

**Abiotic factors structuring habitat use in angel
sharks, *Squatina squatina***

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Abstract

The distribution and degree of habitat specialism in endangered shark species is known to compound the risk of extinction (Walker 1998). However, such information is not known of *Squatina squatina*, despite the critically endangered status of the species (OSPAR commission 2010). As such, this research has used one of the largest online surveys on *S. squatina*'s distribution to gain such information. Similarly, data on *S. squatina*'s habitat associations were collected on SCUBA from visual census surveys at two sites in Lanzarote (Canary Islands, Spain), and analysed with T-tests.

The online survey produced a number of key areas relating to *S. squatina* mating or breeding. However, some sites were associated with both mating and breeding, suggesting the presence of a mating site and nursery area in the same location, something which has seldom been observed in other shark species, but which is thought to be crucial information which can lead to more informed decisions and contribute to the conservation of the species (e.g. MPAs, nature reserves, protection plans etc.) (Carrier and Pratt 1998). Results of the visual census surveys suggest that *S. squatina* has a preference for more complex habitat types (i.e. higher levels of macro algae and loose rock) and a specific range of benthic sediment grade. Furthermore, juvenile *S. squatina* were found to occur at significantly shallower depths than mature *S. squatina*, while gravid females were found to occur in waters which were significantly lower in temperature than non-gravid females. This type of habitat information of an endangered shark species also has the potential to contribute to conservation efforts as it can, for example, allow us to better understand why a species may select certain habitats and therefore better decide which elements of a habitat need preserving and protecting (Springer 1967, Sims 2003).

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Chapter one: General Introduction

Sharks and other elasmobranchs are thought to play a vital role in marine ecosystems, especially in coastal regions (Bascompte et al. 2005; Ferretti et al. 2008; Heithaus et al. 2008). Many marine communities would collapse and trophic cascades could ensue if predatory fish, such as sharks, were removed from marine systems (Dulvy et al. 2000; Shepherd and Myers 2005; Polovina et al. 2009). Apex predators, such as shark species, directly and indirectly affect food webs by regulating prey dynamics through predation, and by altering the behaviours of prey (Roff et al. 2016). Declines of apex predators in an ecosystem, often has cascading effects on lower trophic levels, creating mesopredator release which can cause changes in an ecosystems performance and food web dynamics (Roff et al. 2016).

Shark research has typically focussed on either, conservation (with the weight of research often placed on juveniles and shark nurseries) (Bonfil 1997, Heupel et al. 2007, Kinney and Simpfendorfer 2009), or growth patterns and diet composition (Speed et al. 2010). However, research has recently expanded more to areas such as habitat use and movement of mature sharks once they leave nursery areas (Chapman et al. 2009). Key elements of shark research which have been noted, include understanding the distribution patterns and types of habitats which endangered shark species select, and the reasons for this. This information is thought to be important if effective management is to be implemented (Springer 1967, Sims 2003).

Sharks are an ancient species of cartilaginous fish and a member of the class Chondrichthyes, which fall into the subclass of Elasmobranchii (comprised of sharks and rays) (Compagno 1984). The order Squatiniformes have only one family, Squatinidae, which contains only one genus known as *Squatina* (commonly known as an angel shark) (Ebert et al. 2013). There are currently 23 different angel shark species of the *Squatina* genus that have been identified, however, research indicates that angel shark taxonomy could be uncertain as there could still be undescribed *Squatina* species (Stelbrink et al. 2010; Vaz and de Carvalho 2013). In general, angel sharks face the highest risk of extinction of any of the other orders of sharks (Ebert et al. 2013). The IUCN has listed more than half of all identified angel shark species as threatened with extinction on the IUCN Red List of Threatened Species, however, it is thought that up to 80% of angel sharks could be revealed to be threatened as only two species of angel shark have actually been assessed at Least Concern by the IUCN (Ebert et al. 2013).

Common taxonomic characteristics of all species of the genus *Squatina* (angel sharks) include: a terminal mouth shape, barbels on anterior margin, spiracles on top of the head, long tail and caudal fin, and absence of an anal fin (Compagno 1984). Like all sharks, angel sharks, are known to have a low reproductive output i.e. long gestation periods, slow growth rates, late sexual maturity, small numbers of pups (Compagno 1990, Cortes 2000), which has been noted to compound the risk of extinction associated with a reduced and/or limited geographical distribution and habitat specificity (Walker 1998, Stevens et al., 2000). Furthermore, the survival of shark populations, such as angel sharks, is associated with numbers of well developed young, and their ability to survive long enough to reach sexual maturity and successfully reproduce (Simpfendorfer and Milward 1993).

The angel shark studied in this research is the species *Squatina squatina*, a north-eastern Atlantic, benthic shark with a historical range stretched along a large portion of the eastern Atlantic, ranging from Scandinavia to Mauritania (including the Canary Islands) (Miller 2015). Although historically abundant, there have been significant declines in the past 50-100 years in its former range leading to local extirpations and reduction of its range, leaving the Canary Islands as one of the few places where it can still commonly be seen (OSPAR 2010). As such *S. squatina* has been classified as *Critically Endangered* globally on the IUCN Red List of Threatened Species, and has also been added to the OSPAR List of Threatened and/or declining species and habitats. *S. squatina* is very seldom seen in research vessel surveys or caught in commercial catches as it once was (ICES WGEF 2007), and the lack of research on *S. squatina* means that any areas that have surviving populations are thought to be of regional importance and could be highly useful for study (such as in this case, the Canary Islands) (OSPAR 2010).

The gestation periods for *S. squatina* in the Canary Islands have been estimated at ± 6 months, while they are known to have a three year reproductive cycle (Osaer 2009). In the Mediterranean, *S. squatina* have litter sizes ranging from 7-25 pups per birth (Tonachella 2010), however, litter size is not known for *S. squatina* in the Canary Islands (Miller 2016). *S. squatina* spend a large amount of time buried in the sediment during the day with only their eyes protruding (Day 1880, Tonachella 2010). They are considered high trophic level predators (Cortes 1999) and most angel sharks, including *S. squatina*, are ambush predators, as they lie buried in sediment and wait for their prey to come to them before attacking (Miller

2015). The diet of this species in the Canary Islands consists mainly of teleost prey, especially flatfish (Compagno 1984, and Narvez 2012).

This thesis will focus on the distribution and habitat preferences of *S. squatina*, and will take place in the Canary Islands. This information is likely to help identify and prioritise the potential areas for the conservation of *S. squatina*, which is desperately needed for this critically endangered shark species. This is best studied in an area where *S. squatina* is still reasonably common (i.e. the Canary Islands), and in this case, is also likely to be one of the last places, globally, where *S. squatina* can still be regularly observed.

1.1 Outline of Chapters

In this study the work has been presented as two independent research chapters (each with their own introduction, methods, results and discussion) and one general discussion.

Chapter 2 describes the distribution of *S. squatina* in the Canary Islands. This chapter aims to identify key locations of *S. squatina* occurrence and discusses the importance of the life stages and sexes identified at these geographical areas within the Canary Islands in order to understand the extent of distribution of *S. squatina* and how this may affect their future survival. Additionally, this chapter aims to understand which large scale abiotic factors may be structuring the distribution of *S. squatina*.

Chapter 3 examines the habitat associations of *S. squatina*. This chapter aims to understand the degree to which *S. squatina* is specialised in its habitat use by comparing the fine scale habitat attributes of sites where *S. squatina* are present and absent. This chapter will also compare the fine scale habitat attributes associated with the occurrence of different life stages and sexes of *S. squatina* in order to understand how different subclasses within a population of *S. squatina* may demonstrate habitat specificity.

Chapter 2: Geographical Distribution of *S. squatina*

2.1 Introduction

The geographic distribution of a species population will impact population survival and rate of extinction, with species with a wide geographic distribution predominantly found in high local abundance, while species with narrow geographic distribution predominantly found in low local abundances (Brown 1984). This positive relationship between extent of distribution and population abundance is often attributed to the allee effect (otherwise known as depensation); if a species in a local population is found in high abundance it's population will naturally expand (through the increased interaction and mating of mature male and female individuals within the population) into suitable nearby habitats, with this process continuing (as long as new suitable habitats are available) as populations increase in abundance within new habitats (Caley 1996). Therefore, the likelihood of a species going extinct with these characteristics decreases (Caley 1996). In contrast, species with low local abundance and relatively small or even large geographical ranges will be at a high risk of extinction, as low local abundances are highly susceptible to stochastic environmental declines, while species that have restricted geographical ranges may be highly susceptible to habitat loss and therefore population constriction (Saraux 2014). Therefore, understanding an endangered species distribution will allow us to determine the future survival of the species.

Population numbers are an important factor which are related to the ability of a species to sustain its numbers. The capacity of individuals to find a reproductive partner is associated with adequate numbers (sufficient numbers of individuals which increases the likelihood of mature males and females interacting and mating) of individuals of both sexes, commonly known as the Allee effect (Stephens 1999). However, when individuals in a population become rare, and have a limited distribution with low local abundances, then recovery from population declines become less likely (Stephens 1999). For example, *Haliotis kamtschatkana*, a species of sea snail, formerly had a wide distribution along the British Columbia coast, however, due to fishing pressures *H. kamtschatkana* populations underwent substantial declines in their geographical range and local abundance (PSARC 1998). In an effort to increase the population (and reverse the effects from over fishing) of *H. kamtschatkana* in British Columbia, the fishery around the coast was closed. However, despite closure, the population has still been found to

be in decline, which was related to low local abundances and the restricted geographical range of the species (which was inhibiting population growth) (PSARC 1998). Successful reproduction in an animal species with a very low abundance is thought to increase as concentrations of animals increase (Jamieson, 1989), and so male and female distributions and abundances are crucial when attempting to understand an endangered species survival or risk of extinction. However, as the abundance of an animal species continues to increase, density-dependant effects begin (e.g. increased competition for shared food resources), and as such, negatively impact successful reproduction in the population (Courchamp et al. 1999).

The effects that a limited distribution will have on the population of a marine species can often be dependent on environmental conditions and the physiological limits associated with the species (Brook et al. 2008, Garcia et al. 2008, Field et al. 2009). Ambient water temperature is often associated with marine organism distribution and occurrence as water temperatures will effect metabolism in ectothermic marine species (Brown et al. 2016). For example, Claireaux et al., (1995) fixed ultrasonic transmitters on to *Gadus morhua* L. (Atlantic cod) to monitor their heart rate and movements within 125 cubic metre tank. The cod were then exposed to a variety of heterogeneous and homogenous water temperatures within the tank and their physiological and behavioural responses were recorded. When the temperature of all the water in the tank was raised (homogenously) there were increases in heart rate, heart beat variability and swimming activity in the cod, which was indicative of increased metabolism (Claireaux et al., 1995). However, when the water in the tank was separated by temperature, allowing the cod to choose the water temperature in which it occurred in, they displayed thermoregulatory behaviour by avoiding new temperatures (Claireaux et al., 1995). It was concluded that the cod avoided new temperatures to avoid energetic expenditure associated with acclimatisation of new ambient water temperatures (i.e. associated changes in metabolism) (Claireaux et al., 1995). A 2.5°C increase or decrease in ambient water temperature created changes in metabolic rates of 15-30% (Claireaux et al., 1995). Claireaux's et al., (1995) study demonstrates how even acute temperature changes can effect the physiology of Atlantic cod, and how thermal structures will influence their distribution i.e. Atlantic cod selected water based on minimising the energetic costs associated with changes in water temperature. Di Santo and Bennett (2011) studied the effects of ambient water temperature on the the resting metabolism of two benthic elasmobranch species, *Dasyatis sabina* (Atlantic stingray) and *Chiloscyllium plagiosum* (whitespotted bamboo shark). Di Santo and Bennett's (2011) study kept both elasmobranch species in separate tanks in which the water temperature was fluctuated between 24-27°C for

D. sabina and 23-25°C for *C. plagiosum*. Both elasmobranch species in this study showed increases in metabolism when water temperatures were raised, which resulted in increased oxygen consumption (Di Santo and Bennett 2011). Increases in the uptake of oxygen through thermoregulatory behaviour (e.g. species occurrence associated with warm waters), has been theorised to be advantageous in elasmobranch and shark activities, such as foraging and digestion (Bernal et al., 2001, Dickson and Graham 2004, Di Santo and Bennett 2011).

The effects of ambient water temperatures on the occurrence of shark species in the wild is an important factor associated with the distribution and survival of the species (Simpfendorfer and Heupel 2012). Environmental water temperature have often been associated with shark habitat and shark occurrence (e.g. Simpfendorfer and Heupel 2012). As nearly all species of shark are ectothermic, ambient water temperature is a crucial factor when it comes to understanding occurrence in the wild as it can greatly influence distribution, as it has been shown to control body temperature and regulate metabolic processes related to muscle recovery, digestion, embryo development and gestation (Taylor 1993, Economakis and Lobel 1998). For example, Morrissey and Gruber (1993) implanted ultrasonic transmitters into lemon sharks, *Negaprion brevirostris* so that they were able to track the shark's movements and relate this to environmental variables. It was found that juvenile lemon sharks, *Negaprion brevirostris*, in the Bahamas (Bimini) preferred waters of >30°C. It was hypothesised that the warm waters that lemon sharks chose allowed them to absorb oxygen from the water more efficiently due to the effect that increased ambient temperature had on their metabolic/biological processes (Morrissey and Gruber 1993).

Salinity concentrations can effect where a species is distributed as the physiological tolerances of a species can vary substantially (Elith and Leathwick 2009). Species distribution, based on salinity concentrations has been well noted in many marine species such as, *Salmo gairdneri*, rainbow trout (Rao 1968), *Mugil cephalus* (flathead grey mullet), *Liza dumerili* (grooved mullet) and *Liza Richardson* (southern mullet) (Marais 1978), and *Cyprinodon variegatus* (sheepshead minnow) (Barton and Barton 1987). For *S. gairdneri*, *M. cephalus*, *L. dumerili* and *L. richardson*, changes in water salinity (either increases or decreases) were associated with higher energetic costs (through increased osmoregulation), and as such, these marine species largely avoided varying salinities (Rao 1968, Marais 1978, Barton and Barton 1987).

Salinity has been noted as an important factor in describing elasmobranch and shark habitat and distribution, because of the metabolic costs associated with osmoregulation with changing salinities, which effects all elasmobranch species (Evans et al. 2004). For example, for the coastal elasmobranchs, *Myliobatis californica* (bat rays), *Triakis semifasciata* (leopard sharks) and *Mustelis henlei* (brown smoothhound sharks) in Tomales Bay, California, salinity (and temperature) were found to be the most important environmental factors structuring elasmobranch distribution (Hopkins and Cech 2003). Occurrence of these coastal elasmobranchs in Tomales Bay (*M. californica*, *T. semifasciata* and *M. henlei*) was associated with increasing occurrence as salinity and temperatures began to rise, especially in January and March when salinity and temperatures reached their peak (Hopkins and Cech 2003). For the shark species, *Carcharhinus leucas* (bull shark), Heupel and Simpfendorfer (2008) discovered a relationship between salinity and occurrence. Increased salinity was associated with increased bull shark occurrence. Increased occurrence in relation to increased salinity was more notable in juvenile bull sharks, although it was still observed in adults, but to a lesser degree. Juvenile *C. leucas* were found to avoid areas of salinities of <7, but had a preference for salinities between 7 and 20, this was thought to be because of the physiological capabilities of *C. leucas* (Heupel and Simpfendorfer 2008). Similarly, the occurrence and distribution of *Squatina guggenheim*, an angel shark (not to be confused with the angel shark *S. squatina*) found in the Argentine-Uruguayan common fishing zone, was found to be associated with two environmental variables at certain times of the year, which were found to affect the distribution and population of the species; these were bottom temperature and bottom salinity (Vögler et al. 2008). For *S. guggenheim*, in the Argentine-Uruguayan Common Fishing Zone, distribution was affected by salinity in spring and by temperature in spring and fall, with preferences for salinities ranging from 33.4-33.8 and temperatures ranging from 7.0-18.5°C (Vögler et al. 2008). The salinity and temperature preferences of *S. guggenheim* was speculated to be related to feeding areas (Vögler et al. 2008).

