1 in (Wells et al. 2020b)
	East Side of Entrance Channel	18	27%	0%	1%	3%	8%	60%	Yes	NA	Mosaics 19, 22, 24-27, 34-36, 39-40 in (Wells et al. 2020b)

3.2. Turtle species found

A total of 680 sea turtles was observed in transects between 2000 and 2011: all but one were green turtles, with the single exception positively identified as a hawksbill sea turtle.

3.3. Turtle sampling presence

A total of 464 transects was surveyed between March 2000 and April 2011 in Pearl Harbor. Sampling effort, expressed in number of transects performed per location, was not the same for every year and month (Table 3.2). Years 2001, 2004 and 2011 were poorly sampled when compared with the other years. Despite the overall pattern of transects occurring throughout the year, there are notably few samples that occurred in January.

Sampling effort, expressed both in number of transects performed and average transect length, was also not the same for all locations sampled (Annex Figure 6.4). Several locations were not sampled every year and/or were relatively inadequately sampled (Annex Table 6.3).

Table 3.2 - Number of survey transects performed in each month and year in Pearl Harbor, 2000-2011

Month/Year	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	**Across all years**
January	0	0	0	0	0	0	0	0	0	0	4	0	**4**
February	0	0	18	0	0	0	2	0	0	0	0	0	**20**
March	8	0	13	1	0	0	0	0	0	2	3	0	**27**
April	0	0	19	10	0	6	0	12	0	10	3	2	**62**
May	0	0	2	0	0	8	0	5	0	2	4	0	**21**
June	0	1	14	0	0	0	5	0	18	0	4	0	**42**
July	12	0	2	0	0	0	0	0	3	2	1	0	**20**
August	3	3	4	42	0	5	0	0	0	17	2	0	**76**
September	0	1	0	0	0	41	0	0	0	0	7	0	**49**
October	7	0	0	0	2	0	0	5	11	19	1	0	**45**
November	16	0	17	0	0	0	9	5	12	6	0	0	**65**
December	8	0	5	8	0	0	4	4	0	4	0	0	**33**
Total	**54**	**5**	**94**	**61**	**2**	**60**	**20**	**31**	**44**	**62**	**29**	**2**	**464**

Sea turtles were sighted on 121 transects (26%), while the remaining 343 transects had zero turtle observations (n=464) (Figure 3.1). 448 transects were performed within the 21 locations established and sixteen crossed from at least one location to another. The number of transects that occurred in each location and summary statistics of turtle counts per transect are presented in the Supplementary Material (Annex Table 6.4).

Presence of turtles found in transects across all surveys varied between locations (Figure 3.2). Locations 2, 19 and 21, situated on the entrance channel, had the highest presence of turtles across many surveys - more than 65% of transects in those locations had turtles (Figure 3.2). Locations that had a higher consistency of turtle detection across a relatively large number of surveys (33%) are also situated on the entrance channel - locations 3, 5, 17 and 18 (Figure 3.2). Almost all locations inside the harbor, namely locations 7 to 16, had less than 13% transects with turtles found. Particularly, areas 7, 11, 12 and 15 had zero turtles sighted in transects across ten years of study.

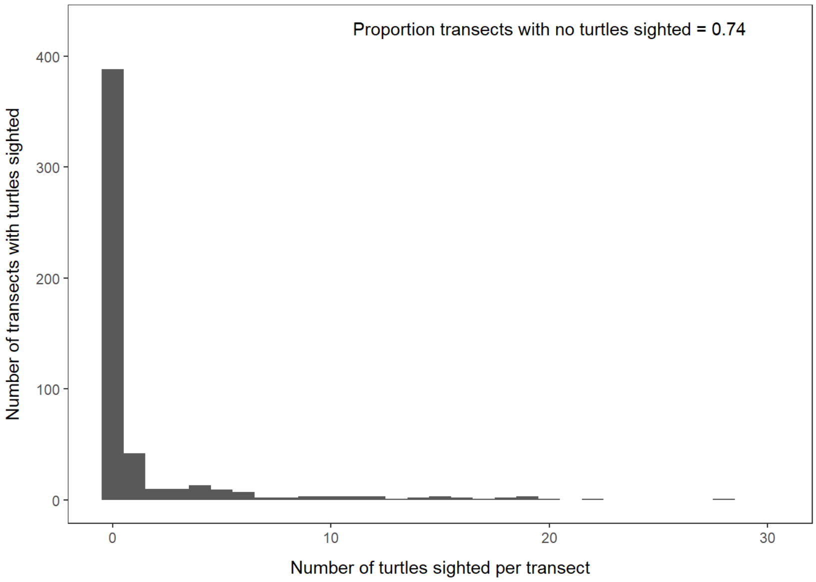

Figure 3.1 - Frequency distribution of sea turtles sighted per transect in Pearl Harbor, 2000-2011

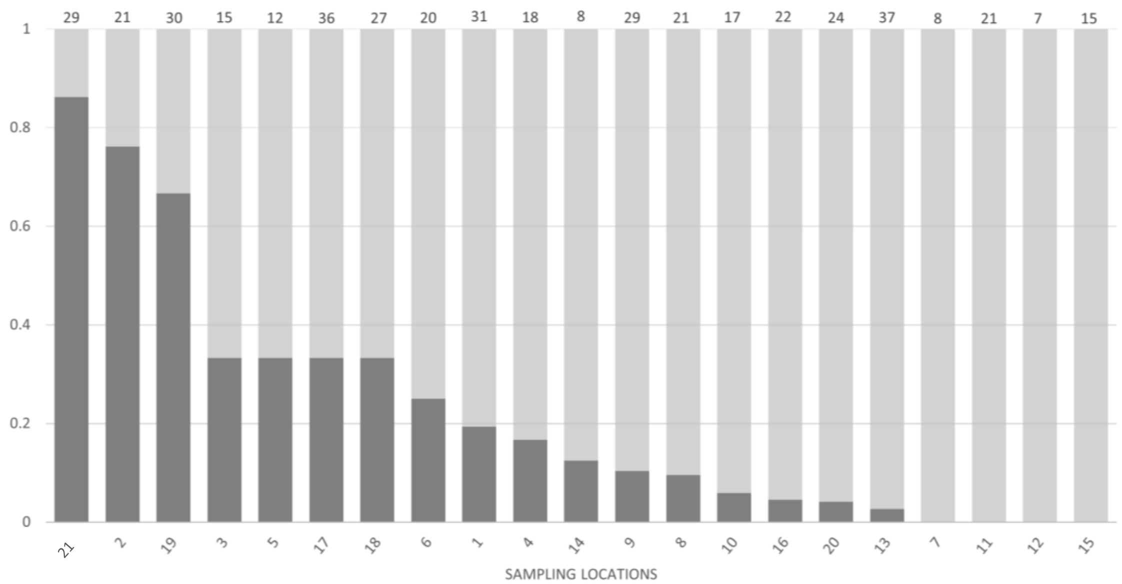

Figure 3.2 – **Proportion of transects where at least one turtle was sighted per sampling location, in Pearl Harbor, 2000-2011**. Numbers above frequency bars represent total transects performed per locations during the time-period examined. Entrance Channel Locations: 1-5 and 17-21. Locations inside the harbor: 6-16.

3.4. Turtle sightings modeling

The optimal model of ZIP-HGAM included all temporal and environmental covariates collected. Covariates Year, Month, SST and Visibility significantly influenced the number of turtles sighted per transect in Pearl Harbor from 2000 to 2011 (Table 3.3). Variable Depth, despite having a p-value slightly higher than the significance level considered, was still included in the optimal ZIP-HGAM considered for further inference as this model yielded the lower AIC.

Table 3.3 - **ZIP-HGAM model results for sea turtle sightings in Pearl Harbor, 2000-2011.** The model covariates and values for effective degrees of freedom (edf), Chi-square (X^2) and p-values are shown. Model presented a deviance explained of 78.6%. Shaded rows correspond to variables or interaction terms statistically significant considering 5% as the significance level.

ZIP-HGAM			
Model Covariates	**edf**	**Chi square**	**p-value**
Year	5.366	27.562	<0.001
Year:Area1	3.497	32.870	0.047
Year:Area2	3.032	14.225	0.003
Year:Area3	9.764E-5	0	0.644
Year:Area4	2.104	37.299	0.050
Year:Area5	1.301E-5	0	1.000
Year:Area6	1.814	24.084	0.006
Year:Area7	4.753E-5	0	0.696
Year:Area8	1.203	13.003	0.040
Year:Area9	3.355E-5	0	0.836
Year:Area10	1.268E-5	0	1.000
Year:Area11	4.084E-4	0	0.409
Year:Area12	2.799E-5	0	0.945
Year:Area13	1.395E-4	0	0.419
Year:Area14	2.284E-5	0	1.000
Year:Area15	2.833E-5	0	0.921
Year:Area16	2.907E-5	0	0.799
Year:Area17	1.024E-2	0.008	0.404
Year:Area18	3.667	111.751	<0.001
Year:Area19	3.937	12.858	0.002
Year:Area20	0.824	55.829	0.131
Year:Area21	0.447	0.508	0.236
Month	1.300	3.604	0.054
SST	6.322	32.863	<0.001
Depth	2.288	6.107	0.073
Visibility	2.416	9.203	0.027
Area	16.850	150.879	<0.001

3.4.1. Annual trends

Global smoother Year (Figure 3.3) and a selected subset of the significant location-specific smoothers (Figure 3.4) illustrate how annual sightings trends per location diverged from the global trend. Year significantly affected the number of turtles sighted (X^2=27.562; p-value <0.001;Table 3.3). The pattern for all locations combined is a general increase in the number of turtles sighted over the years, although we detect a decrease in early years, between years 2003 and 2004 (Figure 3.3). Concerning the significant location-specific smoothers, the seven locations shown are situated either in the entrance channel (1,2,3,18 and 19) or inside the harbor in the West Loch channel (6 and 8). These locations presented significant variations in the number of turtles sighted per transect through the years (Figure 3.4). In Locations 2 and 18 we detected a decrease and, in Location 1 an increase, in turtle abundance at roughly the middle years of the study (2002-2008). Locations 4 and 8 had a general increase in turtles sighted per transect along the years. In Location 6 we found decrease in turtle sightings in early years and then a steadier trend (Figure 3.4).