Chlorophyll-a concentration can be an indicator of marine productivity, and when used in conjunction with sea surface temperature can be an important factor influencing species distribution (Valavanis et al. 2008). For example, a census of cetaceans in the coastal waters of California revealed that their distribution was strongly linked with sea surface chlorophyll (Smith et al., 1986). Cetacean abundance was higher in the chlorophyll rich, productive coastal waters associated with the inshore Californian coast (Smith et al., 1986). Smith et al., (1986)

suggested that chlorophyll concentration was a measure of cetacean habitat and could be used to describe patterns of marine mammal abundance and distribution. An explanation for the link between chlorophyll concentration and cetacean distribution is that chlorophyll rich waters indicate levels of high productivity (Smith et al., 1986). For example, chlorophyll content can be used as a measure of phytoplankton biomass, indicating the possibility that Cetaceans are associated with chlorophyll production because intermediate levels of the food web are associated with chlorophyll (Smith et al., 1986). In a study of elasmobranch habitat, small-spotted *catshark* (*Scyliorhinus canicula*) occurrence in the Mediterranean had a negative relationship with chlorophyll-a concentration and as such chlorophyll-a was concluded to be an important factor in describing the habitat and distribution of *S. canicula* (Pennino et al. 2013). Therefore, the distribution of elasmobranch and shark species may depend on a particular chlorophyll-a concentration.

The historic distribution of *S. squatina* is thought to have once encompassed the North-Eastern Atlantic, ranging from Scandinavia to Mauritania, including the Canary Islands, Mediterranean and Black Seas (OSPAR 2010, Miller 2016). *S. squatina* was also historically relatively common throughout the North-East Atlantic, with frequent sightings on the Southern coast of England, Firth of Clyde (Day 1880), North Sea and Scandinavian waters (Hureau and Monod 1973). However, *S. squatina* has been declared locally extinct from the majority of its former range, with the declines in *S. squatina*'s range thought to occur from over fishing in the last 50 years (OSPAR commission 2010), this species is highly susceptible to bottom longlines, demersal trawls and set nets (OSPAR commission 2010). The current population estimates of *S. squatina* are based on fishery landings, historic data and research surveys (OSPAR 2010). For example, landings of *S. squatina* in the North-East Atlantic dropped from 15 to 20 tons in the 1980s, then to 1 to 2 tons in the 1990s, with the last reported landing in 1998 (ICES WGEF 2004). ICES WGFE (2006) have also noted that *S. squatina* is now no longer seen in research vessel surveys. As a result of these declines, *S. squatina* is now on the IUCN's Red List of Threatened Species and was classified as "Vulnerable" in the year 2000, but because of further estimated and suspected declines in populations of $\geq 80\%$ over three generations *S. squatina* was classified as "Critically Endangered" on a global level in 2006 (IUCN), *S. squatina* was also added to OSPAR's List of Threatened and/or declining species in 2008 (OSPAR commission 2010). However, despite *S. squatina*'s substantial declines it is still thought to be

relatively common in the Canary Islands as it is one of the last places where it is still observed with some frequency in the wild (Muñoz-Chapuli 1985; OSPAR Commission 2010).

Research on *S. squatina* has focussed on the biological processes associated with reproduction (such as gestation periods, litter sizes (Osaer 2009)), diet (Narvaez 2012) and distribution within its former range (Ellis et al. 2004, OSPAR commission 2010). However, as the Canary Islands have been noted as one of the few places where *S. squatina* are thought to still commonly occur, surprisingly little is known about the distribution of *S. squatina* in this area (although recent sightings of *S. squatina* have been observed on El Hierro and La Palma in the Canary Islands, which were not previously thought to be included in *S. squatina*'s distribution (Meyers et al. 2014)). Therefore, the aims and objectives of this study were to determine the distribution of *S. squatina* by locating incidence of the species at various critical life stages throughout its existing range (within the Canary Islands (see Figure 2.1)). And, secondly, to understand how the abiotic factors water temperature, salinity and chlorophyll-a may be structuring the distribution of *S. squatina*, as they may go to some lengths in understanding *S. squatina*'s distribution.



Figure 2.1 Map of Canary Islands

2.2 Materials and Methods

2.2.1 Online survey to examine distribution in Canary Islands region

To determine the extent to which *S. squatina* is distributed in the Canary Islands 37 questions were compiled into an online survey (www.surveymonkey.co.uk) and emailed to a total of 65 dive centres throughout the Canary Islands, encompassing 17 in Lanzarote, 9 in Fuerteventura, 13 in Gran Canaria, 19 in Tenerife, 1 in La Gomera, 2 in La Palma, 3 in El Hierro and 1 in La Graciosa (see Appendix 1). For this survey only ‘well-established’ dive centres were asked to participate in the online survey. A dive centre was considered well established if it been operating in the Canary Islands for more than 5 years. Within each of these dive centres only dive professionals (licensed dive guides and instructors, e.g. PADI Dive Instructor, or members of professional dive organisations) were invited to take part in the online survey. Additionally, each dive professional was only allowed to take part in the online survey if they undertaken a minimum of 100 dives per year for the past 2 years in the Canary Islands. These requirements, which were set for the dive professionals to take part in the online survey, were to ensure that the data collected on *S. squatina* from the online survey were obtained from a reliable source, i.e. diving experts.

Questions categorically examined (1) the geographic distribution of *S. squatina* across the Canary Islands, and (2) the spatial and temporal structure of *S. squatina* occurrence (For a complete list of survey questions used, see Appendix 2). In particular, participants were asked questions relating to the geographical location of *S. squatina* occurrence which they had personally encountered throughout the Canary Islands. However, data was not collected on sites where *S. squatina* were not observed, and therefore, the information collected was presence-only data. Participants were asked to give details of the sites where they had encountered angel sharks. To determine when angel sharks were associated with occurrence in the Canary Islands, participants were asked to give details on which years and which months within those years were associated with angel shark sightings, and the geographical locations which they reported to have seen angel shark occurrence.

To obtain as wide an array of angel shark spatio-temporal occurrence data for the Canary Islands the survey was developed to allow participants with varying levels of knowledge about

S. squatina to complete the questionnaire. For example, an individual who was able to tell the difference between male and female angel sharks was asked questions relating to possible differences in male and female habitat use. Whereas, an individual who did not know how to identify angel sharks by sex would not be asked questions relating to this, but rather, questions relating to angel sharks as a whole (termed as “General” in the results). Similarly, participants were asked about ‘mature’ *S. squatina* (body length of >128cm in females, and >80cm in males), ‘male’ (presence of claspers), ‘female’ (absence of claspers), ‘mating scars’, ‘pregnant’, ‘juvenile’ (body length of <128cm in females, and <80cm in males), and ‘mating’ (insertion of male clasper into female vent). The survey used a range of different types of questions, including multiple choice, scaled/ranked, dichotomous (yes or no questions) and open ended questions.

2.2.2 Temperature, salinity and chlorophyll-a associated with *S. squatina* distribution in the Canary Islands

To determine how abiotic factors impacted the distribution and times of the year associated with *S. squatina* presence in the Canary Islands, environmental data on sea surface temperature (SST), salinity and chlorophyll-a for the Canary Islands were obtained from NOAA's ERDAP database

(<https://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html?page=1&itemsPerPage=1000>).

SST, salinity and chlorophyll-a were expressed as box and whisker plots with added monthly means for each month in the Canary Islands.

2.2.3 Statistical Analysis

The environmental data was only available for the Canary Islands as a whole (rather than specific areas within the Canary Islands which could potentially be sites associated with *S. squatina* presence), therefore, statistical testing (i.e. GLM) was first utilised to show any significant differences in the number of sites in the Canary Islands which were associated with *S. squatina* presence during the course of the year. Followed by separate analysis to show how the environmental conditions (SST, salinity, and Chlorophyll-a) vary over the course of the year and if the variation throughout the year was significant or not (i.e. One-way ANOVA for each environmental variable). In both of the statistical analysis (GLM and one-way ANOVA), the year was separated into individual months.

To determine the effect of month on *S. squatina* presence in the Canary Islands, a binomial Generalised Linear Model (GLM) with a logit link function was conducted. The GLM used the Wald test to show the significance of the variable, month, on predicting *S. squatina* presence, and similarly, if significant, Wald statistics would show which factor of the predictor were significant (i.e. specific months out of the year). Results were considered statistically significant at $P \leq 0.05$. Statistical analysis was performed on SPSS (IBM SPSS Version 23).

To determine if the variation within the SST, Salinity, and Chlorophyll-a data was significantly different in any of the months throughout the year in the Canary Islands, separate one-way ANOVAs were conducted for each variable. If results of the of the ANOVA were significant (considered significant at $P \leq 0.05$) a post hoc Tukey HSD test was conducted to determine which months were significantly different from one another (also considered significant at $P \leq 0.05$). Levene's *F*-test was used to test for the assumption of homogeneity of variance, this being satisfied with $P \geq 0.05$. When homogeneity of variance was not satisfied ($P < 0.05$), the Welch test was used to test for any significance between groups, followed by a Games-Howell post hoc test if significant (both significant at $P \geq 0.05$). Statistical analysis was performed on SPSS (IBM SPSS Version 23).

2.3 Results

A total of 19 online surveys were completed and encapsulated responses from six of the Canary Islands (Tenerife, Fuerteventura, Gran Canaria, Lanzarote, La Gomera and El Hierro), excluding La Palma and La Graciosa, with every respondent reporting the occurrence of *S. squatina*. Similarly, every island with responses also had a number of *S. squatina* sites which were identified, with the exception of the island El Hierro (which had a single response but no sites identified) (see Table 2.1).

Responses from the islands Gran Canaria and Lanzarote, which are home to just over half of the dive centres which were contacted in this study, contributed to more than half of the total number of responses from all participants (see Table 2.1). Interestingly, there were more responses from the island Gran Canaria, despite having fewer dive centres than Lanzarote. Furthermore, Gran Canaria was host to over double the amount of *S. squatina* sites than Lanzarote, and contributed to over 50% of the total number of *S. squatina* sites identified in the survey.

Although the islands of Tenerife and Fuerteventura made up the second largest group of dive centres which were contacted (after the largest group, Gran Canaria and Lanzarote), they made up less than a quarter of all responses collected (see Table 2.1). However, these two islands did contribute to over a quarter of all *S. squatina* sites.

The islands La Gomera and El Hierro had the lowest number of responses (>0) out of all the islands, although, they also had the lowest number of dive centres on (out of all the islands which gave responses). Only a single *S. squatina* site was identified from the responses over these two island (found at La Gomera), despite both islands having responses from participants.

Table 2.1 Responses of the online survey by individual island

Island	Number of Dive Centres which were contacted	Number of Responses from participants	Number of Participants who reported <i>S. squatina</i> occurrence	Number of <i>S. squatina</i> sites identified
Tenerife	12	1	1	3
Fuerteventura	10	3	3	2
Gran Canaria	13	7	7	10
Lanzarote	18	6	6	3
La Palma	2	0	0	0
La Gomera	2	1	1	1
El Hierro	3	1	1	0
La Graciosa	1	0	0	0
Total	61	19	19	19

2.3.1 Sites where ‘General’ *S. squatina* were observed

Responses, from the participants, of General *S. squatina* sightings were fairly consistent throughout the individual sites which were identified, as only under a third of the sites (Arinaga, Arguineguin, Artificial Reef, Puerto Mogán, and Sardina Del Norte found at the island Gran Canaria, and Puerto Del Carmen found at Lanzarote) were identified by more than one respondent, in each case (see Figure 2.2). Nearly all of these sites, which had the highest responses, also had the highest number of months in the year in which they were observed (with the exception of Puerto Mogán at Gran Canaria, which had one of the lowest number of months in the year in which *S. squatina* was observed, despite having more than one response) (see Figure 2.2 and Figure 2.3). However, there were some sites (although, less than a quarter) which had the lowest number of responses, but some of the highest number of months throughout the year in which *S. squatina* were observed (Amadores Beach, and Tufia found at Gran Canaria, El Jablito found at Fuerteventura, and Playa Flamingo found at Lanzarote).

2.3.2 Sites where mature male and mature female *S. squatina* were observed

All of the sites which had female and/or male *S. squatina* observations were identified with only a single response at each site. However, less than half of all the sites identified in the survey had observations of male *S. squatina*, and under a quarter of all sites had observations

of female *S. squatina* (see Figure 2.2). Every site which had female sightings, also had male sightings (i.e. Abades, Poris de Abona, and Las Eras on the island Tenerife, and Puerto Rico on the island Gran Canaria), however, there were also sites with male only sightings (Anfi Beach, Arguineguin, El Pajar and Artificial Reef, all of which are found at the island Gran Canaria). The site Abades (Tenerife) had over twice the amount of months at which male and female *S. squatina* were observed than Puerto Rico (Gran Canaria), which ranked second in terms of the number of months in which male and females were reported (see Figure 2.3). Abades had five times the amount of months, with *S. squatina* observations, than the rest of the sites which had male and female reports (excluding Puerto Rico). Similarly, Puerto Rico had twice the amount of months with *S. squatina* reports, than all the other sites which had male and female sightings (other than Abades).

2.3.3 Sites where matings and *S. squatina* with mating scars were observed

A little more than a third of all the sites identified in the survey had observations of *S. squatina* with mating scars. Similarly, less than a quarter of all sites had reports of *S. squatina* mating (see Figure 2.2). However, the number of responses from participants was fairly consistent at the sites which had observations of *S. squatina* mating and/or *S. squatina* with mating scars, with the exception of Puerto Del Carmen (Lanzarote), which had double the amount of responses regarding mating scars. Less than a quarter of the mating scars/mating sites had the presence of both mating scars and mating (Puerto Del Carmen found at Lanzarote, and El Jablito found at Fuerteventura). However, *S. squatina* mating was only reported during a single month at a single site (El Jablito found at Fuerteventura). Whereas, the site Puerto Del Carmen (Lanzarote) had no reported months in which mating was known to occur, despite having a single respondent reporting the occurrence of mating at this site, although, *S. squatina* with mating scars were reported to occur for a single month out of the year.

The sites Amadores Beach, Sardina del Norte (Gran Canaria), and El Jablito (Fuerteventura), which contributed to under half of the mating scar sites, had the highest number of months in which *S. squatina* with mating scars was observed throughout the year, and, was equal to twice the amount at the sites Artificial Reef and Arinaga (Gran Canaria), which had the next highest number of months in the year in which *S. squatina* mating scars occurred.

2.3.4 Sites where gravid *S. squatina* were observed

There was only a single site throughout the whole Canary Islands at which respondents reported any observations of gravid *S. squatina* (Puerto Del Carmen, Lanzarote) (see Fig 2.2). Furthermore, the sighting of gravid females was limited to only one month of the year (see Fig 2.3).

2.3.5 Sites where juvenile/pups were observed

Less than a quarter of all the sites identified had observations of *S. squatina* juveniles/pups (Amadores Beach and Anfi Beach found at Gran Canaria, El Jablito found at Fuerteventura, and Puerto Del Carmen found at Lanzarote). However, Amadores Beach and El Jablito had over 10 times as many months in which juvenile *S. squatina* were observed than Anfi Beach, and Puerto Del Carm had over 5 times as many month than Anfi Beach (see Fig 2.3).

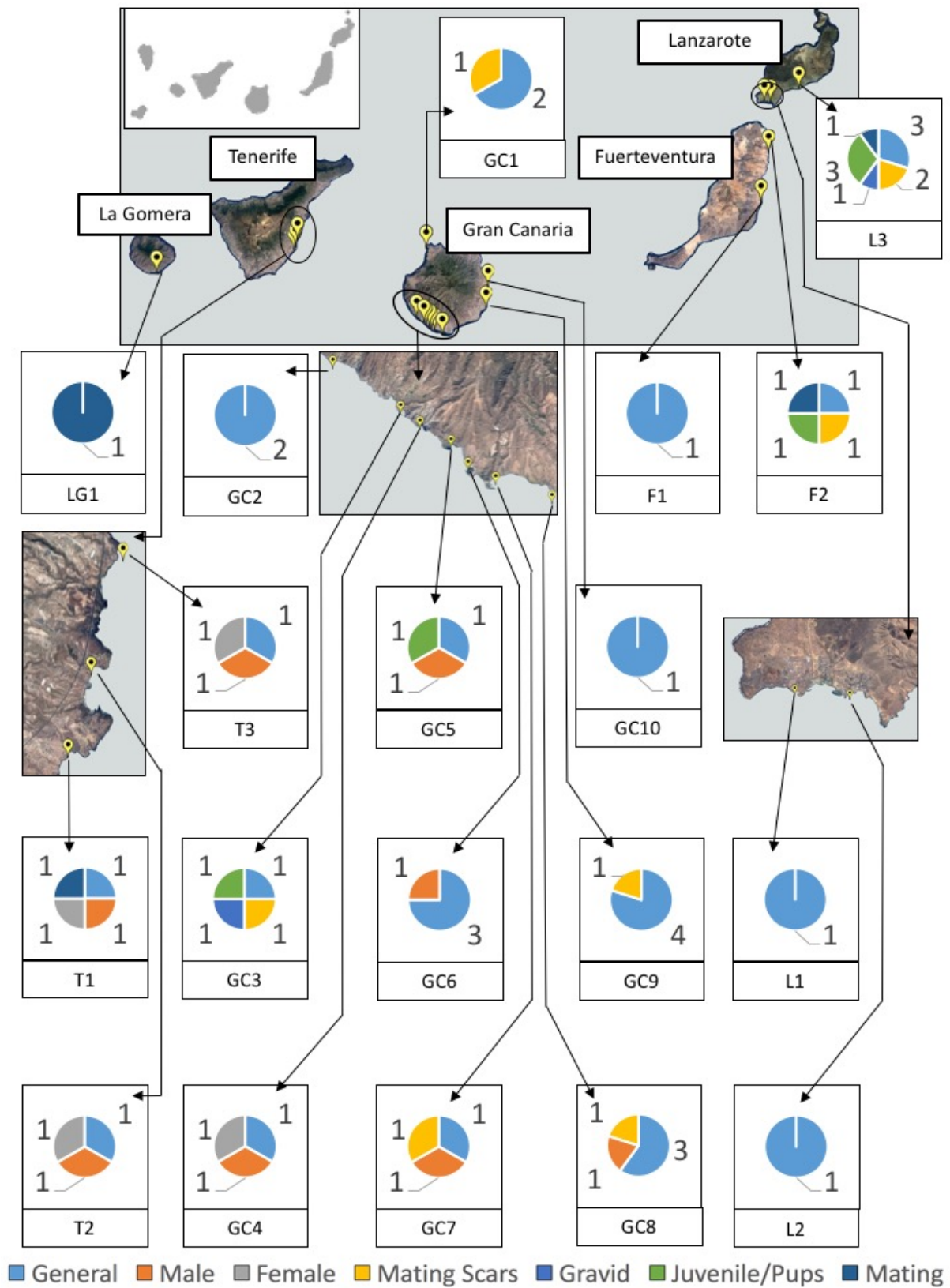


Figure 2.2 Number of respondents who reported observations of *S. squatina* at individual sites. Dive sites: LG1=Playa de Santiago, T1=Abades, T2=Poris de Abona, T3=Las Eras, GC1=Sardina del Norte, GC2=Puerto Mogan, GC3=Amadores Beach, GC4=Puerto Rico, GC5=Anfi Beach, GC6=Arguineguin, GC7=El Pajar, GC8=Artificial Reef, GC9=Arinaga, GC10=Tufia, F1=Las Salinas, F2=El Jablito, L1=Playa Flamingo, L2=Punta Berrugo, and L3= Puerto Del Carmen

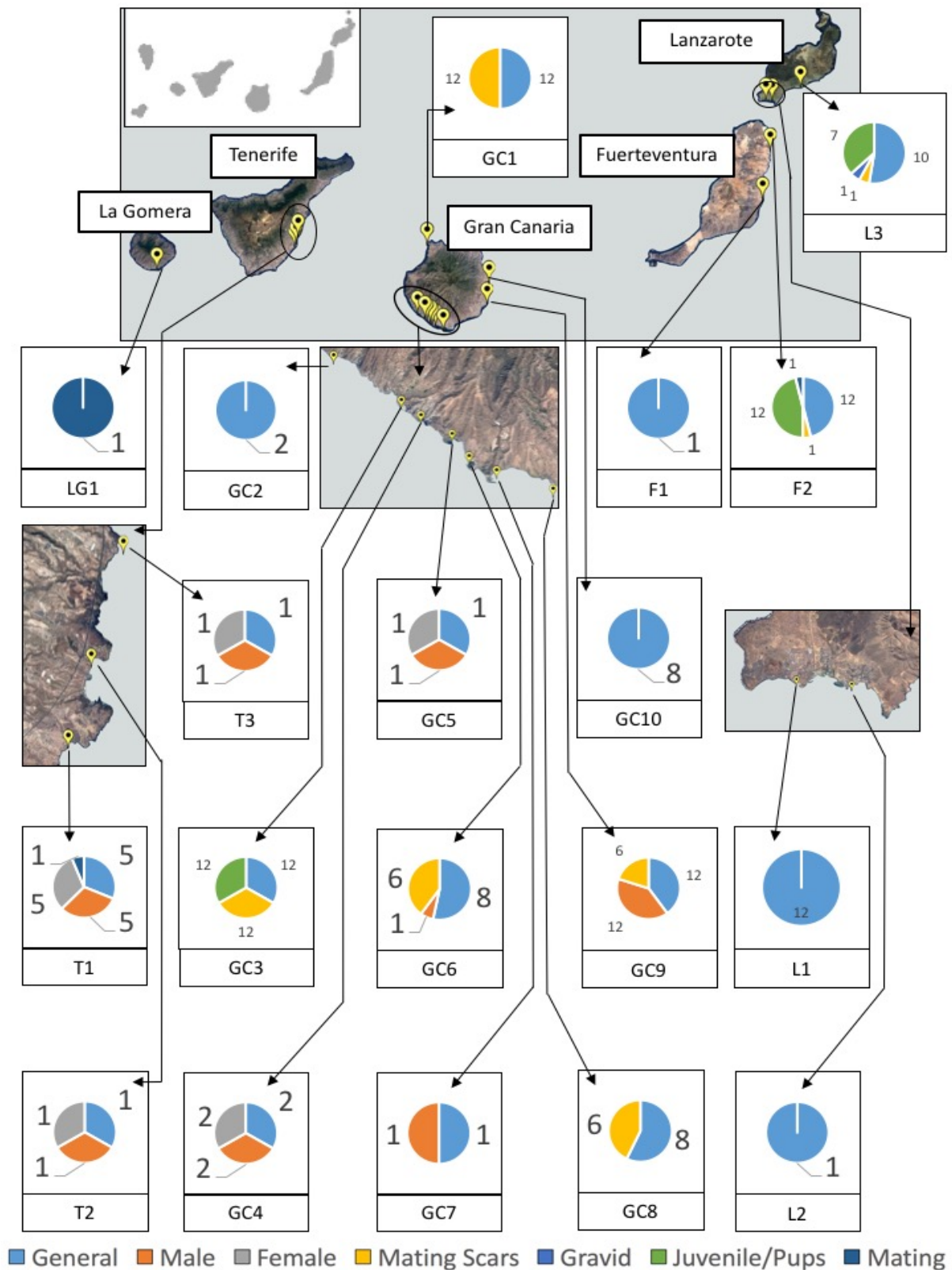


Figure 2.3 Number of months *S. squatina* was present at individual sites. Dive sites: LG1=Playa de Santiago, T1=Abades, T2=Poris de Abona, T3=Las Eras, GC1=Sardina del Norte, GC2=Puerto Mogan, GC3=Amadores Beach, GC4=Puerto Rico, GC5=Anfi Beach, GC6=Arguineguin, GC7=El Pajar, GC8=Artificial Reef, GC9=Arinaga, GC10=Tufia, F1=Las Salinas, F2=El Jablito, L1=Playa Flamingo, L2=Punta Berrugo, and L3= Puerto Del Carmen

Although, the proportion of sites occupied by *S. squatina* varied throughout the year, with the highest proportion occurring in March and February (which had over twice as many sites occupied as the month with lowest proportion, in July) (see Fig 2.4), there was no significant difference in the number of sites occupied between months, suggesting that month was not a suitable predictor for *S. squatina* occurrence in the Canary Islands (Wald test: $W = 13.669$, $df = 11$, $p = 0.252$).

SST was significantly different between months in the Canary Islands (One-way ANOVA: $F = 693.412$, $df = 11$, $p = 0.000$). There were only three pairs of the monthly SST data which did not significantly differ (i.e. February and March, August and November, and January and April) (see Fig 2.5), whereas the rest of year was associated with significantly different monthly SSTs. However, salinity concentrations (PSU) in the Canary Islands remained fairly consistent throughout the year (see Fig 2.6). As such the salinity (PSU) did not significantly differ in any month (One-way ANOVA: $F = 0.629$, $df = 11$, $p = 0.801$). Whereas, the variation in chlorophyll-a concentrations (mg/m³) (see Fig 2.7) did differ significantly throughout months (Welch test: $F = 288.596$, $df = 11$, $p = 0.000$).

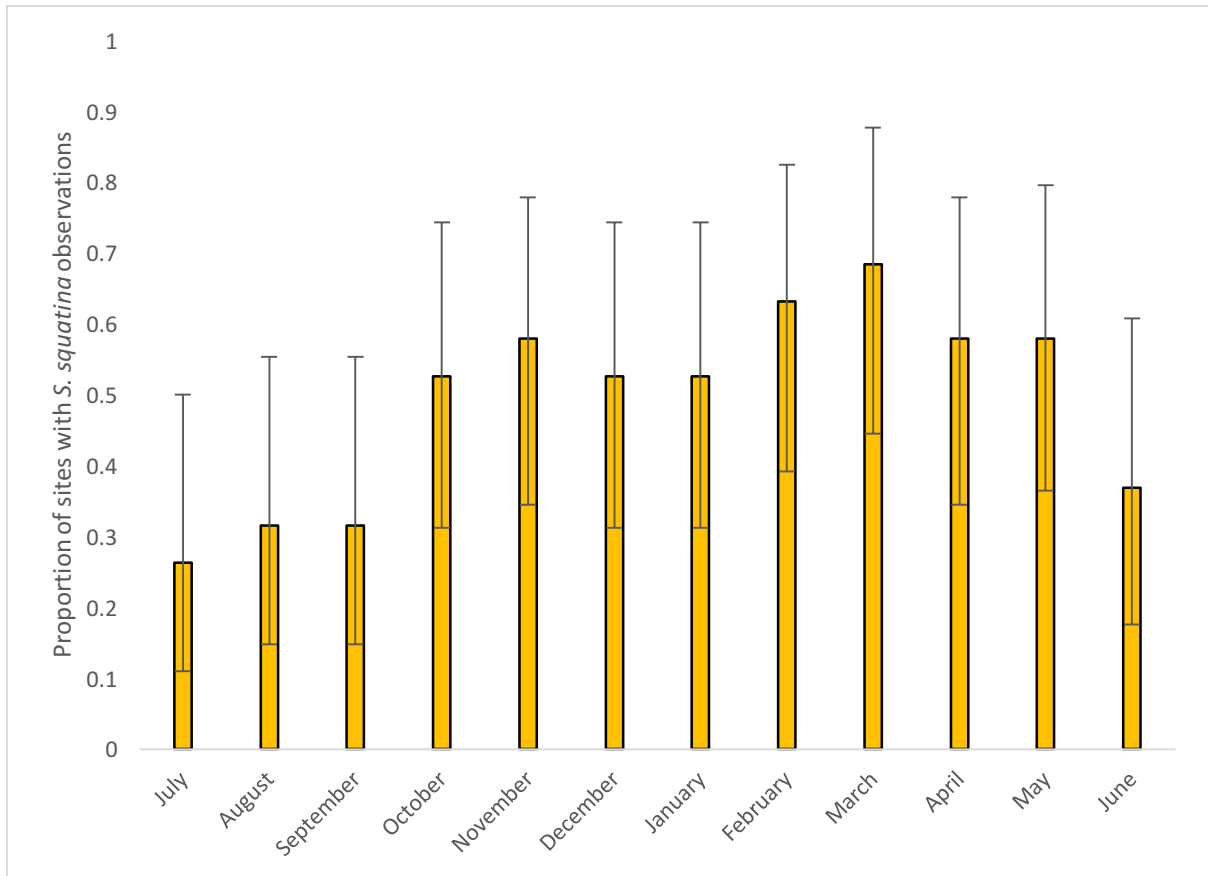


Figure 2.4 Proportion of sites with *S. squatina* observations by month in the Canary Islands.

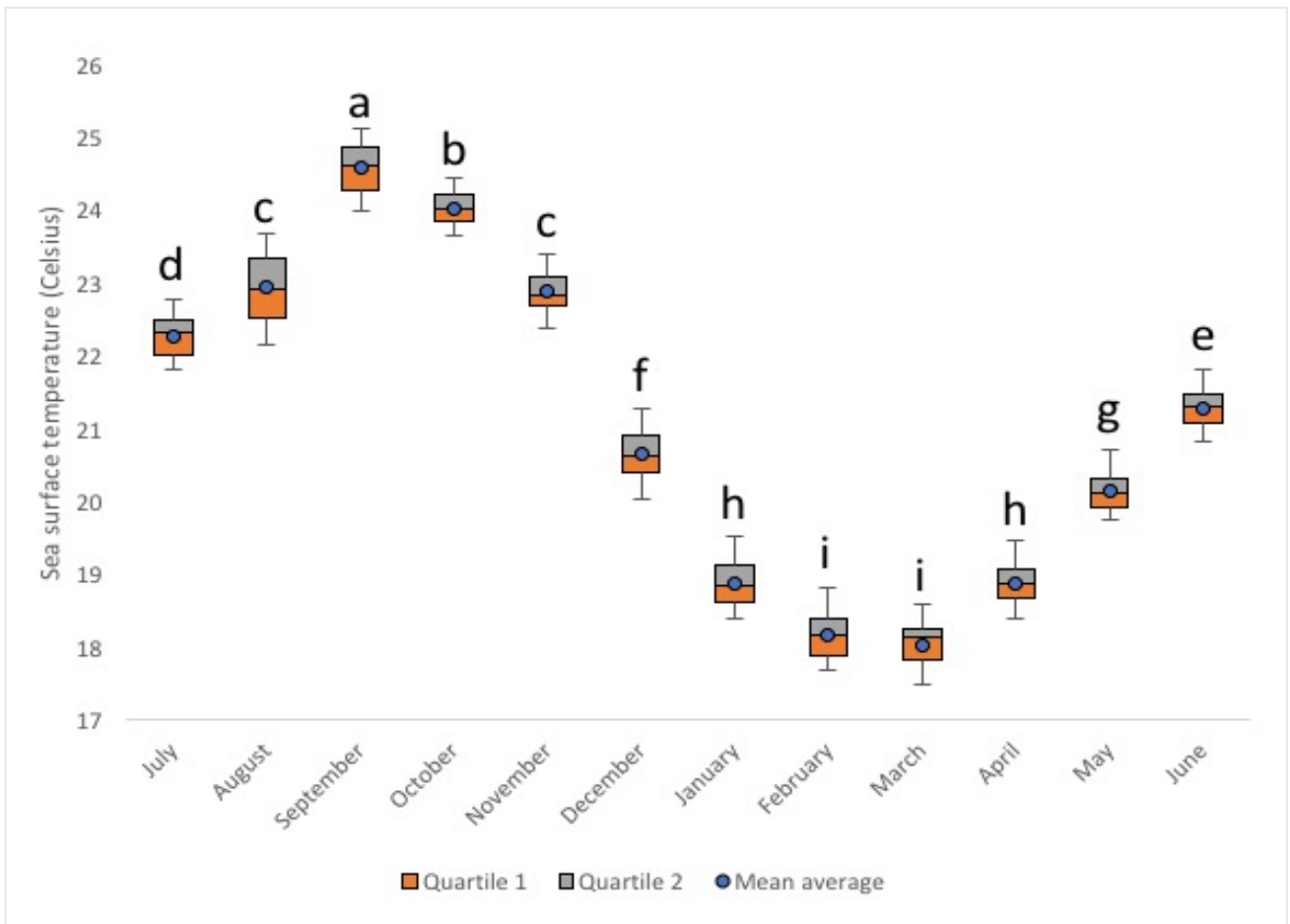


Fig 2.5 Sea surface temperature (Celsius) by month in the Canary Islands. Monthly SST which is not significantly different is represented with the same letter.