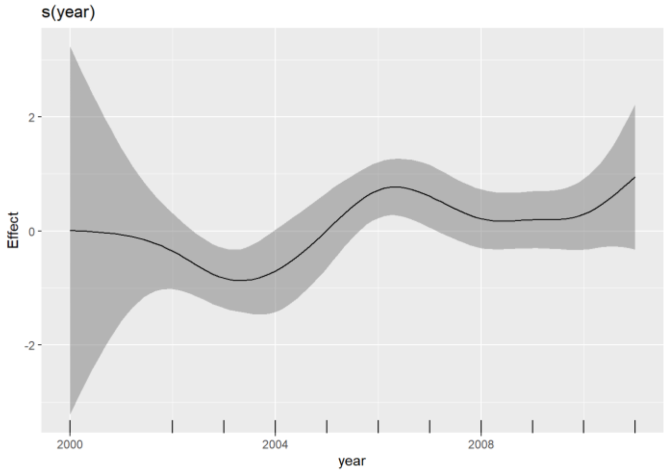

Figure 3.3 - **Response curve for variable Year of ZIP-HGAM.** Shaded areas show 95% confidence intervals.

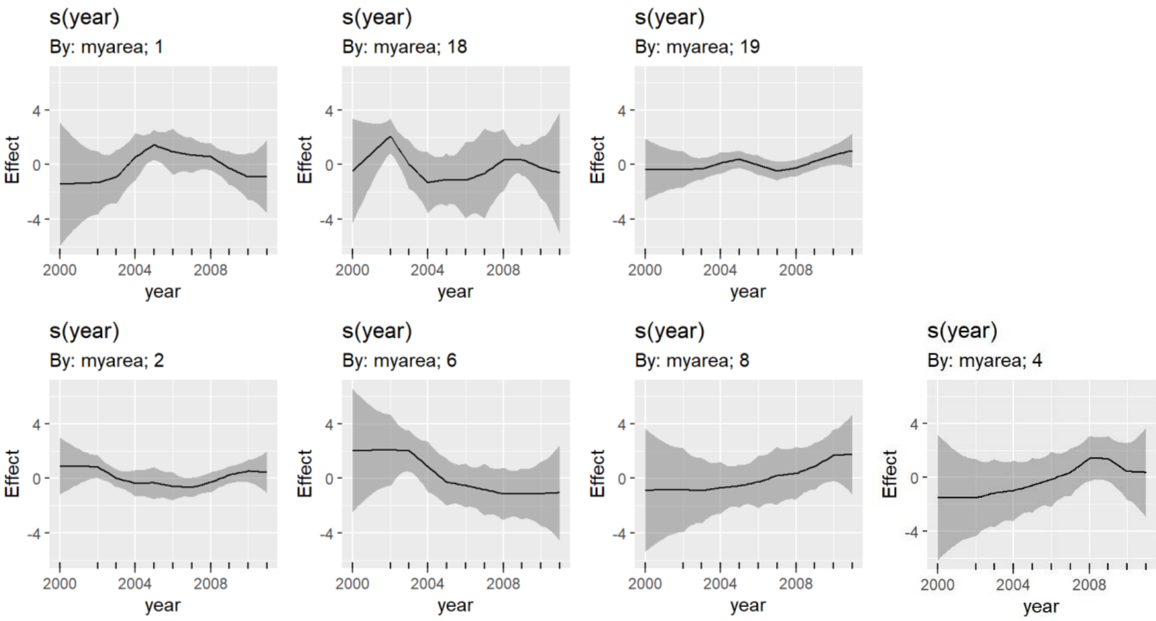

Figure 3.4 - **Response curves for the significant interaction terms between Year and Area of ZIP-HGAM.** Shaded areas show 95% confidence intervals.

3.4.2. Seasonal patterns and environmental associations

We found variable Month to be a significant predictor of the number of turtles sighted per transect (X^2=3.604; p-value = 0.05,Table 3.3). There is a slight decrease in the number of turtles sighted in early months of the year, between approximately March and June (Figure 3.5). Consequently, we detect a larger number of turtles sighted in the later months of the year.

For SST, we found that a bimodal response including two main peaks, one between 24 and 25ºC, and the other at approximately 26.5ºC, is associated with higher numbers of turtles sighted (Figure 3.5). We found the mean monthly sea surface temperatures from murSST dataset to have a range average of

25.1ºC in the cool season and 26.4ºC in the warm season. Distribution of temperature values observed differed significantly between the two general seasons in Hawaii (Mann-Whitney U=8.02; p-value <0.001; Annex Figure 6.5).

Underwater visibility had a positive effect on the number of turtles sighted. Turtle sightings increased until a peak was reached, at about 20m of underwater visibility. Beyond 20m, further increases in visibility did not affect number of turtles sighted per transect (Figure 3.5).

Considering the significance level of 5%, we found variable Depth to be a statistically non-significant predictor for the number of turtles sighted (X^2=6.107; p-value = 0.07, Table 3.3). Although, when observing the partial effect of depth in turtle sightings (Figure 3.5), one may verify that turtles were mostly sighted in a depth range of approximately 5 to 20m. At greater than 20m depth, the number of turtles sighted per transect started to decrease.

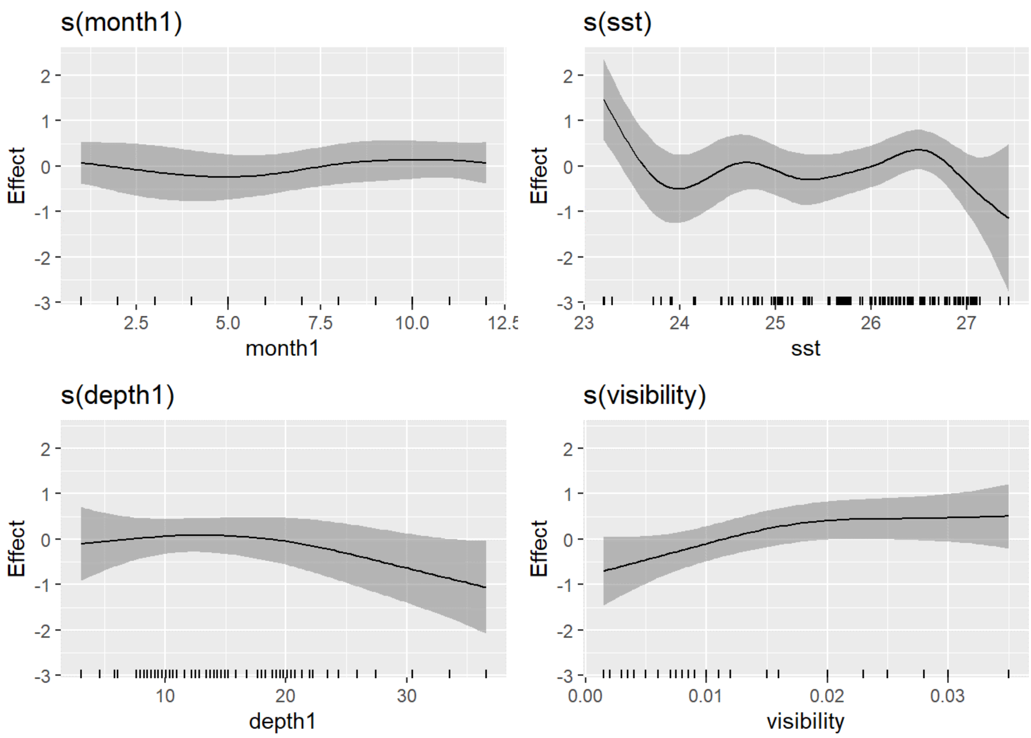

Figure 3.5 - **Response curves for significant variables - Month, SST and Visibility - and non-significant variables – Depth - of ZIP-HGAM, given a significance level of 5%.** Shaded areas show 95% confidence intervals and bottom vertical lines represent observations.

3.4.3. Model predictions

We found a non-uniform spatial distribution of green turtles in the study region, according to the prediction map based on the optimal ZIP-HGAM (Figure 3.6 b)). There is a clear concentration of sea turtles in two particular locations of the Pearl Harbor Entrance Channel, with the maximum turtles sighted per transect expected to be found in locations 19 and 21. In the remaining locations, this predicted abundance is much lower. Particularly in all locations inside Pearl Harbor and also areas 4, 18 and 20, the number of turtles is expected to vary between 0 and 1 (Annex Table 6.5). The predicted distribution is consistent with the observed distribution, shown in the average turtles sighted per transect map presented in Figure 3.6 a).

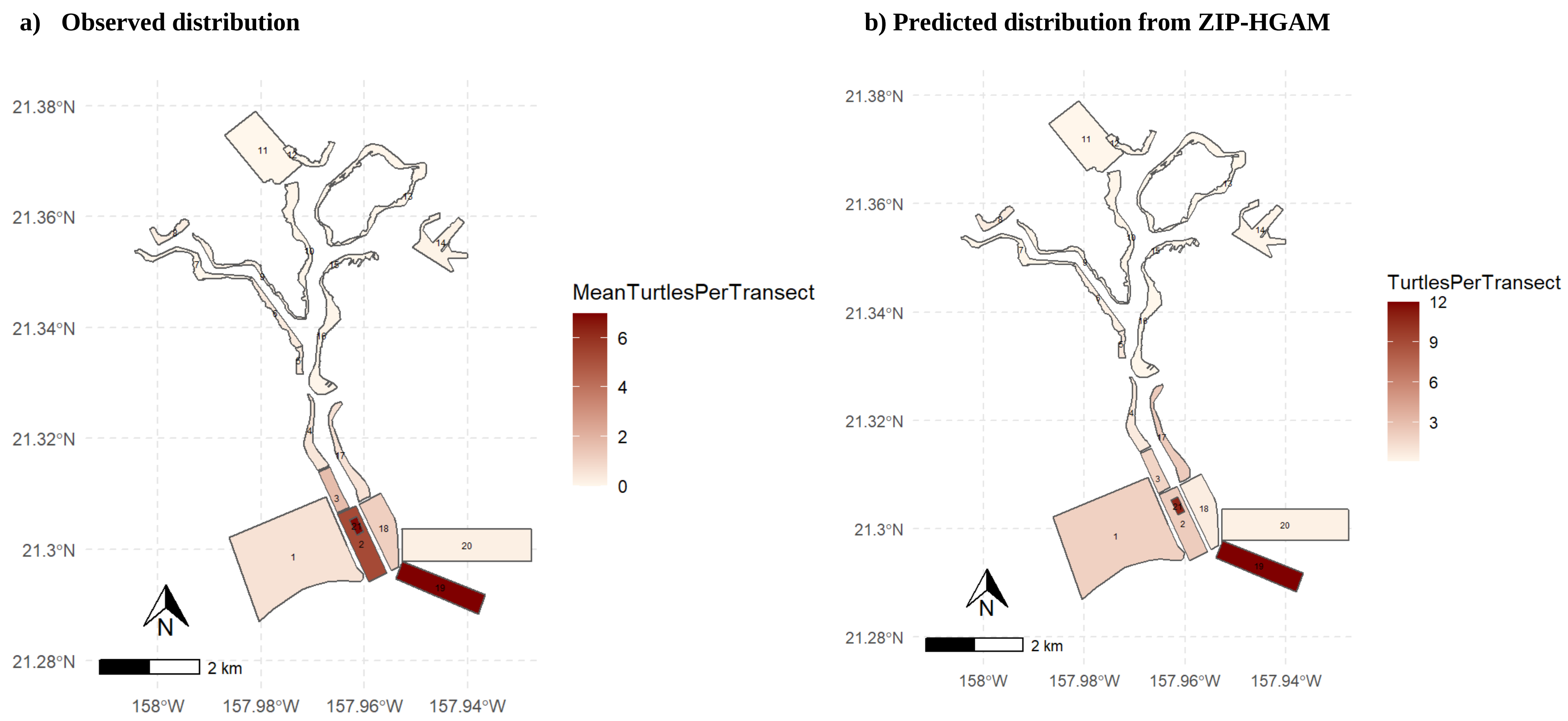

Figure 3.6 - a) **Observed distribution** (Average number of turtles sighted per transect per location, in Pearl Harbor, 2000-2011), b) **Predicted distribution of turtles based on the ZIP-HGAM** (Number of turtles expected to be sighted per transect). Predictions used average values of environmental predictors, depth, SST and visibility, and transect length, incorporated as offset term the model.

3.2. Qualitative observations: behaviour and size-class distribution

For 569 of the 680 sea turtles observed in Pearl Harbor during the surveys (83.7%), it was possible to record their behaviour when first sighted along survey transects. The remaining 106 individuals' behaviour was registered as Not Recorded. Green turtles were observed swimming (50.4%), resting (43.9%) and being cleaned or hovering at cleaning stations (5.6%) (*n*=569 observations). No turtles were observed foraging across the sampling period examined. Behaviours displayed per location and additional sighting and location information are presented Table 3.4.

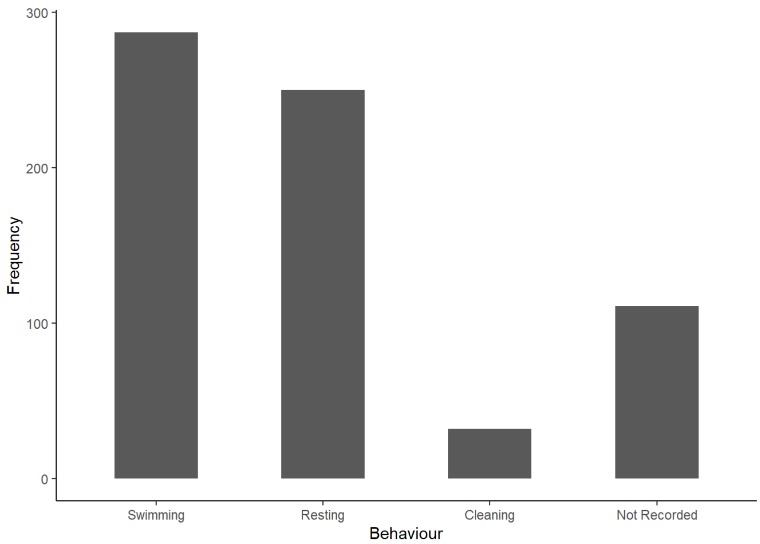

Figure 3.7 - Frequency distribution of the behaviours turtles were performing when first sighted (*n* = 680)

Table 3.4 - **Summary table of green turtle behaviours by sampling location and region in Pearl Harbor, 2000-2011**. Additional observations concerning resting features and particular observations are listed. Total number of turtles observed per location (n) is shown. {-} means no behaviours were observed given the fact no turtles were observed.

<table>
<tr><th colspan="2">Region</th><th>Location</th><th>Behaviour</th><th>Additional qualitative observations</th></tr>
<tr><td rowspan="7">Pearl Harbor Entrance Channel</td><td rowspan="4">West side of Entrance Channel</td><td>2 (n=111)</td><td rowspan="4">Swimming
Resting
Cleaning</td><td rowspan="4">Resting spots in location 21 are underwater caves
Positively identified hawksbill in location 4 (n=1)</td></tr>
<tr><td>21 (n=200)</td></tr>
<tr><td>3 (n=26)</td></tr>
<tr><td>4 (n=9)</td></tr>
<tr><td rowspan="3">East side of Entrance Channel</td><td>17 (n=22)</td><td rowspan="2">Swimming
Resting</td><td rowspan="2"></td></tr>
<tr><td>18 (n=32)</td></tr>
<tr><td>19 (n=211)</td><td>Swimming
Resting
Cleaning</td><td>Cleaning stations observed
Resting locations are under a large pipe that runs downhill</td></tr>
<tr><td rowspan="14">Pearl Harbor</td><td rowspan="3"></td><td>1 (n=19)</td><td rowspan="2">Swimming
Resting</td><td rowspan="2">Resting spots comprised undercut ledges in location 1</td></tr>
<tr><td>20 (n=5)</td></tr>
<tr><td>5 (n=4)</td><td>Resting</td><td></td></tr>
<tr><td rowspan="4">West Loch Channel</td><td>6 (n=7)</td><td rowspan="2">Swimming
Resting</td><td rowspan="3">Resting spots are outflow points of freshwater springs</td></tr>
<tr><td>9 (n=3)</td></tr>
<tr><td>10 (n=1)</td><td>Resting</td></tr>
<tr><td>8 (n=5)</td><td rowspan="4">Swimming</td><td rowspan="4"></td></tr>
<tr><td rowspan="4"></td><td>13 (n=1)</td></tr>
<tr><td>14 (n=1)</td></tr>
<tr><td>16 (n=1)</td></tr>
<tr><td>7 (n=0)</td><td rowspan="4">-</td><td rowspan="4"></td></tr>
<tr><td>Middle Loch</td><td>11 (n=0)</td></tr>
<tr><td></td><td>12 (n=0)</td></tr>
<tr><td></td><td>15 (n=0)</td></tr>
</table>

Locations which had the highest turtle presence, locations 2, 19 and 21, differed significantly in the behaviours' observed frequency (X^2=153.64; p-value < 0.001). Behaviour of all turtles sighted in Location 19 was successfully identified and, approximately 50% of the turtles were found resting (*n*=211). Locations 2 and 21 had a considerable proportion of turtles with activities not recorded (31% and 26% respectively). For individuals where behaviour was positively identified, in Location 2 resting and swimming turtles were found at similar proportions (*n*=77) (Figure 3.8), whereas in area 21 the dominant activity was swimming (60%) and resting comprised 34% of turtles sighted (*n*=148).

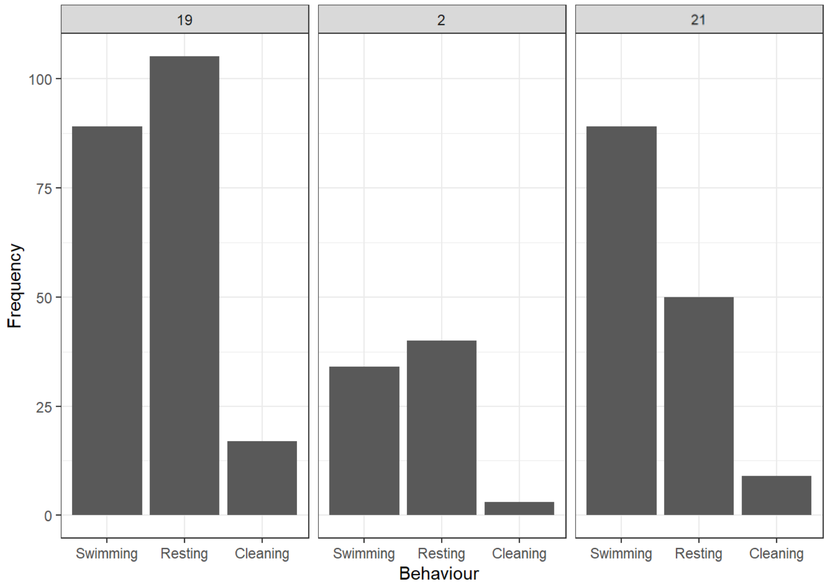

Figure 3.8 - **Frequency distribution of the behaviours green turtles were observed performing, per location where higher turtle presence was found**. Location 19: *n*=211; Location 2: *n*=77; Location 21: *n*=148.