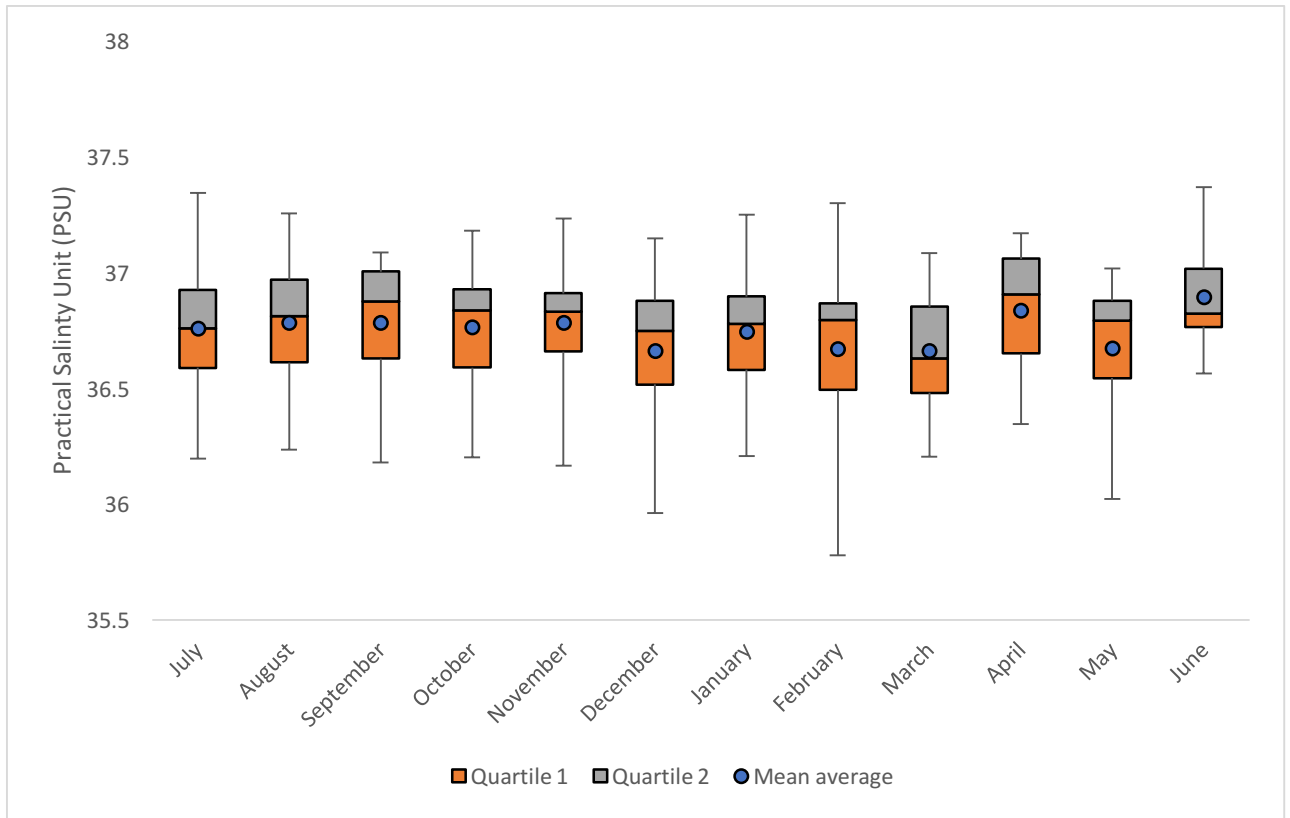


Fig 2.6 Sea surface salinity (PSU) by month in the Canary Islands

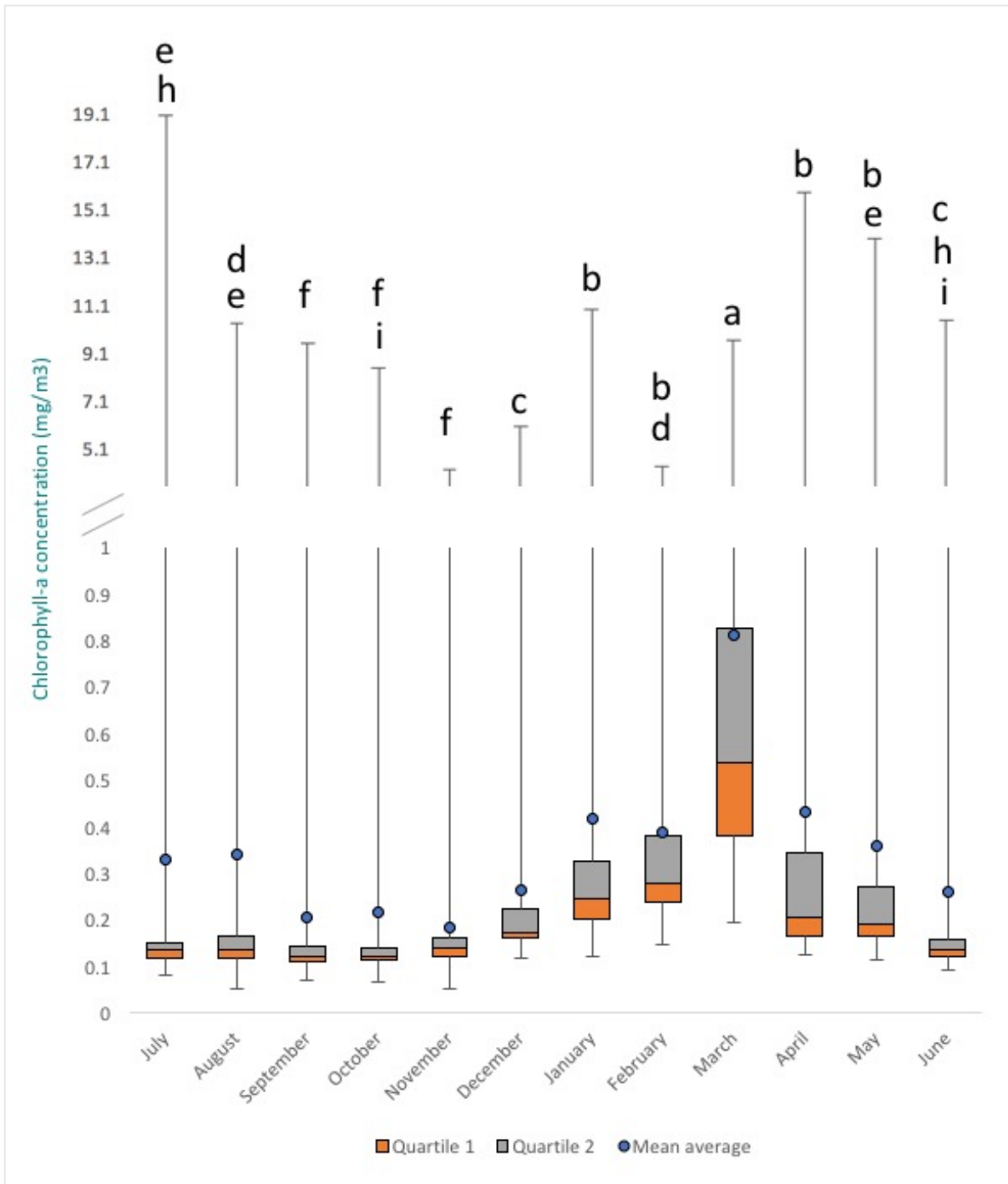


Fig 2.7 Chlorophyll-a concentration (mg/m³) by month in the Canary Islands. Monthly chlorophyll-a concentrations which are not significantly different are represented with the same letter.

2.4 Discussion

Many of the sites identified in the online survey were associated with a number of key life stages of *S. squatina*, and while no single site had observations of all of the life stages that this study sought to collect information on, there were a number of sites which had the presence of several life stages which might indicate the existence of nursery areas and mating sites. Similarly, other sites were associated with life stages which might indicate either the existence of mating sites or nursery sites.

Several key areas were identified in the Canary Islands which are likely to be nursery sites for *S. squatina*. The strongest candidates for nursery sites were Amadores Beach (Gran Canaria), and El Jablito (Fuerteventura) as they both had reports of year round presence of juvenile *S. squatina* and *S. squatina* pups. *S. squatina* might benefit from some sort of protection or conservation management of such sites because the importance of geographical locations which are known to have the incidence of juvenile sharks cannot be understated as these areas are thought to be crucial in the maintenance of endangered shark populations (Brewster-Geisz and Miller 2000). For example, Brewster-Geisz and Miller (2000) created a stage based model of the management implications of *Carcharhinus plumbeus*, a large coastal shark considered to be overfished in the Atlantic. Projections of their stage-based model demonstrated the importance of management which protects juvenile and sub-adult *C. plumbeus* from mortality, which in turn facilitates the rebuilding of stock (i.e. reaching sexual maturity and successfully reproducing) (Brewster-Geisz and Miller 2000).

Similarly, it is suggested that Puerto Del Carmen (Lanzarote) should also be considered a nursery site for *S. squatina*, as it had reports of juvenile presence for 7 months out of the year. Previous research (i.e. Meyers cited in Miller 2015) has already identified Puerto Del Carmen as a potential nursery site for juvenile *S. squatina*, and the results of the online survey gives this further credibility. However, Puerto Del Carmen was also the only site identified in the online survey, which had reports of gravid *S. squatina*. The presence of both gravid and juvenile life stages of a shark species at one site has been noted as a strong indicator of a primary nursery site (Bass 1978 and Castro 1993). Primary nursing sites are areas where gravid sharks, give birth and where the newly born pups live for a period of time (often this is a short period of time, but can range from weeks to months or even years, depending on the species)

which they then often leave to move into a secondary nursing site before reaching maturity (Bass 1978). Although, it is important to note that primary and secondary nursing sites can occur in the same location for some species of elasmobranch (Simpfendorfer and Milward 1993).

For example, the blacktip shark (*Carcharhinus limbatus*) was found to use the area Caicara do Norte in Brazil as a seasonal primary nursery area, as fisherman reported the frequent landings of small *C. limbatus*, which were consistent with the length of new born pups, during the months of January and February (Yokota and Lessa 2006). While, the absence of *C. limbatus* was noted during the rest of the year, suggesting the area was only used by newly born *C. limbatus* (Yokota and Lessa 2006). As Puerto Del Carmen did not have year round incidence of juvenile *S. squatina* it is worth considering that this area could be a primary nursing site which newly born pups temporarily occupy before moving to another site (i.e. a secondary nursing site). However, Yolota and Lessa's (2006) study highlights one of the limitations of the methodology of this study, the categories used to define *S. squatina*'s different life stages were fairly broad and not based on exact measurements of *S. squatina*'s total length (i.e. juvenile *S. squatina* data was based on each individual participant's ability to correctly judge total length underwater as either above or below a certain length associated with juvenile/mature *S. squatina*, and did not differentiate between newly born pups and older juveniles which may be nearing sexual maturity). Therefore, it is beyond the scope of this research to answer such questions about the potential primary and secondary nursing sites which *S. squatina* may utilize. However, the identification of locations which are associated with the presence of juvenile life stages of endangered shark species (either newly born or nearing sexual maturity) is potentially critical information to be utilized in the conservation of that species (Bonfil 1997 and Camhi 1998).

Furthermore, all the sites which are suggested as potential nursery sites (i.e. Amadores Beach, El Jablito, and Puerto Del Carmen) also had the presence of life stages which would suggest that these areas are also mating sites. For example, Amadores Beach not only had the presence of juvenile *S. squatina*, it also had year round incidence of *S. squatina* with mating scars. Similarly, El Jablito also had the presence of *S. squatina* with mating scars and even reports of *S. squatina* mating events (although, both for one month out of the year). Puerto Del Carmen also had incidence of *S. squatina* with mating scars for a month out of the year. In general, shark mating is known to be an incredibly rare event to witness, especially in the wild (Bres

1993) and the presence of mating scars at sites could suggest the existence of mating sites (Feldheim et al. 2001). Shark mating sites are areas in which individuals repeatedly occur to engage in copulation (Pratt and Carrier 2001) and have been noted in few shark species due to the cryptic nature of shark mating (shark species with observed mating sites include *Ginglymostoma cirratum*, in the Dry Tortugas island cluster, Florida Keys (Carrier et al. 1994, and Carrier and Pratt 1998), and *Carcharias taurus*, on the east central coast of Florida (Gilmore et al 1983) as multiple mating events were observed in these locations with some frequency).

The identification of areas which are likely to be both nursery areas and mating sites is known to be rare and critical to the protection of endangered shark species. For example, Carrier and Pratt (1998) implemented a protection plan for nurse sharks (*Ginglymostoma cirratum*) in the Dry Tortugas, Florida Keys. Their study was unique in that they identified one site which was both a mating site and a nursing area. Their protection plan had three main elements, the first was to identify a specific area which was unique and critical for the breeding of *G. cirratum*. Second, was to identify key times of year which were associated with mating and breeding in the identified area, and to restrict public access during the key times of year (the third element of their protection plan was to educate and inform the public of *G. cirratum*'s mating and breeding). Carrier and Pratt (1998) demonstrated the potential that such spatio-temporal information, about important life stages in sharks, has to contribute in the design and implementation of effective conservation strategies. However, due to the patchiness in sampling effort and response rates in the online survey employed in this research, it is entirely plausible that other sites identified have the potential to be nursery and/or mating grounds for *S. squatina*, as well as other sites not identified in the survey. Therefore, the results of the online survey should not be viewed as a definitive list of *S. squatina* mating and nursery sites in the Canary Islands.