During data collection, it was possible to assign 630 of the total 680 sea turtles sighted to a 50cm size-class. Turtles with an estimated SCL ranging from 50cm to 1.0m were the most abundant (Figure 3.9), accounting for 60% of the observations (*n*=630). Size-class containing individuals larger than 1.0m in SCL accounted for 36.8% of the observations, whereas turtles smaller than 0.5m only contributed with 3.2% to the total observations (*n*=630).

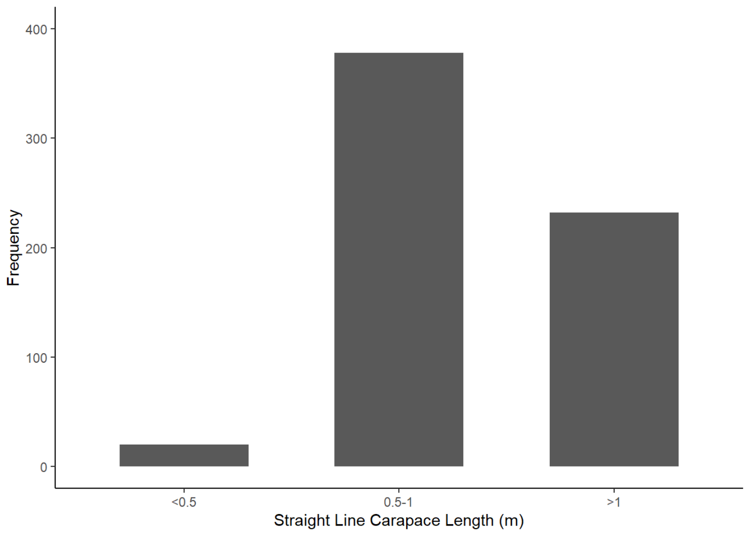

Figure 3.9 - Size-class distribution found of the green turtles sighted in Pearl Harbor, 2000-2011, based on in-water direct observations (*n*=630)

The use of depth by the different size categories varied significantly between size groups (Kruskal-Wallis, K= 39.95; p-value < 0.001, Figure 3.10). The smallest individuals were found in transects performed at shallower locations. Turtles with an estimated SCL ranging from 50cm to 1.0m were found at relatively deeper sites when compared with the smallest size-category ($P_{\text{Holm-corrected}} < 0.01$). Individuals larger than 1.0m in SCL were found at relatively deeper locations than 50cm-1.0m SCL turtles ($P_{\text{Holm-corrected}} < 0.01$) (Figure 3.10).

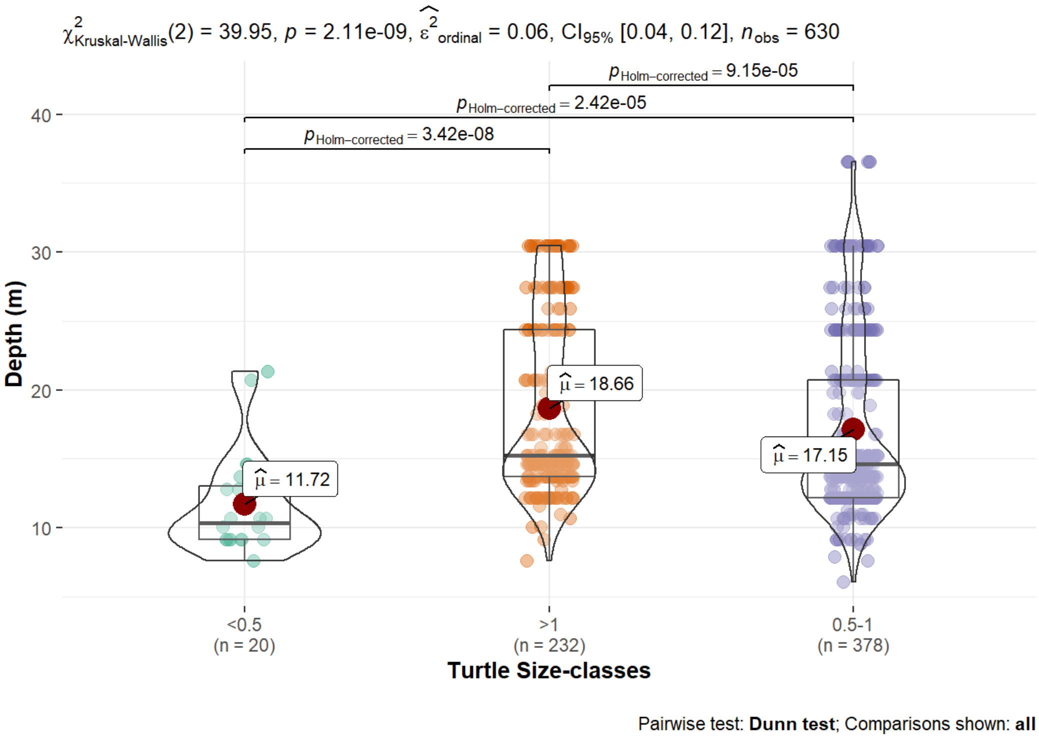

Figure 3.10 - **Kruskal-Wallis comparing the three turtle size categories across transect depth (m) in which individuals were recorded.** <0.5 represents the smallest size class, with individuals up to 50cm in Straight-Line Carapace Length; 0.5-1 represents medium size class with turtles ranging from 50cm to 1.0m SCL; >1 represents large size class, with individuals estimated to be above 1.0m in SCL. $P_{Holm-corrected}$ represent Holm adjusted p-values used in the Dunn's pairwise comparisons.

4. Discussion

Green turtles are not uniformly distributed within Pearl Harbor, Oahu, Hawaii. We found evidence of a regular presence in entrance channel locations and increased number of turtle records per transect, between 2000 and 2011. In Pearl Harbor entrance channel, two main locations provided significant resting habitat for green turtles, confirmed by the annual trends found, qualitative sighting data concerning turtle behaviour and environmental features documented. We also found evidence of spatial variability in the behaviours exhibited by turtles, with resting and cleaning activities almost exclusively restricted to entrance channel locations. During the time period examined, we found resting habitat restricted to a particular region within the harbor, West Loch Channel, where green turtles were sighted resting in freshwater springs. Inside the harbor, turtle sightings were uncommon, leading to a high proportion of transects with zero observations. The lower number of turtles detected in transects inside the harbor is likely due to the true absence of turtles or a failure in turtle detection due to poor visibility conditions. The absence of significant foraging and resting elements found inside the harbor during our surveys may have leaded to the notable absence of turtles. We found evidence of seasonality in the presence of *C.mydas*, with a slightly lower number of records in early months of the year. Juvenile, subadult and adult green turtles were present in the study area during the time-period considered, with the most abundant individuals belonging to the medium size category, SCL ranging from 50cm to 1.0m. Between the three turtle size categories, we detected differential distributions in their use of water depth.

4.1. Spatio-temporal distribution of green turtles

4.1.1. Annual trends, habitat associations and behaviours

For all locations combined, there was a general increase in number of green turtles observed over the 10-year period (Figure 3.3), analyzed in this historical dataset. These results suggest that Pearl Harbor may be important habitat for the Hawaiian subpopulation. Reasons for this increase may be attributed to the conservation efforts that have targeted the Hawaiian green turtle subpopulation and the suitable turtle habitat found in some regions of Pearl Harbor. The Hawaiian green turtle subpopulation is limited to the Hawaiian island chain, with turtles residing in foraging grounds around the Main Hawaiian Islands in between breeding migrations (Balazs & Chaloupka 2004). Hawaiian green turtles have been demonstrating promising signs of recovery after a long period of protection, with an increasing population trend observed (Balazs & Chaloupka 2006; Humburg & Balazs 2015; Valdivia et al. 2019). We consider the general increase found in records from 2000 to 2011 to be mostly a result of the conservation measures applied and, thus, a reflection of the green turtle increased presence in the Hawaiian Archipelago. The greater presence of green turtles into the study area was also likely affected by the suitability of habitat. Hawaiian green turtles have been showing strong fidelity for chosen foraging locations (Keuper-Bennett & Bennett 2000; King 2007; Balazs et al. 2017). However, methods used in our study do not allow us to assess site fidelity of turtles.

We found green turtles to have a patchy distribution in Pearl Harbor. For the entire study region, it would be inadequate to pool survey results, therefore we analyzed sampling areas or regions in particular. Presence of turtles was the highest on transects performed in the entrance channel (Figure 3.2), where potential foraging and resting habitats are found in several locations. Of the total 21 locations sampled, we identify three important areas situated at the opening of the entrance channel - 2, 19 and 21 -, accounting for approximately 76.7% of total turtles sighted in transects (*n*=680).

Location 21 is a specific reef feature within Location 2, and these two areas together had almost half of total turtles sighted across the study period of 10 years. The number of turtle records in both locations was relatively constant throughout the years, although annual trends in Location 2 fluctuated at the significance level considered (Figure 3.4). A decrease in turtle sightings was found in the middle years of the study for Location 2, attributed to the absence of surveys in this this area between 2004 and 2006 (Annex Table 6.3). Concerning benthic characterization, recent surveys revealed these two locations to have diverse biotic cover that includes macroalgae, turf algae, and a notable amount of live coral (Table *3.1*) (Wells et al. 2020b).

Within locations 2 and 21, we found most turtles resting and swimming and, to a lesser extent, being cleaned (Figure 3.8). Underwater caves are present in both locations and turtles were observed to rest within these features (Table 3.4). Hawaiian green turtles have been found to spend a lot of time resting in coral reefs and underwater caves within foraging grounds, commonly in association with marine algae pastures (Balazs 1980; Balazs et al. 1987). Further, green turtles are frequently seen being cleaned within resting sites, suggesting the two behaviours are performed within the same habitats, thus behaviours observed in locations 2 and 21 were expected. Turtles were not observed foraging in these locations or any other in Pearl Harbor, although the macroalgae cover and seagrass presence in locations 2 and 21 may provide forage for the turtles. Hawaiian green turtles consume native and introduced algae and, around Oahu, predominantly forage on red algae (Balazs et al. 1987; Arthur & Balazs 2008). We cannot confirm the occurrence of red algae in locations 2 and 21 for the time-period considered, given the absence of data, however its generalized presence in the entrance channel region was detected in recent surveys (Wells et al. 2020b).

We found a significant increase in the number of turtle records in location 19 in last years of the study (Figure 3.4). Location 19 begins where the Fort Kamehameha Wastewater Treatment Outfall pipe emerges from the seafloor. The pipe was installed in the latter half of 2004 and became operational in January 2005. Green turtles in this area were observed swimming, resting and, to a lesser extent, stationary at cleaning stations (Table 3.4, Figure 3.8). The divers observed turtles congregating around the outfall pipe and resting near this feature; cleaning stations were also observed to become established shoreward of the pipe. The regular presence of turtles in Location 19 after the installation of the pipe may indicate this is a significant habitat feature for them. Similarly, green turtles were observed to crowd within a plume of warm water close to an outfall can in Maui (Balazs et al. 1987), an important foraging ground for the Hawaiian *C.mydas* (Balazs et al. 2017). Balazs 1987 attributed this behavior to thermoregulation (Balazs et al. 1987). It is thus possible that resting close to this feature has thermal benefits for green turtles. No foraging activity was observed, despite the extensive seagrass beds adjacent to this location found in the surveys. Seagrass species are a significant component of the diet of green turtles residing in Kaneohe Bay, Oahu (Arthur & Balazs 2008), although the extent in which Hawaiian green turtles incorporate seagrasses in their diet seems be a function of its availability in the landscape (Russell et al. 2003). Similar to Locations 2 and 21, we found Location 19 to be used as resting habitat by approximately half of turtles sighted in this area.

Turtle records per transect in the remaining entrance channel locations were relatively lower (Figure 3.6). Some locations such 3, 17 and 18 though had a relatively higher presence of turtles across the many transects performed (Figure 3.2). Locations 3 and 17 showed no difference from the global trend (Table 3.3), hence we found a generalized increase in turtle records in these locations. Location 18 presented a significant decrease of turtle sightings in middle years of the study (Figure 3.4), attributed to the absence of surveys between 2006 and 2008 (Annex Table 6.3). Once again, no turtles were detected foraging. In more recent data, these locations were found to have either notable live coral (Location 18) or macro and turf algae (Location 3) cover, as well as seagrass present in both locations (Table 3.1) (Wells et al. 2020b), potentially providing forage and resting sites for green turtles.

Possibilities for the absence of observed foraging activity in our surveys include a differential distribution of turtles' foraging and resting areas, variations in temporal and spatial distribution of turtle forage within the study region and sampling bias. Foraging sites of Hawaiian green turtles have been found in proximity with resting habitats, usually only within a few kilometers of each other (Balazs et al. 1987). Green turtles tend to use Locations 2, 19 and 21 mainly as resting spots, or were found just passing by (swimming). Foraging could occur in other nearby locations outside Pearl Harbor, which might present food sources in a relatively higher quality or quantity. Recent benthic cover and the amount of potential turtle forage observed in current surveys may not reflect its availability between 2000 and 2011 (Wells et al. 2020b). It is also important to refer we do not know the exact location where turtles were sighted within the sampling areas, since the location of transects performed was not recorded. Spatial distribution of transects performed within a given area, which is unknown, may have not coincided with the spatial distribution of food sources in the landscape. Another possibility for the absence of observed foraging activity is linked with a particular sampling aspect, regarding transects' time of day. Time of day at which surveys happened was not recorded, although it is known that nearly all the surveys happened at daytime. Green turtles have been reported to feed at night (Bjorndal 1980; Balazs et al. 1987), thus the prevalence of daytime transects might have leaded to a failure in the detection of this behaviour.

We found a much lower number of turtles detected in transects inside the harbor. Several locations, namely 7 and 10 to 16, had a total of zero to one turtle sighted in transects across the 10-year period examined (Figure 3.6). Consequently, it was not possible to establish annual trends and we consider most of these areas to be of negligible use by turtles. Locations 5, 6, 8 and 9 in the West Loch Channel had greater and more regular turtle presence than most other areas inside Pearl Harbor (Figure 3.2). Several freshwater springs were found in West Loch Channel during the surveys which, when flowing, spring discharge water was cooler than the sea water. Green turtles were observed positioning themselves on the flows of freshwater springs. Freshwater springs are present in several nearshore areas around the main Hawaiian Islands but, green turtles have not been sighted using these features (Balazs et al. 1987). To our knowledge, this behaviour has not been reported elsewhere. None of the springs where turtles were observed during our surveys have shown any signs of outflow for several years, however, it could be important to determine the role of the cooler water flows provided by springs in thermal biology of sea turtles.

4.1.2. Sources of zero observations

The lower number of turtles sighted within the harbor can be, in part, due to the absence of suitable resting and foraging turtle habitat found during the surveys in this region. Most harbor floor on locations inside Pearl Harbor is essentially featureless, with flat silty seafloors with ship mooring and debris scattered throughout. Corals and seagrass, which could provide potential forage and resting sites, are either absent or sparse and patchy (Wells et al. 2018, 2020b; Wells 2020). Most locations also presented high sedimentation and turbidity during the surveys, naturally affecting underwater visibility estimates. We found underwater visibility to significantly influence the number of turtles sighted per transect and, consequently, to possible influence their detectability. As seems intuitive, greater visibility leaded to a greater number of turtle records (Figure 3.5). Further, locations with relatively lower turtle sightings and locations with the worst visibility conditions, situated inside the harbor, are coincident (Figure 3.6 and Annex Figure 6.2). We consider underwater visibility to play a role in the high proportion of zero observations found and, ultimately, in detectability of sea turtles.

When using line transect sampling, the probability of detecting individuals on or near the transect is expected to be high (Buckland et al. 2001), being assumed to be 1 on the line for conventional distance sampling. Divers performed transects close to the bottom, which is the location where turtles are expected to be more difficult to detect, thus the likelihood for detecting all turtles on or near the track line was increased. However, most locations inside Pearl Harbor had poor visibility conditions, which might violate the perfect detectability assumption considered in line transect sampling (Gates et al. 1981). Visibility and, thus, detectability problems when using a line-transect methodology can be dealt with by taking measurements such as the distance and angle of the individual sighted from the track line (Marshall et al. 2008). Methods used in our study did not considered these kinds of measurements, required for standard distance sampling, so we were not able to calculate a detection function for observing turtles. However, we can examine possible sources for such a high proportion of transects with zero observations.

In ecological count data, zero observations can have several causes; we consider the zero counts found inside the harbor to have two possible sources. The first is a true zero, where the study species does not occur in the landscape because the habitat is unsuitable (Martin et al. 2005). As already mentioned, most of the locations inside the harbor have low habitat complexity. Consequently, green turtles might have not been able to find suitable foraging and resting habitat in this region. The harbor is also a site of human activity, which might suppress turtle presence. Considering this source, detectability of individuals would then be just related to habitat characteristics. The other possible source is a false zero, the species occurs at a site and is present during the survey, but the observer fails to detect it (Martin et al. 2005). Sighting and environmental conditions do not affect true density, but might alter the area an observer is able to search (Beavers & Ramsey 1998). Water visibility has been demonstrated to influence sea turtle detectability when used as predictor in estimating turtle abundance (Williams et al. 2017). Further, Balazs et al. (1987) have noticed, in an assessment of Hawaiian green turtle foraging grounds that, under turbid conditions, green turtles can detect the proximity of the diver and swim away before entering its field of vision. This causes the number of turtles sighted to be small since the area that could be observed is restricted. We thus consider this oceanographic covariate to partially explain the high proportion of zero turtle records found inside the harbor, coupled with a possible unsuitability of the habitat. Owing to limited visibility, it is likely that more sea turtles went undetected and hence were present within Pearl Harbor.

Lately, green turtles have been found to have a generalized distribution inside the harbor. During our surveys, we found resting habitat restricted to the West Loch Channel. Recent surveys concerning turtle habitat inside the harbor have shown a patchy distribution of turtle resting sites (Wells 2020), that were not documented before. It is crucial to note that we are analyzing an historic data set that shows changes in the turtle population over time. Green turtles may have been able to change their use patterns of different parts of the harbor, expanding their use of this region.