Salinity concentrations (PSU) in the Canary Islands remained fairly consistent throughout the year and did not significantly differ by month, suggesting there may be a link between *S. squatina* occurrence and salinity (PSU) (as *S. squatina* presence in the Canary Islands also did not significantly differ by month, however, this link is somewhat tenuous). Whereas, both chlorophyll-a (mg/m³) and SST (Celsius) in the Canary Islands did differ significantly throughout certain months, potentially indicating that these two environmental factors are not structuring Canary Island wide *S. squatina* occurrence. However, due to the resolution of the

environmental data (i.e. not specific to individual sites associated with *S. squatina* occurrence) it was not possible to suggest how these variables may be affecting *S. squatina* occurrence at each site (although, it does highlight the need to collect such data at the sites identified in this study). Although, ambient water temperature has been linked to *S. squatina* incidence at a single site in the Canary Islands: Narv ez et al., (2008) has linked occurrence of *S. squatina*, at Arinaga (Gran Canaria), to ambient water temperature, as peaks of sightings occurred once the water temperature dropped below 21 C soon after autumn. The sightings of *S. squatina* in Arinaga remained high until water temperatures reached >21 C in the summer months (Narv ez et al., 2008).

The effects of environmental variables on shark occurrence has been well studied before (e.g. Hueter and Manire 1994, Hopkins and Cech 2003, Hussey et al. 2009, Ubeda et al. 2009, etc.), and there has even been some research into this on other species of angel shark distributions. For example, V ogler et al. (2008) examined the spatial distribution of *Squatina guggenheim* in the Argentine-Uruguayan Common Fishing Zone and found that they were most affected by water temperature during spring and fall (with temperature preferences ranging from 7.0 - 18.5 C) and only affected by salinity during spring (with preferences for salinity values ranging from 33.4 – 33.8).

S. squatina did not appear to have a well defined season for when they were present throughout the Canary Islands as a whole. However, the lack of a clear season may indicate that the times of year in which *S. squatina* is present in the Canary Islands is dependent upon each individual site, rather than as a whole. Not all of the sites had year round observations of *S. squatina*, and where they go when they're not observed is not obvious. However, many species of shark will undertake seasonal migrations, often along coast lines (Bres 1993, Bruce et al. 2006). Migrations in sharks have been noted to mainly occur because of shifts in prey distributions and changing water temperatures (Springer 1967). For example, Sims et al. (2003) linked the migrations of basking sharks with occurrence of high prey availability. While, blacktip sharks migrate with seasonal water temperature declines (<21 C) (Hueter and Manire 1994).

However, Pacific angel sharks (*Squatina californica*) are known to have low dispersal capabilities and remain within inshore areas, with little or no mixing with nearby groups of *S. californica*, and the idea has been put forth that this may be true of most benthic elasmobranchs,

suggesting that it is unlikely that other angel shark species undertake migrations (Standora and Nelson 1977, Gaida 1997). Conversely, Escobar-Sánchez (2006) has noted the absence of *S. californica* during the summer months in the Gulf of California and has suggested the existence of a seasonal migration in the species. Nevertheless, the question of whether *S. squatina* migrate remains to be seen, and is one that obviously needs its own research. However, as an alternative explanation, many sharks are known spend long periods of time at depth, making them hard to observe, especially as this often exceeds the safe depth limits of recreational diving. For example, White sharks are known to spend the majority of their time at an average of 60m (Domeier and Nasby-Lucas 2008). While, juvenile sandbar sharks around the east coast of North America, which are nearing sexual maturity, will spend large amounts of time in deeper waters during the winter than summer (up to 72m in winter compared with up to 24m in the summer) (Conrath and Musick 2008).

Chapter 3: Habitat Associations of *S. squatina*

3.1 Introduction

A species occurrence can often be related to a particular set of habitat associations (Kolasa and Li 2003). However, if the habitat parameters associated with the occurrence of a species is very narrow, then that species is considered to be a part of the broad category of a habitat specialist (Vanderpham et al. 2016). Whereas, a species which has a wide set of habitat parameters associated with occurrence is considered to be a part of the broad category of a habitat generalist (Vanderpham et al. 2016). For example, the Koala almost exclusively feeds on the leaves of eucalyptus trees and as such is considered a habitat specialist as it's occurrence is dependent on an adequate supply of eucalyptus (Moore et al. 2005). Whereas, a species like the raccoon is considered a habitat generalist as it able to tolerate a wide variety of environmental conditions and food sources (Sidorovich et al. 2000). However, what actually constitutes as a species 'habitat' varies from species to species and is based on the environmental tolerances of the species.

A habitat specialist is, in general, much more vulnerable to extinction and population declines than habitat generalists, as changes to their habitat can have a more compounded effect on their abundance and distribution (Baines et al. 2016). Habitat specificity is known to be even more detrimental to shark species in decline, as their low reproductive output (i.e. long gestation periods, slow growth rate) can increase the risk of extinction (Compagno 1990, Cortes 2000).

The habitat associations of a shark species can be different based on the differing physiological needs of the different life stages within that species (Hopkins 2003). Many juvenile sharks in a species are associated with occurrence in warmer ambient water temperatures (and also shallower depths, which are often associated with warmer waters), than non-juveniles in their population (Morrissey and Gruber 1993). The association of juvenile sharks with warmer habitats has been shown to occur for reasons relating to changes in metabolism of the juveniles (Morrissey and Gruber 1993).

All sharks, and other elasmobranchs, are known to have a low reproductive output i.e. long gestation periods, slow growth rates, late sexual maturity, small numbers of pups (Compagno

1990, Cortes 2000). As a result of this low reproductive output, the stability and growth of sharks relies on small numbers of well developed young, and their ability to survive long enough to reach sexual maturity and successfully reproduce (Simpfendorfer and Milward 1993). For example, in shark and ray species such as *Rhizoprionodon tayloris*, *Squalus acanthias*, and *Dipturus batis* the survival of juveniles nearing sexual maturity have been found to be the most important life stage in population maintenance and recovery of the target species (Gallucci et al 2006, Brander 1981). Threats to juvenile sharks, and other elasmobranchs, come under two main categories, predation (i.e. non-conspecific and conspecific predation) and a lack of resources necessary for growth and development (e.g. adequate prey, optimal environmental conditions such as water temperatures, salinity) (Morrissey and Gruber 1993). These two main threats (predation and lack of resources) to juvenile sharks are often reduced through their habitat selection i.e. juvenile sharks which occur in habitats with enough resources for growth and development and which reduces predation, have a higher chance of reaching sexual maturity and successfully reproducing (Morrissey and Gruber 1993). The general term used for these types of habitats which reduce threats of predation and lack of resources to juvenile sharks is 'nursery' (Heupel et al. 2007). However, there has been a lack of distinction involved in what actually constitute a shark nursery (Heupel et al. 2007). Although, the idea behind a shark nursery is tied up in survival i.e. predator avoidance and access to an adequate source of prey (Branstetter 1990). For example, Morrissey and Gruber (1993) attached ultrasonic transmitters to juvenile lemon sharks in Bimini, and found that juvenile lemon sharks were segregating themselves from mature lemon sharks. This segregation happened by depth, with juveniles being associated with shallower waters- it was suggested that juvenile lemon shark habitat selection was based on predator avoidance of conspecifics and heterospecifics (by occupying a shallower depth level where mature lemon sharks and other predators were not found) and which had access to smaller prey which was more suitable for juvenile lemon sharks. The shallower depths which juvenile lemon sharks were associated with also had higher temperatures which were suggested to increase metabolism and promote growth and development (Morrissey and Gruber 1993). Segregation of juvenile and mature groups of sharks in a population is associated with juvenile survival which is a precursor to reproductive success, as it is known to reduce conspecific predation of juveniles and increase their exposure to important resources (Morrissey and Gruber 1993). The mechanism behind segregation in juvenile and mature groups of sharks is often related to separation by geographical areas (increasing distance between juvenile and mature groups) and depth of occurrence (Heupel et al. 2007). Juveniles will often select shallow habitats as larger

predators, both conspecifics and heterospecifics, are more likely to occur in deeper waters due to the restrictions which shallower depths place on larger predators (Morrissey and Gruber 1993). The benefit of shallower waters for juveniles is also often associated with warmer temperatures and higher abundance of food prey suitable for smaller sized sharks (i.e. smaller sized sharks have a smaller gape and must feed on smaller prey than larger sharks (Morrissey and Gruber 1993)).

Sex specific habitat associations have been observed in many coastal shark species such as, *Negrapion brevirostris* (Feldheim et al., 2002), *Mustelus schimitti* (Van der Molen and Caille 2001) and a variety of shark species of the genus *Carcharhinus* (Cliff and Dudley 1992, Simpfendorfer and Milward 1993). Mechanisms of sexual segregation in mature male and mature female sharks is by depth (Klimley 1987). Segregation of the sexes by differing habitat associations in sharks have been hypothesised to occur for reasons such as dietary preferences (Klimley 1987) and spreading of male selective pressures and support of female choice of mates (Klimley 1985, Klimley 1987, Pratt Jr and Carrier 2001). For example, in the Gulf of California, female scalloped hammerhead sharks move to offshore sites before males (Klimley 1987). Klimley (1987) explained this pattern in the Gulf of California through the different dietary needs of male and female scalloped hammerhead sharks. Klimley (1987) suggested that the different distributions of the hammerheads were based on females needing larger body sizes, compared to the males, for the greater energy needs during gestation and embryonic development, and therefore, moved to offshore sites where they had more predatory success on pelagic fish to increase their body size.

There has been an absence of research on the specific habitat attributes associated with *S. squatina* occurrence as little is known about their habitat preferences. For example, *S. squatina* is known to spend large amounts of time buried under the sand (Compagno 1984), however, the sediment composition associated with *S. squatina* occurrence is not known.

The aims of this chapter were to understand how habitat attributes such as quantities of sediment grade and benthos type (e.g. sand, rock etc.) were associated with *S. squatina* occurrence, and which habitat attributes (such as water temperature and depth), if any, were specifically associated with the occurrence of *S. squatina* at different life stages and sexes (such as juvenile and mature, male and female, and gravid and non gravid), as such habitat specialism in endangered marine species is known to exacerbate population declines (Walker 1998).

3.2 Materials and Methods

3.2.2 Benthic cover and sediment composition of sites

To determine the habitat associations of *S. squatina*, sediment composition and benthic cover were estimated throughout 4 sites occurring on the south coast of Lanzarote: Playa Flamingo, Puerto Del Carmen, Mala, Costa Teguisse (see Figure 3.1). The sites Playa Flamingo and Puerto Del Carmen were chosen due to the high frequency with which *S. squatina* is sighted there (Miller 2016). Whereas, the sites Costa Teguisse and Mala were chosen for their lack of *S. squatina* sightings and for their geographical location. As a result, all 4 sites are roughly equally spaced along the south coast of Lanzarote giving a fairly even distribution of sites along the coast (see Figure 3.1). The sediment composition and benthic cover at each site were defined in terms of the percentage of macro algae, sand, loose rock and bedrock and the percentage composition of infaunal sediments. Infaunal sediment percentage was determined from the wet sieving of core samples of the substrate taken haphazardly at each site. While, benthic cover percentages were estimated using a transect based sampling method on SCUBA. A total of 8 transects were laid in the Puerto Del Carmen site. Each transect started at the waters edge and ran perpendicular to shore (each were approximately 50m apart). The transects ended when either the reef edge was met, or when the depth exceeded 25 metres (average transect length was 102m, minimum transect length was 52m and maximum transect length was 175m). At the Playa Flamingo site, transects were laid as above, however due to the smaller size of the site, 6 transects were placed perpendicular to shore (30m in length) and were placed 25m apart. At both sites, divers placed a 25cm quadrat every metre on the substrate along each transects, a single photograph of the quadrat was then taken.

To estimate the percentage of benthic cover (macro algae, sand, loose rock and bedrock) Coral Point Count with excel (CPCe) extensions software was used to analyse the photos of the substrate which were taken with the quadrats (Kohler and Gill 2006). CPCe software randomly distributes points onto uploaded photographic images. Each point is then visually identified and annotated by the user for the features found under each separate point and recorded by the software (i.e. macroalgae, sand, loose rock and bedrock). Once all the photos of a sites substrate (along the transects) are uploaded and annotated the software will output estimates of percentages of the habitat categories previously defined (i.e. macro algae, sand, loose rock and bedrock) for that site. The number of points which CPCe overlays onto uploaded images is

user defined. Initial tests were conducted in order to find the optimal number of points with which to overlay the images. This was achieved by testing varying numbers of points (i.e. 10, 25, 50, 80, 100) on images which were representative of the study sites substrate. It was found that 50 points was the optimal number with which to overlay the images. In the Puerto Del Carmen site a total of 873 pictures of the substrate were taken, which resulted in 43,650 point counts of habitat type. In the Playa Flamingo site, a total of 150 pictures of the substrate were taken, which resulted in 7,500 point counts of habitat type.

To estimate sediment composition a number of core samples of the substrate were taken at both sites (a total of 30 from Playa Flamingo and 48 from Puerto Del Carmen). The process involved inserting a 25cm length of PVC pipe (2.5cm diameter) vertically into the substrate to fill it up with sediment; 25cm is roughly the depth to which *S. squatina* will typically bury itself (pers obs). A cap was then put on the exposed end, allowing the pipe to be pulled out with the sample still inside the tube, and then another cap was put on the other end, sealing the sample for analysis once out of the water. At both sites the sediment samples were taken in-between the transects which were laid. Core samples were distributed in a haphazard manner throughout sites. A total of 30 samples were taken at the Playa Flamingo site, and 48 at Puerto Del Carmen. To gain percentage estimates of sediment composition wet sieving was undertaken, as described by Kingsford and Battershill (2000). Samples were sieved through 6 stackable meshes of decreasing size, 4000, 2000, 500, 250, 125 and 63 microns. The weight of each sieved sample was expressed as a percentage of the whole sample, derived from subtracting the weight of the empty meshes before wet sieving from the weight of the meshes after wet sieving. The percentage of the sediment within samples were averaged across the site, giving a percentage gradient of sediment for each site.

To compare habitat attributes of sites associated with *S. squatina* presence and absence benthic cover and sediment composition were also estimated at two other sites on the south coast of Lanzarote, Costa Teguisse and Mala (see Figure 3.1). These sites were selected for comparison against the two main sites (Puerto Del Carmen and Playa Flamingo) as they were known to only have *S. squatina* sightings very rarely. Benthic cover and sediment composition at the comparison sites was derived from the same method as above (i.e. transects, quadrats, CPCe, core samples). However, the transects of the comparison sites differed from the main sites in that 4 transects running parallel to shore were laid at depths of 20m, 15m, 10m, and 5m. Each of the transects was 50m long. Similar to above, photos were taken of the substrate every metre

along the transects and analysed with CPCe software. A total of 200 photos were taken, which resulted in 10,000 habitat point counts at each comparison site. Three core samples were taken along each transect at each depth at the comparison sites and wet sieved afterwards in the same way as described above. A total of 12 core samples were taken from each comparison site and averaged together to give an estimate of sediment composition at each site.