4.1.3. Seasonal patterns and environmental associations

We found seasonal fluctuations in the presence of green turtles in the study region. From the model results (Figure 3.5), we detected a decrease in turtle records per transect between approximately March and June, just partially coinciding with the warm season, May through October. Hawaiian *C.mydas* reproductive migrations may explain the lower number of sightings during these months. Hawaiian green turtles forage in the Main Hawaiian Islands and, every three to four years, females migrate to French Frigate Shoals to nest, on the Northwest Hawaiian Islands (Balazs & Chaloupka 2004; Humburg & Balazs 2015; Balazs et al. 2017). Green turtles' trip from the Main Hawaiian Islands to FFS has been found to range between 16 to 94 days (Balazs et al. 2017). Nesting activity at FFS increases in May, has a peak between June and early August and starts to decline in late August (Niethammer et al. 1997). Further, Balazs (1980) found that copulations in the waters of FFS took place even earlier than the nesting period, starting in middle of April. It is possible that green turtles found in Pearl Harbor are leaving this region during the early months of the year, migrate to FFS and then return when the nesting season ends, explaining the peak of observations found in September and October. Seasonality in green turtle occurrence in Pearl Harbor have been observed in more recent surveys. Scientists found an analogous seasonal pattern in turtle sightings, with peaks occurring in the winter and a break in turtle records in May, June and July (Richie et al. 2016). As the authors stated, a long-term study would be required to establish if these fluctuations found are factual. In our study, sampling effort was irregular, with a notable absence of transects in several months across all years, particularly in January (Table *3.2*). More regular, systematic sampling could have improved the significance of this result, allowing us to infer more reliable conclusions on green turtle seasonal patterns in Pearl Harbor.

We found sea surface temperature to significantly affect the number of turtle records in Pearl Harbor. The available water temperature range for the turtles to occupy was 23.2ºC to 27.4ºC (Table *2.1*). Two peaks in SST, associated with a higher number of turtles, occurred at about 24-25ºC and around 26.5ºC (Figure 3.5). Sea surface temperature has been found to determine spatio-temporal distribution of green turtles (Spotila et al. 1997; Becker et al. 2019), however we consider the pattern observed to be a reflection of the water temperatures found for the two general seasons. In the cool season, average of mean monthly water temperature values found was 25.1ºC and, in the warm season, the average was 26.4ºC (Annex Figure 6.5). The peaks observed in the sea surface temperature smoother plot are somewhat coincident with the average water temperature values found. Since water temperatures are commonly dependent on season, using changes in temperature between months might have improved predicting turtles' preferred temperature range (Shimada et al. 2016).

Based on previous assessments, water temperatures in Pearl Harbor vary annually from 23 to 29ºC (Coles et al. 1999). We found our remotely collected temperature data, extracted from 2002 until 2011, to be consistent with historic water temperatures. Concerning the predictive ability of models with remotely sensed covariates such as sea surface temperature, these have been found to generally produce similar results when compared with models using *in situ* measures (Becker et al. 2010). However, given both the dimensions and division of the sampling areas in our study, fine scale differences in water temperature might have been missed. We selected the finer spatial resolution available, 1km resolution, but it is still much wider than some of the areas within the harbor. It is thus possible that remotely sensed sea surface temperature is not accurate for some regions of Pearl Harbor. We strongly recommend using sea surface temperature collected *in situ* or, if not possible, at a higher spatial and temporal resolution in future studies.

4.2. Size-class distribution and depth preferences

The data set contained sightings of juvenile, subadult and adult green turtles in Pearl Harbor (Figure 3.9), during the time-period examined. The estimated sizes of sea turtles in our study were reported in 50cm categories. Balazs (1980) defined size categories for Hawaiian *C.mydas* in the following categories: juveniles are comprised of post hatchling to 65cm SCL; subadult - 65 to 81cm SCL individuals; and adults comprised of individuals with SCL above 81cm. We found the medium size category, from 50cm to 1.0m SCL, to be the most frequently observed in Pearl Harbor (Figure 3.9), which overlaps Balazs' juveniles, subadults and adults size classes. Smaller turtles, from post hatchling to 50cm SCL individuals, were rarely sighted. The size-class distribution found followed the relative size-class structure of green turtles encountered in Hawaiian foraging grounds prior to our study, where juveniles above 35 cm SCL and subadults were most numerous (Balazs et al. 1987). Further, green turtle stranding data from four Hawaiian Islands, Kauai, Oahu, Maui and Hawaii, revealed an incidence of small juveniles ranging from 40 to 60cm SCL (Chaloupka et al. 2008b). The lower number of smaller individuals found was expected, since the observed minimum SCL at which Hawaiian green turtles recruit to nearshore habitats from the pelagic environment is documented to be 35cm (Balazs 1980; Balazs et al. 2015).

Concerning distribution of turtles by depth, we found distinct depth preferences across the three size categories considered (Figure 3.10). Smaller turtles were sighted in transects performed at relatively shallower sites, whereas larger individuals were sighted in relatively deeper habitats within the study region. Spatial segregation by size in green turtles have been found in foraging grounds worldwide (Bresette et al. 2010; López-Castro et al. 2010), and turtles have been hypothesized to display this behaviour both due to distinct habitat requirements and to reduce predation risk. Similarly in Hawaii, Balazs (1980) observed a tendency among juveniles and subadults to use resting sites located at shallower depths. Some insights into the turtles comprising the medium size category can also be obtained when looking at depth distribution. The significant difference between medium and large categories regarding depth preferences, and the size-class distribution observed in stranding data (Chaloupka et al. 2008b), may indicate that medium size category is likely to include a large proportion of juveniles. However, we were not able to quantitatively estimate the proportions of juveniles, subadults, and adults present in this size category.

Depth was not a significant environmental predictor for the number of turtles sighted per transect, however green turtles in Pearl Harbor were mostly sighted in a depth range of 5 to 20m (Figure 3.5). Depth of transects performed ranged from 3.0m to 36.6m (Table *2.1*). The results found regarding depth distribution should be considered carefully since survey transects were performed at pre-established depths. The preferred depth range found could reflect the performed transect depth since, as already mentioned, sea turtles recorded in the surveys were on or near the track line. Estimates based on transects might not reflect turtles' optimal depth range in the region, although the results likely identify an accurate depth distribution pattern.

4.3. Suggestions for future improvement and final considerations

The present study suggests there was a regular and continued concentration of green turtles in Pearl Harbor Entrance Channel between 2000 and 2011. A generalized presence of green turtles throughout Pearl Harbor has been found in recent surveys. Apparently, anthropogenic activities in Pearl Harbor do not seem to bother the turtles or are not sufficiently disturbing to discourage them from using this region. Nonetheless, and given the increased turtle presence in Pearl Harbor, future studies should consider the quantification of turtle mortality by vessel strike in this location and, if necessary, the definition of zones with reduced boat speed to minimize vessel-turtle collisions (Shimada et al. 2017). Boat strike was found to be the most likely human-related cause of green turtles dead strandings on the main Hawaiian Islands (Chaloupka et al. 2008b). We further recommend future studies in Pearl Harbor to also include photo-identification of turtles sighted (Williams et al. 2017) as a complementary methodology to the U.S. Navy monitoring activities to assess site fidelity, if physical mark and recapture methods of assessing population structure is not feasible. Recording distances and angle of turtles sighted from the track line would allow to use standard distance sampling methods and calculate a detection function (Buckland et al. 2001), thus improving the analytical methods used.

Maintaining and improving the monitoring activities described in our study is crucial, and an important step in complying with the Sikes Act and other natural resource relevant laws. By investigating temporal and spatial patterns of use of the environment, we reconstructed green turtle's past use of an historic location such as Pearl Harbor, from a decade of observations, and identified significant resting habitat. Further, the analysis of the qualitative sighting data allowed us to assess the relative population structure of green turtles found in Pearl Harbor environment. A continuous analysis of the type of data presented in our study is needed for the Navy and Regulatory Agencies to manage turtle populations on a scale that is relevant to the U.S. Navy activities. Ultimately, by analyzing this detailed information, we hope to contribute to the extensive knowledge on distribution and ecology of Hawaiian green turtles. Determining habitat use within foraging grounds is critical for the conservation of this subpopulation.