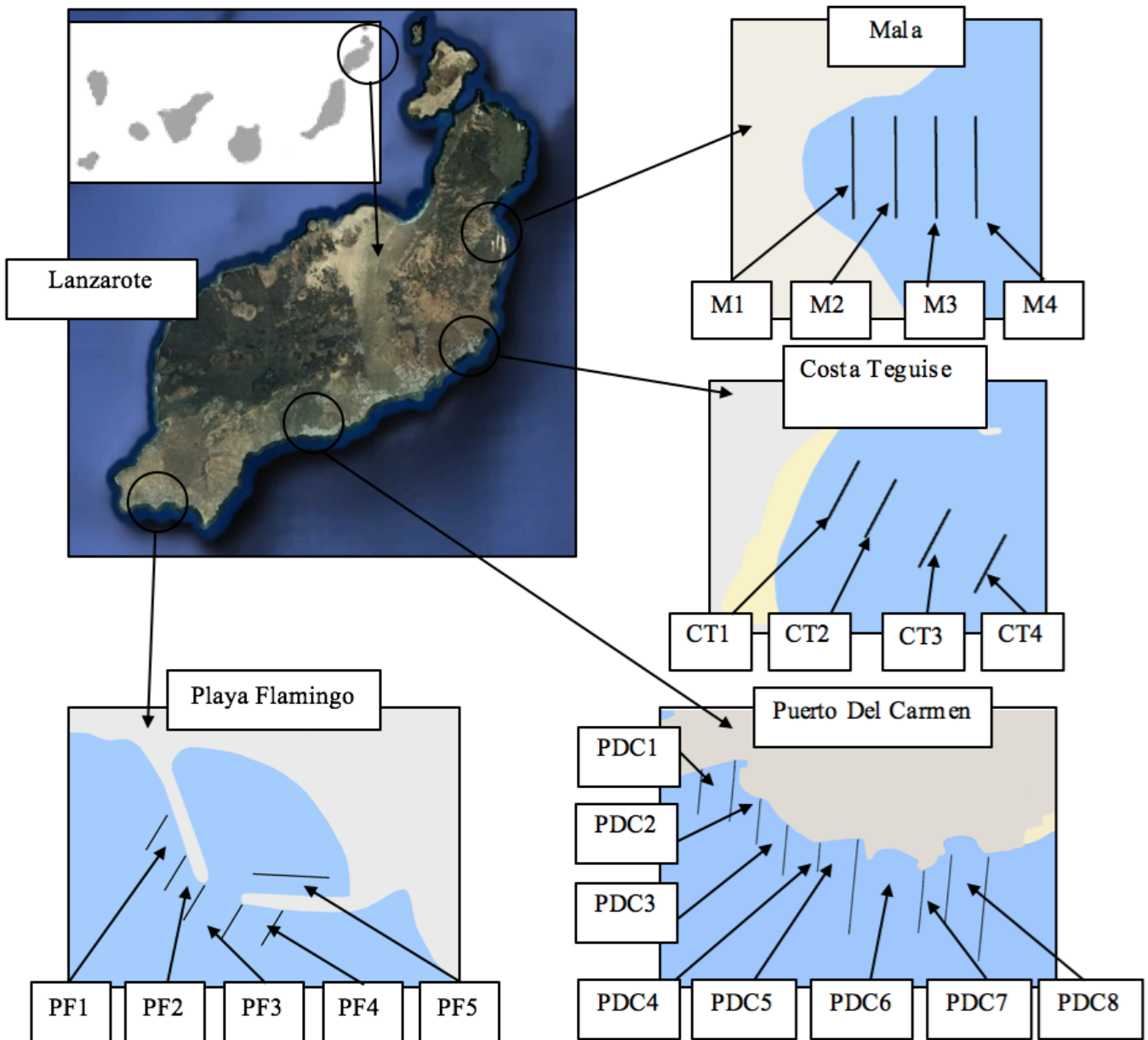


Figure 3.1 Study sites with transect and area locations

3.2.3 Observations of *S. squatina* and associated abiotic factors structuring habitat use

Underwater visual population surveys, using SCUBA, were conducted at the sites Puerto Del Carmen and Playa Flamingo, located on the island Lanzarote, between March 2015 and March 2016 to determine if *S. squatina* have different habitat associations at different life stages and sexes. Puerto Del Carmen and Playa Flamingo were picked as replicate sites for population surveys as high sightings of *S. squatina* have been reported in both locations, with Puerto Del Carmen recently being declared a nursery ground (Miller 2016). With every individual observation of *S. squatina* at the sites Puerto Del Carmen and Playa Flamingo, variables were

noted down on waterproof paper (i.e. date, time, location (in relation to transects previously laid), depth (m) at sighting and sea temperature (determined from the primary authors dive computer). In addition to this, each individual's sex was determined from the presence of clasper (male) or lack of claspers (female) (Pratt and Carrier 2001), while total length was measured with a 2m length of tape which was placed beside any encountered *S. squatina*; this method only posed a problem when *S. squatina* was active and swimming, however, *S. squatina* is a sedentary species (Miller 2016) so this problem was not often encountered. Lastly, level of pregnancy in females was quantified by visually assessing females girth; those who had a much larger girth than usual and body shapes which were not consistent with their typical flat shape were considered pregnant (Whitney et al 2012).

3.2.4 Statistical Analysis

To determine the main abiotic factors structuring habitat use of *S. squatina*, a series of independent two sample *t*-tests were used to determine if the means associated with groups of *S. squatina* were associated with a statistically significant difference. Results of something were considered statistically significant at $P \leq 0.05$. Levene's *F*-test was used to test for the assumption of homogeneity of variance, this being satisfied with $P \geq 0.05$. When homogeneity of variance was not satisfied ($P < 0.05$) the Mann-Whitney U test was used as it allowed for accurate results with data which was not normally distributed. Statistical analysis was performed on SPSS (IBM SPSS Version 23).

3.3 Results

The site Puerto Del Carmen had over five times more observations of *S. squatina* than the site Playa Flamingo (see Figure 3.2). However, there were over three times as many surveys conducted at the site Puerto Del Carmen than Playa Flamingo. The area PDC1 in Puerto Del Carmen had the highest number of *S. squatina* observations than any other area within the site, and amounted to nearly half of all the observations at Puerto Del Carmen. Whereas, the area PDC8 did not contribute to any of the *S. squatina* observations, and PDC2 and PDC3 each contributed to less than 3% of all observations. All of the areas at Playa Flamingo had *S. squatina* observations. Most of the areas within this site had fairly similar numbers of sightings, however, the area PF5 had at least half the amount of *S. squatina* observations than the rest of the areas.

The sites Puerto Del Carmen, Costa Teguisse, and Mala were best characterised by the sand category (see Figure 3.3) as this contributed to over 80% of the benthos in each case. Whereas, at the site Playa Flamingo, the benthos category sand contributed to less than 5% of the benthos. While, the categories bedrock and loose rock made up the majority of the benthos at Playa Flamingo, as they contributed to nearly 90%.

The sediment grade categories 250 and 125 microns contributed to well over half of the sediment at the sites Puerto Del Carmen and Mala (see Figure 3.4). Whereas, Playa Flamingo was best characterised by the large proportion of sediment categories 500 and 250 microns. Although, Costa Teguisse had a fairly high percentage of the 250 micron sediment grade category, the 125 micron category made up the majority of sediment at the site, and contributed to over half of the sediment.

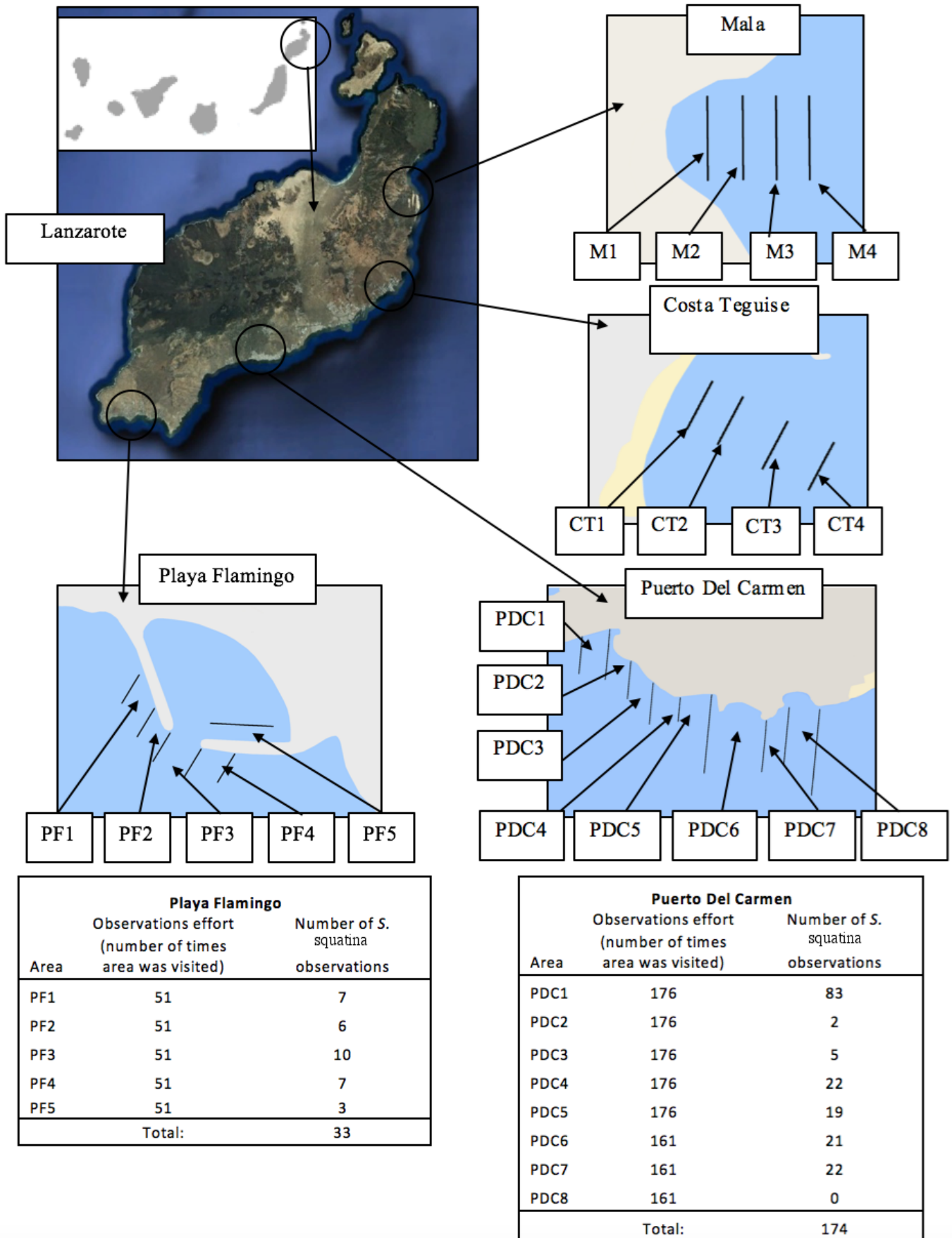


Figure 3.2 Study sites with observation effort and number of *S. squatina* observations

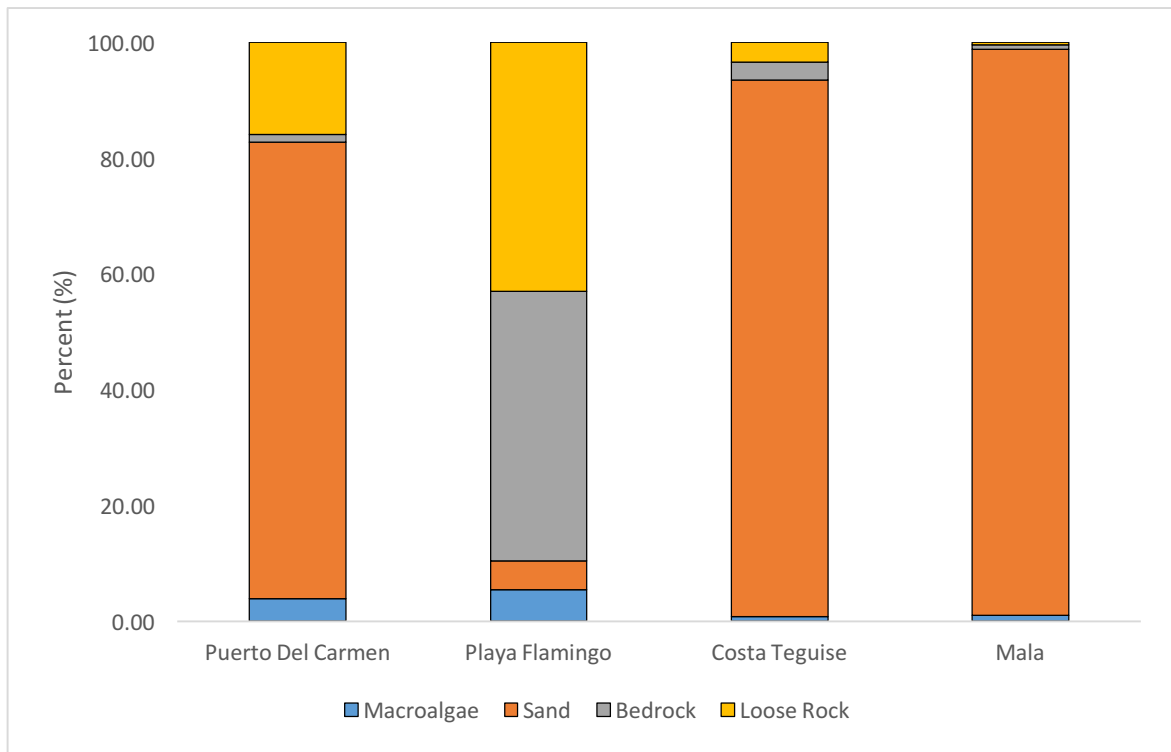


Figure 3.3 Percentage of benthos types at study sites

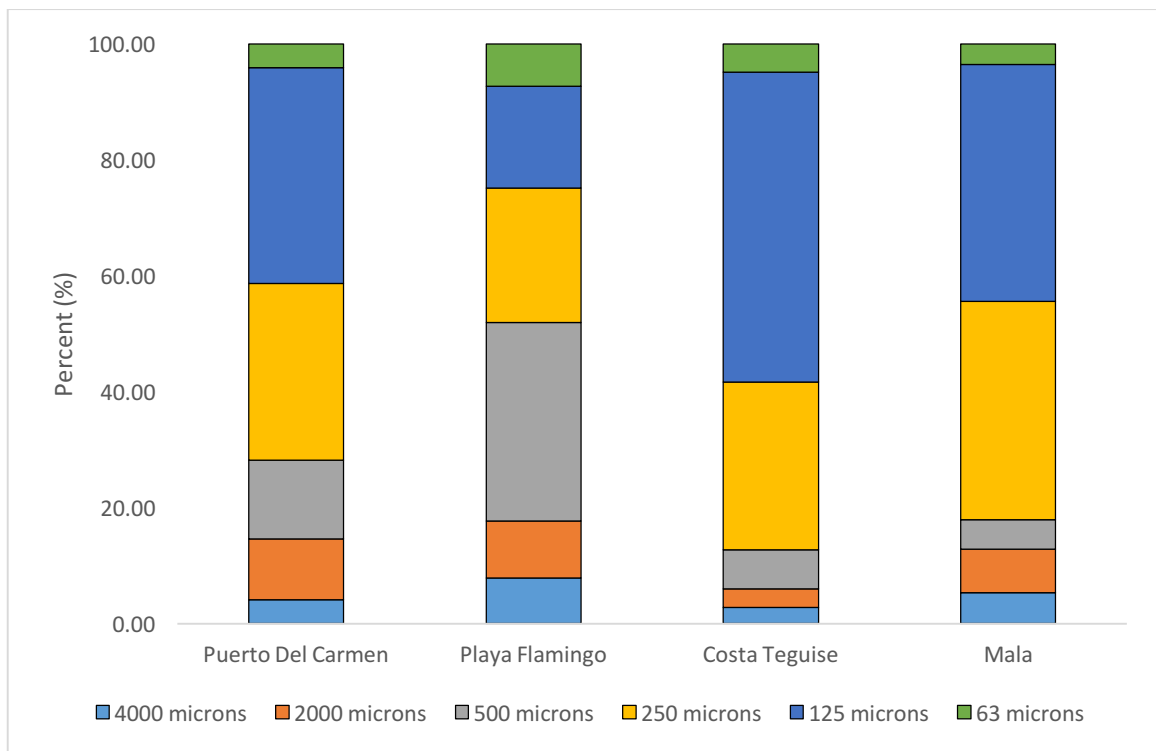


Figure 3.4 Percentage of sediment grade at study sites

Macroalgae cover was found to be significantly different between locations at which *S. squatina* had been observed and those at which it had not been observed (see Figure 3.5) (T-test: $T = 3.38$, $df = 15$, $p = 0.004$). Similarly, there was a significant difference in benthic sand cover between locations at which *S. squatina* had been observed and those at which it had not been observed (Mann-Whitney test: $U = 4.13$, $df = 11.67$, $p = 0.001$). Although there was a difference in the amount of bedrock at sites which had *S. squatina* sightings and those sites which did not, there was no significant difference between the two groups (T-test: $T = 0.90$, $df = 15$, $p = 0.386$). Whereas, loose rock at areas with *S. squatina* sightings was, on average, much higher than at areas without *S. squatina* sightings and found to be significant (Mann-Whitney test: $U = 4.05$, $df = 11.24$, $p = 0.002$).