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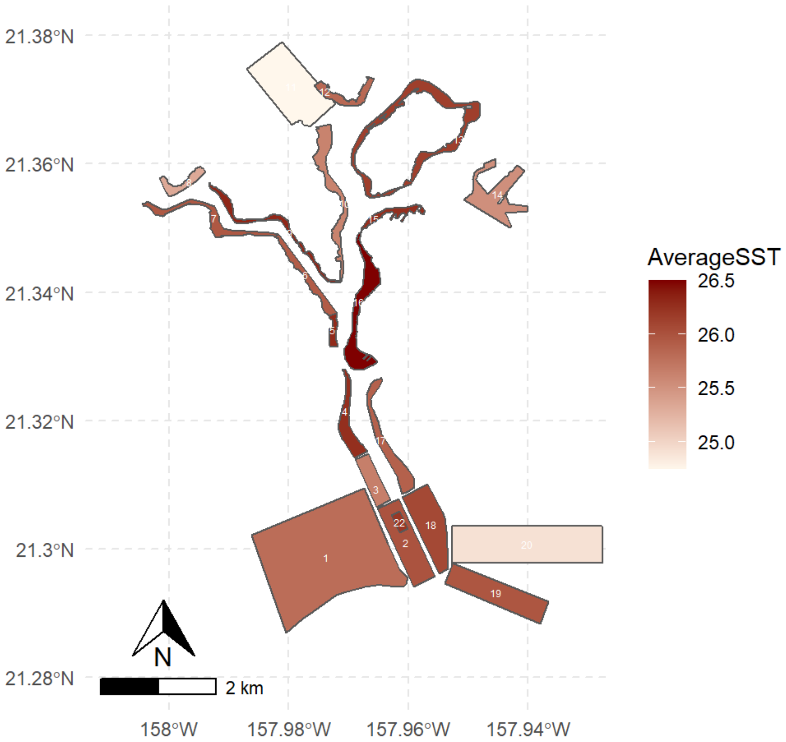
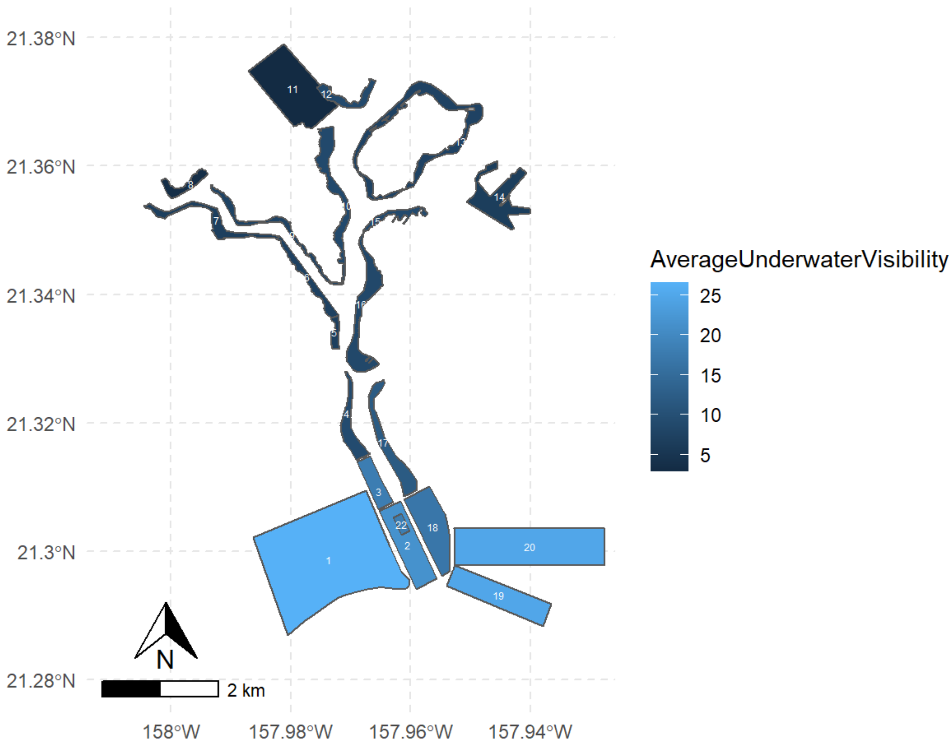
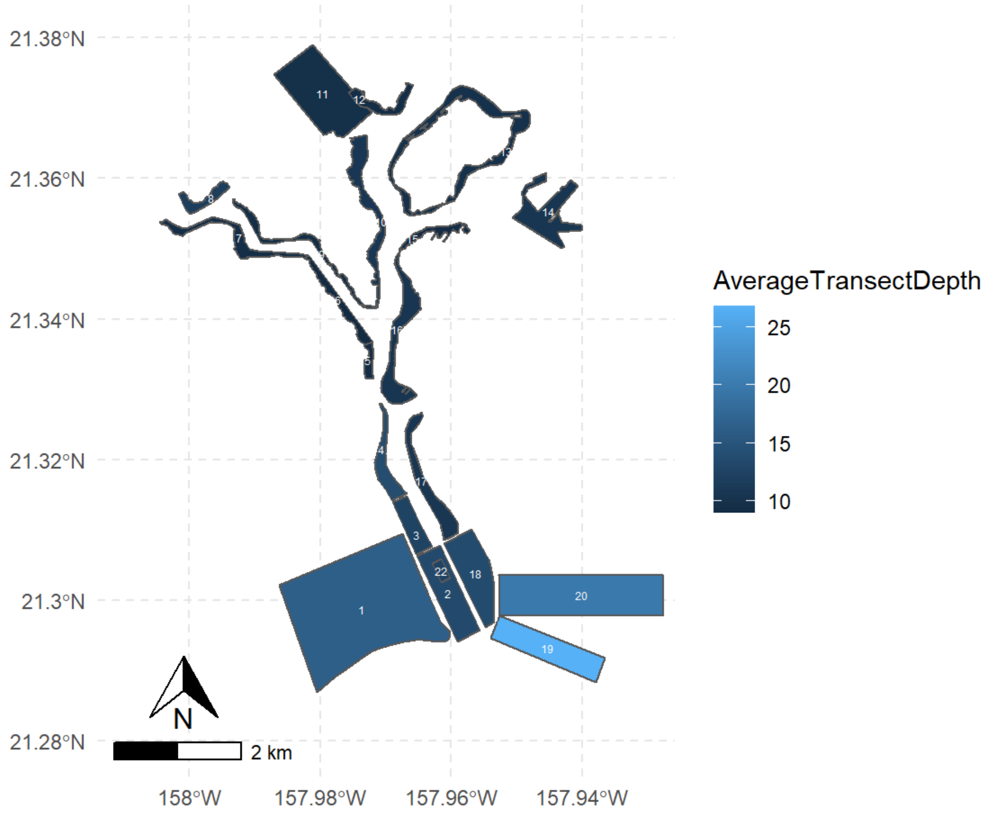
6. Supplementary Material



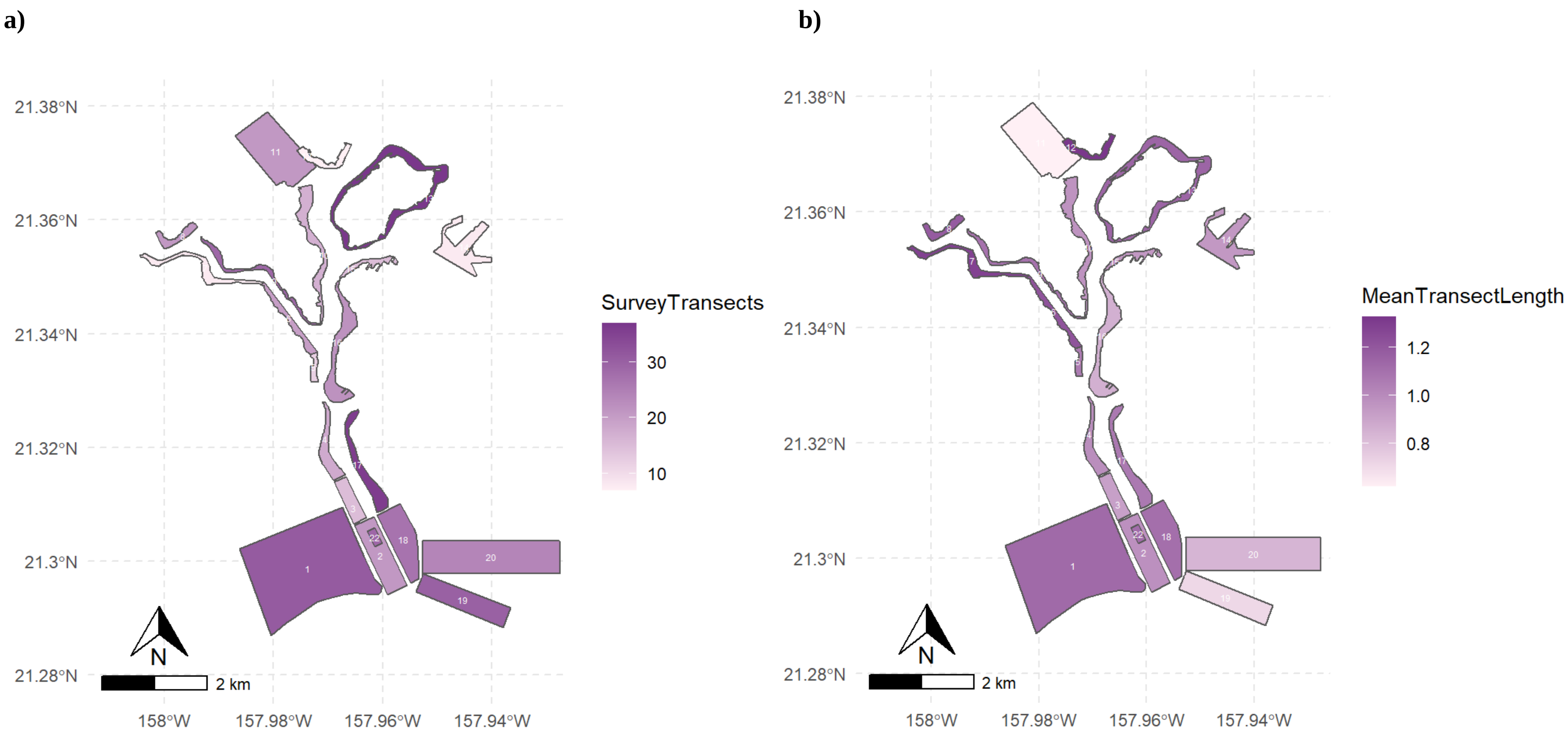
Annex Figure 6.1 - Spatial variability of sea surface temperature monthly means, remotely extracted and averaged for the time-period examined, 2002-2011, in Pearl Harbor