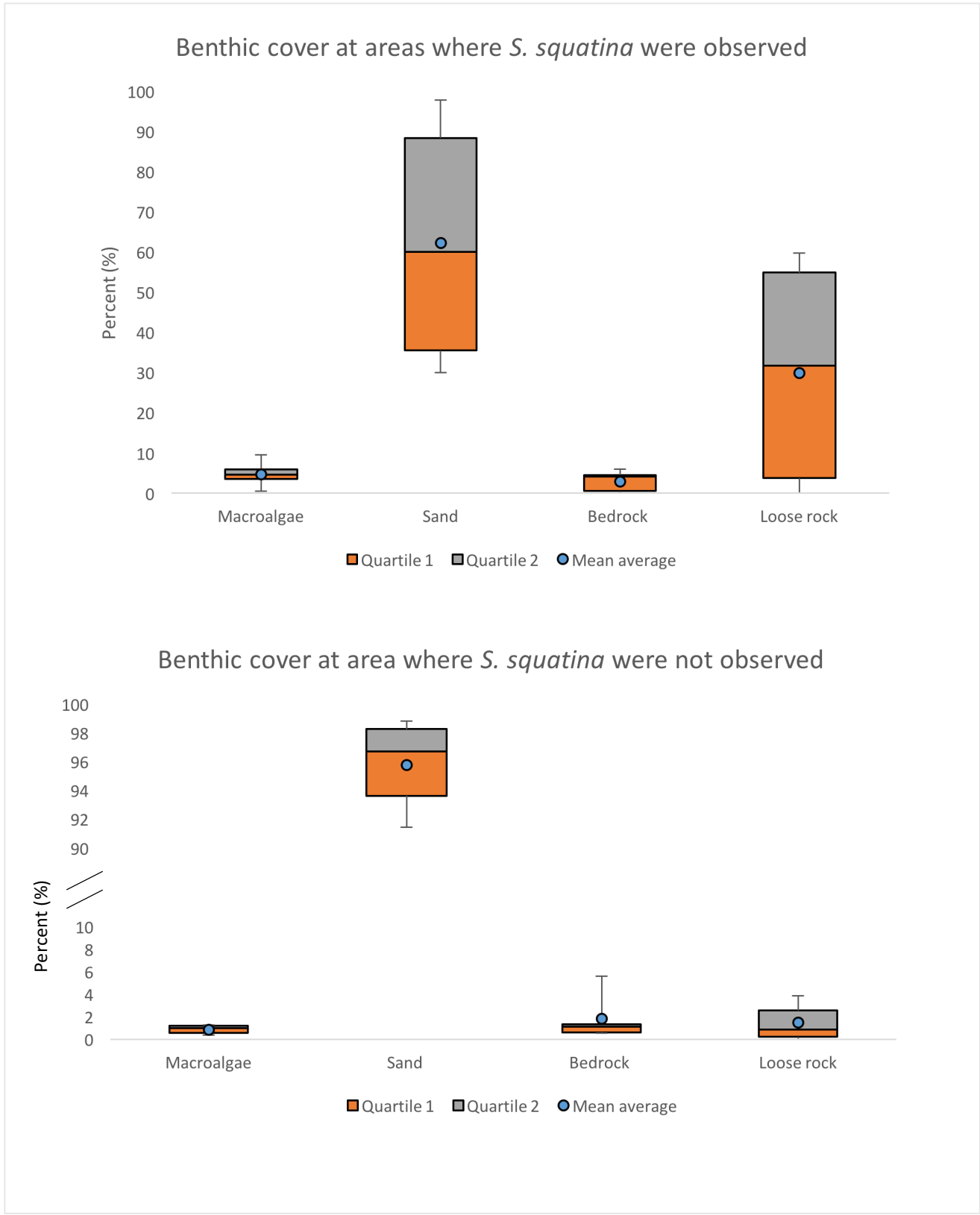


Figure 3.5 Box plots of benthic cover types at locations where *S. squatina* was and was not observed

The amount of both 4000 micron and 2000 micron sediment at locations where *S. squatina* was observed and was not observed (see fig 3.6) was not significantly different (T-test: $T = 1.66$, $df = 12.12$, $p = 0.118$, and T-test: $T = 0.96$, $df = 15$, $p = 0.352$, respectively). Similarly, the amount of 250 micron and 63 micron sediment was also not significantly different between areas where *S. squatina* was observed and areas where *S. squatina* was not observed (T-test: $T = 0.87$, $df = 15$, $p = 0.397$, and T-test: $T = 1.43$, $df = 15$, $p = 0.172$, respectively). However, the amount of 500 micron and 125 micron sediment at locations where *S. squatina* was observed was significantly different than the sediment at locations where *S. squatina* was not observed (Mann-Whitney test: $U = 3.82$, $df = 11.47$, $p = 0.003$, and T-test: $T = 2.67$, $df = 15$, $p = 0.017$, respectively).

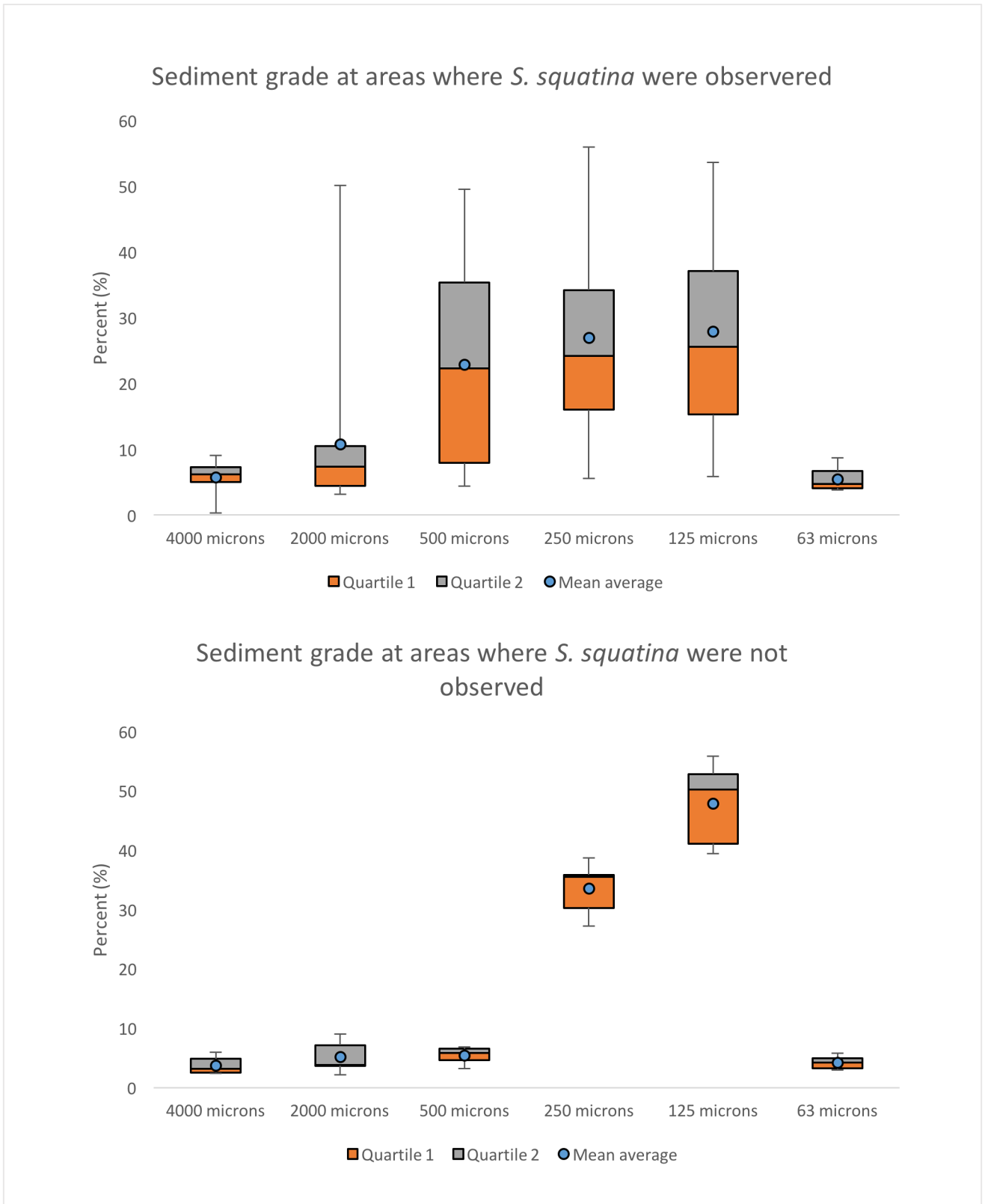


Figure 3.6 Box plots of sediment grade at locations where *S. squatina* was and was not observed

There was a significant difference in the depths at which juvenile and mature *S. squatina* were observed at (T-test: $T = 2.27$, $df = 133$, $p = 0.025$). Although, juvenile *S. squatina* were associated with significantly shallower depths than mature *S. squatina* (see Figure 3.7), there was no significant difference in ambient water temperature between juvenile and mature *S. squatina* (Mann-Whitney test: $U = 1.04$, $df = 98$, $p = 0.299$).

Whereas, there was no significant difference in either the depths or ambient water temperatures associated with mature male and mature female *S. squatina* occurrence (see Figure 3.8) (Depth T-test: $T = 1.98$, $df = 51$, $p = 0.065$, and ambient water temperature T-test: $T = 1.61$, $df = 31.1$, $p = 0.118$).

Similarly, the depths at which observably gravid and non observably gravid *S. squatina* occurred (see Figure 3.9) showed no significant difference (T-test: $T = 0.297$, $df = 130$, $p = 0.767$). However, there was a significant difference in the ambient water temperatures at which observably gravid and non observably gravid *S. squatina* occurred (T-test: $T = 2.32$, $df = 96$, $p = 0.023$).

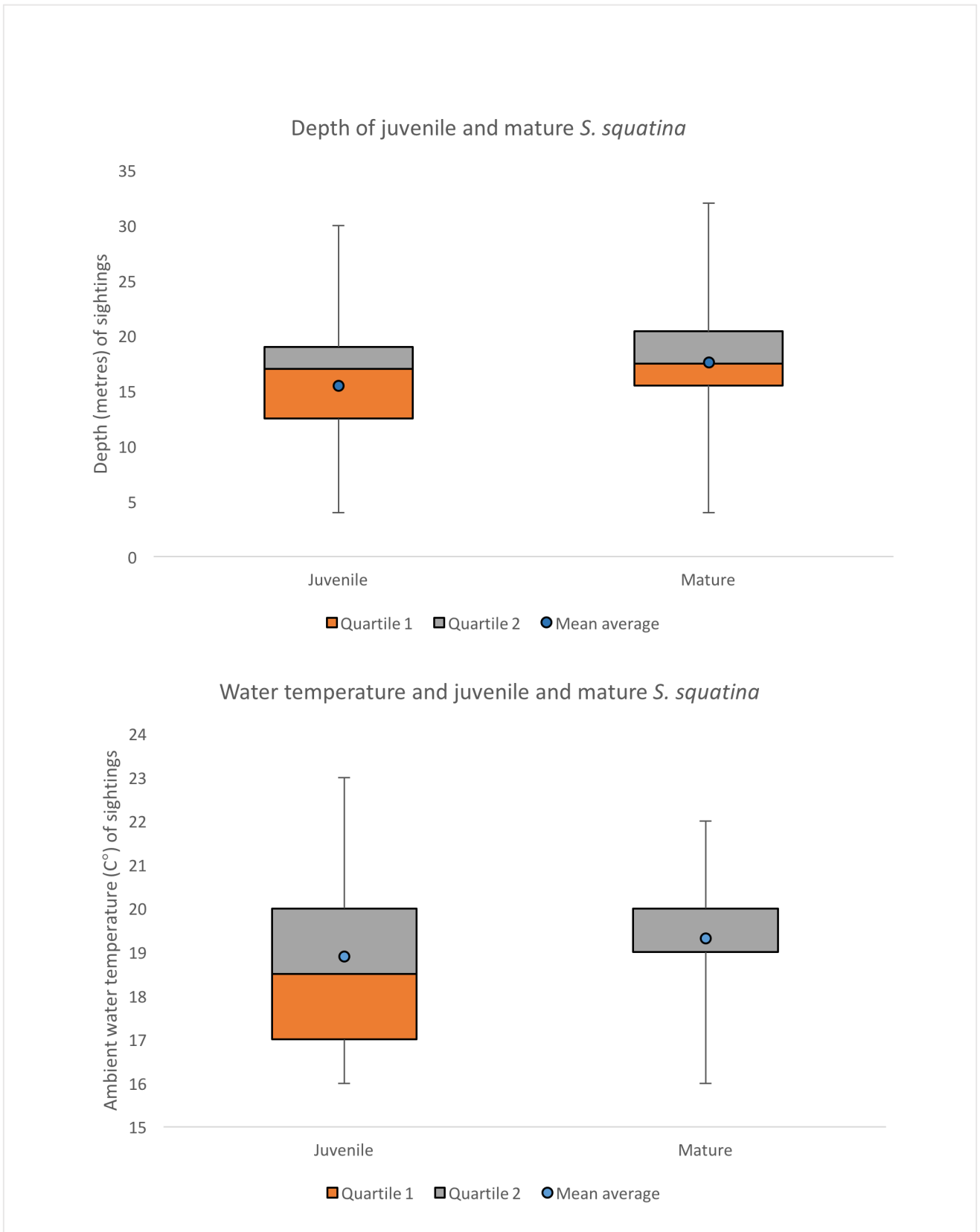


Figure 3.7 Box plots of depth and ambient water temperature at which juvenile and mature *S. squatina* were sighted