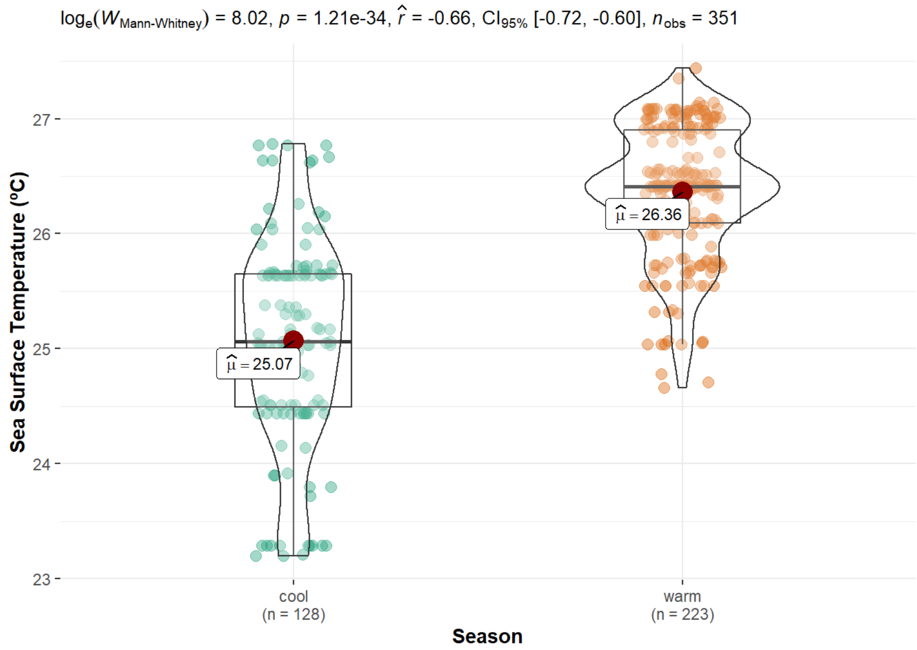
Annex Figure 6.2 - Spatial variability of the average underwater visibility, in meters, estimated in transect surveys per location, Pearl Harbor, 2000-2011



Annex Figure 6.3 - Spatial variability of the average depth, in meters, of transect surveys per location, Pearl Harbor, 2000-2011



Annex Figure 6.4 - **Sampling effort per location in Pearl Harbor, 2000-2011**, expressed in a) Total transects performed per location, b) Average transect length, in kilometers, of all transects performed per location



Annex Figure 6.5 - Mann-Whitney test comparing mean monthly sea surface temperatures found for two general seasons in Hawaii, from 2002-2011 in Pearl Harbor.

Annex Table 6.1 - Spearman correlation coefficient calculated between covariates incorporated in the ZIP-HGAM optimal model

	Year	Month	SST	Depth	Visibility
Year	1	0.031714	-0.1272156	0.1005903	0.1397607
Month	0.031714	1	0.3911167	-0.02584116	0.1802453
SST	-0.1272156	0.3911167	1	-0.09971367	0.09708254
Depth	0.1005903	-0.02584116	-0.09971367	1	0.5935674
Visibility	0.1397607	0.1802453	0.09708254	0.5935674	1

Annex Table 6.2 - **Comparison between models results for the number of turtles sighted per transect in Pearl Harbor, 2000-2011.** Distribution of families considered during the statistical analysis are presented in the first column. Temporal and environmental variables, Akaike's Information Criterion (AIC) and explained deviance values of each model considered are shown. Interaction terms between sampling area and year were incorporated in all models but are not shown

Model	Covariates	Effective degrees of freedom	Chi square	p-value	AIC	Deviance explained (%)
ZIP-HGAM	Year	6.526	52.557	<0.001	769.7	78.5
	Month	2.328	6.846	0.021		
	SST	4.164	14.874	0.010		
	Depth	2.376	6.765	0.071		
	Visibility	1.002	5.251	0.022		
ZIP-HGAM (backward elimination)	Year	6.106	39.713	<0.001	773.6	77.3
	SST	5.097	25.135	<0.001		
	Visibility	1.671	6.182	0.049		
Poisson-HGAM	Year	1.000	4.424	0.035	861.4	81.5
	Month	1.881	13.790	<0.001		
	SST	6.980	52.080	<0.001		
	Depth	3.383	21.451	<0.001		
	Visibility	2.772	12.807	0.009		
Negative Binomial-HGAM	Year	1.000	1.474	0.225	812	69.7
	Month	1.078E-5	0	0.478		
	SST	1.664	11.075	0.004		
	Depth	2.335	3.898	0.265		
	Visibility	1.000	1.914	0.167		
Model	**Covariates**	**Effective degrees of freedom**	**F-value**	**p-value**		
Tweedie-HGAM	Year	1.000	2.620	0.1065	864.5	69.6
	Month	3.106E-5	0	0.386		
	SST	1.651	0.800	0.445		
	Depth	2.674	2.011	0.105		
	Visibility	1.000	2.406	0.122		
Model	**Covariates**	**Slope**	**Z-value**	**p-value**	**AIC**	
ZI-NB Count model	Month	-0.027	-0.598	0.550	1086.1	
	SST	0.220	1.595	0.111		
	Depth	0.072	3.066	0.083		
	Visibility	65.255	3.485	<0.001		
ZI-NB ZI model	Month	-0.036	-0.542	0.588		
	SST	0.331	1.640	0.101		
	Depth	-0.007	-0.237	0.813		
	Visibility	-49.781	-2.151	0.031		

Annex Table 6.3 - **Summary data: total transects performed per location per year**. {-} represents no turtle surveys were performed in the given location in that year. The first part of the table presents transects performed within locations. The second part, separated by a shaded row, presents transects that crossed locations, as indicated by location names that are separated by hyphens.

Location /Year	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011		Total transects performed
1	7	-	4	2	-	2	-	1	4	3	7	1		31
2	-	-	8	5	-	-	-	2	1	3	2	-		21
3	3	-	4	2	-	-	-	2	1	2	1	-		15
4	1	-	5	-	-	2	-	1	2	4	3	-		18
5	-	-	3	-	-	3	-	1	2	2	1	-		12
6	-	-	4	4	1	4	3	1	-	1	2	-		20
7	-	-	2	2	-	-	3	-	1	-	-	-		8
8	-	-	1	3	-	14	-	-	-	2	1	-		21
9	2	-	6	6	-	6	4	-	1	3	1	-		29
10	2	-	4	2	-	-	1	1	3	4	-	-		17
11	4	-	5	-	-	1	-	11	-	-	-	-		21
12	1	-	2	-	-	-	-	-	2	2	-	-		7
13	15	-	2	2	-	2	-	1	8	5	2	-		37
14	1	-	3	-	-	-	-	2	1	1	-	-		8
15	1	-	3	-	-	2	1	1	4	2	1	-		15
16	-	-	5	-	-	4	-	4	2	5	2	-		22
17	6	-	10	13	-	3	2	1	-	1	-	-		36
18	7	-	5	5	-	5	-	-	-	4	1	-		27
19	3	-	-	1	1	5	3	1	6	6	3	1		30
20	-	4	5	4	-	-	-	-	1	10	-	-		24
21	-	-	4	10	-	7	3	-	2	1	2	-		29
1-2-18	-	-	4	-	-	-	-	-	-	-	-	-		4
2-1	-	1	-	-	-	-	-	-	-	-	-	-		1
6-7	-	-	1	-	-	-	-	-	-	-	-	-		1
19C	1	-	-	-	-	-	-	-	-	-	-	-		1
4-5	-	-	1	-	-	-	-	-	-	-	-	-		1
3-4	-	-	2	-	-	-	-	-	-	-	-	-		2
2-3-4	-	-	1	-	-	-	-	-	-	-	-	-		1
2-21	-	-	-	-	-	-	-	1	-	-	-	-		1
19-2	-	-	-	-	-	-	-	-	3	1	-	-		4
Total records per year	**54**	**5**	**94**	**61**	**2**	**60**	**20**	**31**	**44**	**62**	**29**	**2**		**464**

Annex Table 6.4 – **Number of total transects performed in each location, number of transects with sea turtles sighted, and summary statistics of the counts per transect.** The first part of the table presents transects performed within locations. The second part, separated by a shaded row, presents transects that crossed locations, as indicated by location names that are separated by hyphens.

Location	**No. of transects**	**No. of transects w/ turtles**	**% Transects w/ turtles**	**Count**			
				Min	Max	Mean	SE
1	31	6	19.4%	0	8	0.61	0.30
2	21	16	76.2%	0	19	5.29	1.13
3	15	5	33.3%	0	17	1.73	1.14
4	18	3	16.7%	0	4	0.50	0.31
5	12	4	33.3%	0	1	0.33	0.14
6	20	5	25%	0	3	0.35	0.17
7	8	0	0%	0	0	0.00	0.00
8	21	2	9.5%	0	4	0.24	0.19
9	29	3	10.3%	0	1	0.10	0.06
10	17	1	5.9%	0	1	0.06	0.06
11	21	0	0%	0	0	0.00	0.00
12	7	0	0%	0	0	0.00	0.00
13	37	1	2.7%	0	1	0.03	0.03
14	8	1	12.5%	0	1	0.13	0.13
15	15	0	0%	0	0	0.00	0.00
16	22	1	4.5%	0	1	0.05	0.05
17	36	12	33.3%	0	6	0.61	0.20
18	27	9	33.3%	0	10	1.19	0.47
19	30	20	66.7%	0	28	7.03	1.44
20	24	1	4.2%	0	5	0.21	0.21
21	29	25	86.2%	0	22	6.90	1.15
1-2-18	4	0	0%	0	0	0.00	0.00
2-1	1	0	0%	0	0	0.00	-
2-21	1	1	100%	14	14	14.0	-
2-3-4	1	1	100%	3	3	3.0	-
3-4	2	2	100%	1	2	1.50	0.50
4-5	1	0	0%	0	0	0.00	-
6-7	1	0	0%	0	0	0.00	-
19-2	4	2	50%	0	1	0.50	0.29
Total	464	121					

Annex Table 6.5 - **Number of turtles expected to be sighted in transects per location, based on the optimal ZIP-HGAM**. Predictions used average values of environmental predictors, depth, SST and visibility, and transect length, incorporated as offset term the model.

Location	Number of turtles expected to be sighted per transect
1	1.98
2	2.24
3	1.81
4	0.73
5	0.72
6	0.36
7	0.15
8	0.56
9	0.20
10	0.20
11	0.14
12	0.19
13	0.10
14	0.18
15	0.12
16	0.10
17	2.28
18	0.56
19	12.00
20	0.38
21	10.91