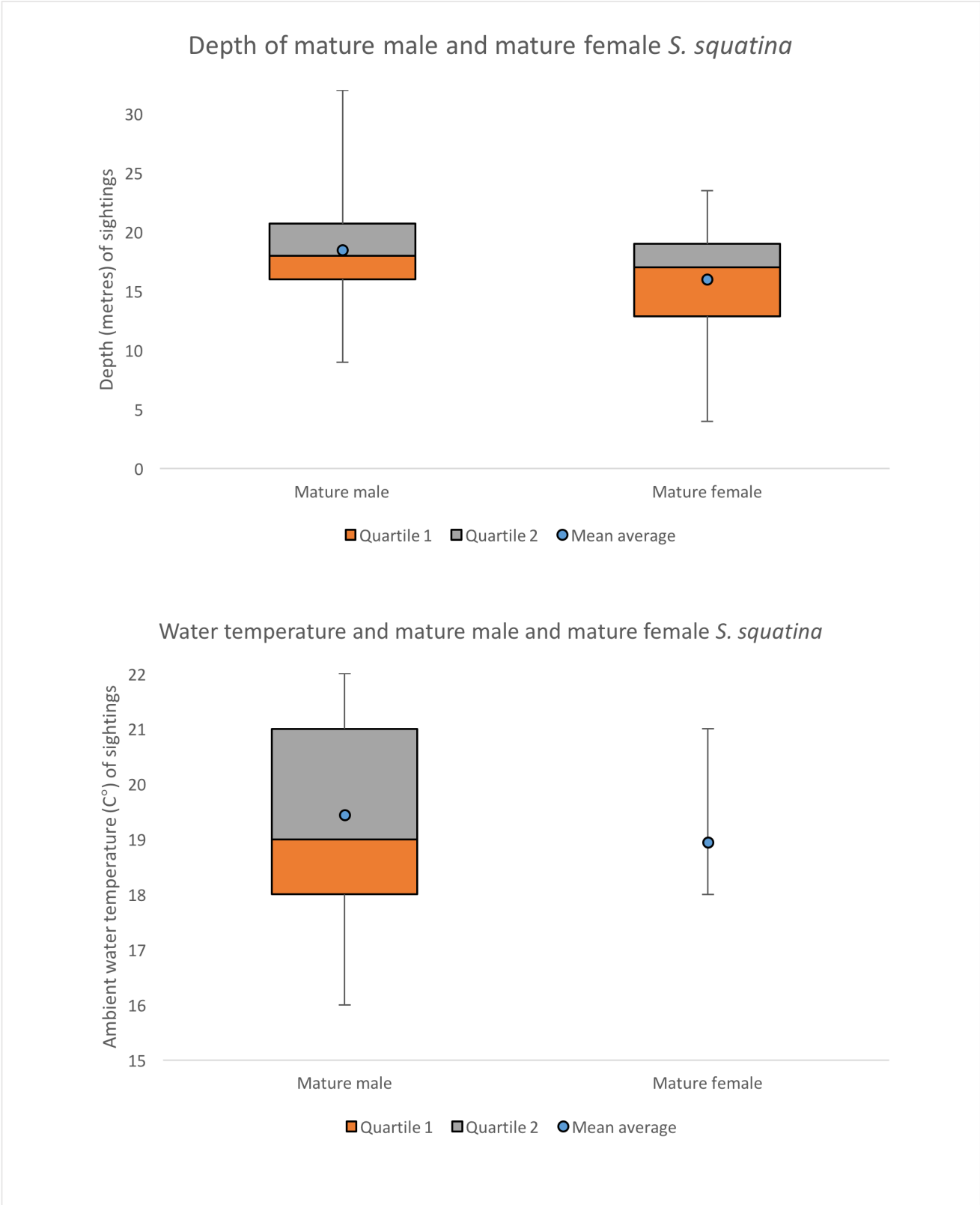


Figure 3.8 Box plots of depth and ambient water temperature at which mature male and mature female *S. squatina* were sighted

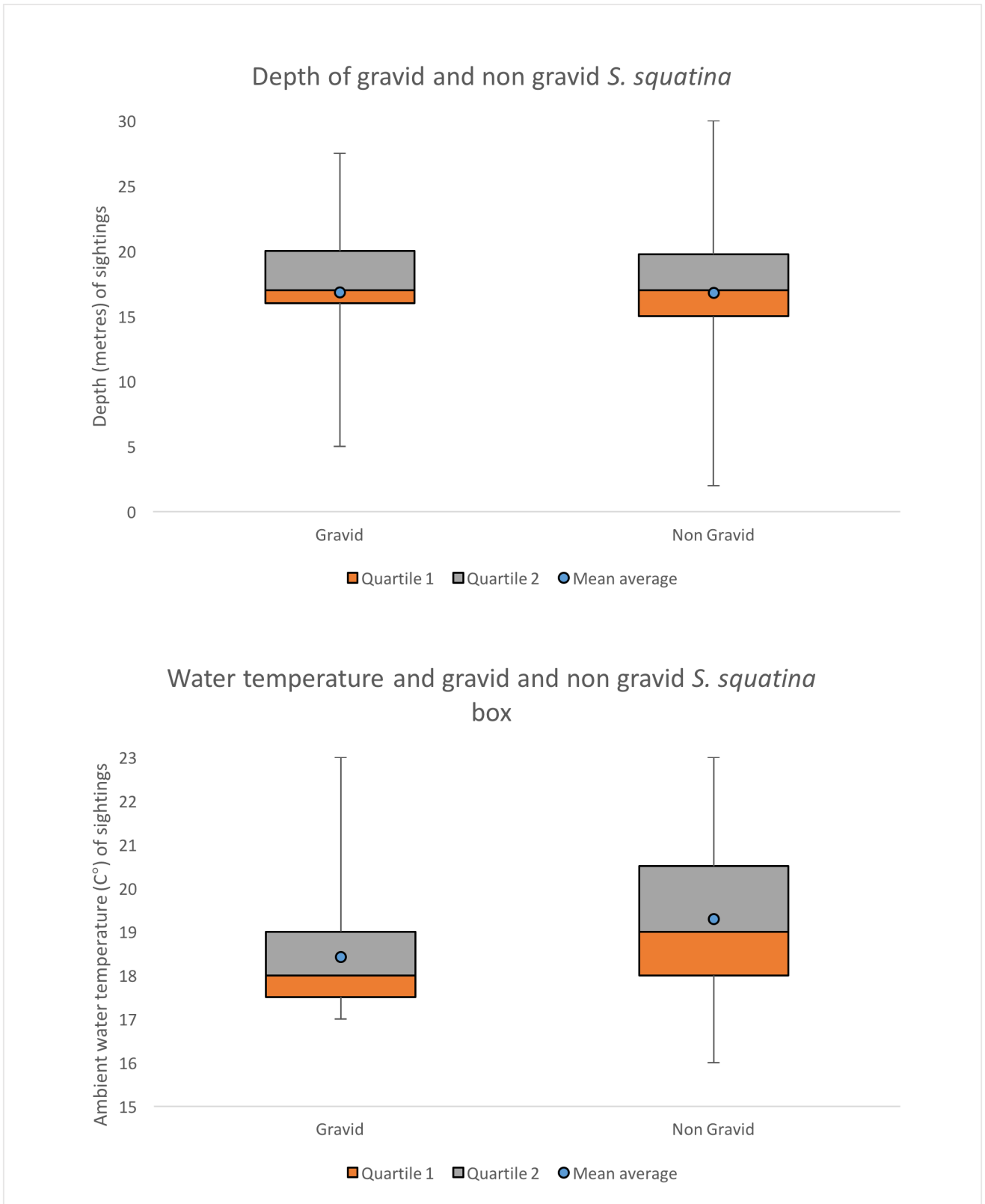


Figure 3.9 Box plots of depth and ambient water temperature at which gravid and non gravid *S. squatina* were sighted

3.4 Discussion

The benthic habitat associated with *S. squatina* presence at Puerto Del Carmen and Playa Flamingo was most strongly described by the percentage of benthic cover of macro algae, sand and loose rock, as the *t*-tests suggest that these habitat attributes are significantly different from areas where *S. squatina* was absent. The quantity of macro algae and loose rock cover was significantly higher in areas where *S. squatina* was present than in areas where *S. squatina* was absent, on average, 3.84% and 28.52% higher, respectively. Additionally, the quantity of sand cover was significantly lower in areas where *S. squatina* was present than in areas where *S. squatina* was absent, on average 33.46% lower. The significantly higher quantities of macro algae, loose rock and significantly lower quantities of sand cover indicate that the areas where *S. squatina* are present, have a more complex benthos, and that they are selecting their habitat based on this complexity. However, the relationship between habitat complexity and predatory success is not straight forward (i.e. habitat complexity can be associated with both predatory success through increased prey densities and refuge for prey from predation (Crowder and Cooper 1982, Canion and Heck 2009)). Although, *S. squatina* are known to be ambush predators (Miller 2016), which could potentially increase the chances of successful predation through increased camouflage and reduced predator detection by prey and/or increased prey densities in complex habitats (Crowder and Cooper 1982, Winfield 1986). Habitat complexity has been shown to be an important factor in structuring the occurrence of shark species (Espinoza et al. 2014)). For example, Espinoza et al. (2014), studied shark species-specific habitat associations along the Great Barrier Reef Marine Park throughout a 10 year period, with baited underwater video stations (BRUVS). A total of 21 species were recorded with 64% of the shark abundance being made up of the shark species *Carcharhinus amblyrhynchos*, *C. albimarginatus*, *Galeocerdo cuvier*, and *Loxodon macrorhinus*. Along the Great Barrier Reef Marine Park, nearshore habitats with greater complexity (e.g. high quantities of macro algae and marine plants, rocky shoals, and coral reef) were associated with higher occurrence of a wider variety of shark species than nearshore habitats which were associated with less complexity (Espinoza et al. 2014).

Sediment grain size was found to be an important habitat factor associated with *S. squatina* occurrence as the sediment structure was significantly different (on two levels: 500 micron and

125 micron sediment grade categories), in areas where *S. squatina* were present and absent. There was on average 17.51% more sediment of the 500 micron sediment grade category in areas where *S. squatina* were present than in areas where the species was absent, and on average 19.82% less sediment of the 125 micron sediment grade category in areas where the species was present, although the 500 micron and 125 micron sediment grade category were found in similar quantities at the areas where *S. squatina* were present (22.92% and 27.96%, respectively). Similarly, sediment grade size preferences have been noted in other elasmobranch species such as skates and rays (*Raja clavata*, *R. radula*, *R. asterias*, *Dasyatis pastinaca* and *Gymnura altavela*) in the Northeastern Mediterranean (Yeldan and Avsar 2005): from May 1999 to May 2000 in the Northeastern Mediterranean coast of Turkey, Yeldan and Avsar (2005) identified the sediment structure associated with skate and ray species occurrence. Sediment structure was determined by grain size analysis of core samples of the benthos and put into gravel, sand and silt, and clay categories (defined as, gravel: 2000-1000 microns, sand and silt: 1000-240 microns, and clay: <240 microns). Skates in the Northeastern Mediterranean were found to prefer highly silty substrates, while rays were found to prefer sandy silts found in shallower waters (Yeldan and Avsar 2005). However, the role of sediment grade size in structuring elasmobranch and shark species occurrence is not well understood. The sediment preferences of *S. squatina*'s prey could explain the variation of the 500 micron and 125 micron sediment grade categories between the areas where *S. squatina* were present and absent, which would suggest that *S. squatina* could select habitats which were associated with higher prey density. For example, *S. squatina*'s prey is comprised mainly of flatfish, crustaceans and mollusks (Day 1880, Compagno 1984; Ellis et al. 1996) and flatfish have demonstrated strong habitat preferences for various sediment grain sizes (with a general trend occurrence in coarser sediments with increasing size) Tanda 1990, Minami et al 1994, Gibson and Robb 1992, Phelan et al. 2001). However, associations between shark and elasmobranch occurrence and sediment types may not be causal. For example, Martin et al. (2012) modelled the habitat of *R. clavata* and *S. canicula* (commonly known as the thornback ray and small spotted catshark, respectively) in the eastern English channel and found that the younger (neonate and juvenile) life stages had a strong preference for softer and less coarse sediments (categorised as mud and fine sand in the study), as opposed to the harder and more coarse substrates (categorised as coarse sand, gravel, and pebbles). But, that this preference for softer sediments was likely due to the fact that they are often found in calm sheltered shallow coastal areas, such as bays, which are often preferred by younger sharks and rays for their protective

benefit (i.e. less predation, warmer water conditions, and sufficient food resources) and not necessarily a particular sediment grade.

The depths associated with juvenile *S. squatina* presence were found to be significantly shallower than mature *S. squatina* at both sites, Puerto Del Carmen and Playa Flamingo. Juvenile *S. squatina*, on average, occurred 2.1 metres shallower than mature *S. squatina*, indicating that juvenile and mature *S. squatina* are selecting habitat based on depth. However, the shallower occurrence of juvenile *S. squatina* was not associated with a significant difference in ambient water temperatures when compared to the ambient water temperatures associated with mature *S. squatina* occurrence. Juvenile and mature shark segregation has been well researched, with depth often being the mechanism associated with this type of segregation, however, this has often been related to the differing physiological needs of juveniles and matures and the benefits of increased metabolism through thermoregulatory behaviour in juveniles associated with occurrence in shallower and warmer waters i.e. *Negaprion brevirostris* (Morrissey and Gruber 1993), *Carcharhinus plumbeus* (Conrath and Musick 2008). However, it would appear that juvenile *S. squatina* occur at shallower depths for a different reason as temperature was not associated with a significant difference in mature and juvenile *S. squatina* presence. One explanation for the observed differences in depth occurrences of juvenile and mature *S. squatina* could be related to predator avoidance on behalf of the juveniles. It is well known that mature sharks will eat other sharks, often smaller juveniles (van der Elst 1979, Compagno 1984, Harvey 1989). Intraspecific predation is a major mortality factor in a variety of vertebrates (Hutton 1989), and it is known that many sharks engage in this behaviour, for example, lemon sharks are cannibalistic (Vorenberg 1962, personal observation), and Morrissey and Gruber (1993) suggest that the segregation of juvenile and mature lemon sharks is related to the avoidance of major predators, which predominantly includes larger conspecifics.

The water temperatures associated with observably pregnant *S. squatina* were significantly lower than the temperatures associated with non-observably pregnant *S. squatina*, suggesting that they utilise habitats with these lower temperatures (M=18.43 (SD=1.29)). As water temperatures have been noted to effect marine organism's metabolism (often with increased temperatures associated with increased metabolism and decreases in temperature associated with decreases in metabolism) (Gillooly et al. 2001).

Chapter 4: General Discussion

The aims of this study were to determine the spatio-temporal distribution of *S. squatina* by locating incidence of the species at various critical life stages throughout its existing range (within the Canary Islands), and to determine the habitat associations of occurred in the species.

The distribution of *S. squatina* in the Canary Islands allowed us to see the extent of their distribution in the Canary Islands, despite substantial reductions in their former range over the past 50-100 years (OSPAR commission 2010). This study brought to light a number of potential breeding sites, nursery sites, and even mating sites and the times of year associated with occurrence in the Canary Islands, which were previously not known to occur. The implications of this, and practical uses, could prove useful in the conservation of *S. squatina*, with the aim of increasing population numbers through the recolonization of their former range, as certain areas which may be critical for *S. squatina* reproduction were highlighted in this study. For example, the conservation of *G. cirratum* in Florida and the Caribbean has shown great success from restricting the public's access to waters used by *G. cirratum* at certain key times of year associated with mating and parturition (Carrier and Pratt 1998).

The habitat associations of *S. squatina* could have an impact on how the species is managed, as it is suggested that *S. squatina* are selecting habitats based on several environmental aspects (macro algae, loose rock, sand, and sediment composition). It is likely that this is positively related to increased habitat complexity, possibly due to increased prey interactions (Crowder and Cooper 1982, Winfield 1986). However, these are obviously by no means the only habitat attributes which *S. squatina* are basing their habitat selection on, but it is suggested that these attributes (benthos type and sediment type) will go some ways to understanding *S. squatina*'s occurrence as the risk of extinction, for a critically endangered species like *S. squatina*, is thought to be higher if it is indeed selecting habitats based on an ecological niche (Walker 1998).

The incidence of *S. squatina* in the Canary Islands appears to be fairly wide spread, however, it would seem that *S. squatina* are selectively choosing habitats based on a few variables. All of which, indicates that even though *S. squatina* may show some degree of habitat specificity, that the Canary Islands may have high availability of the specific habitat attributes that *S.*

squatina select. This further gives credence to the importance of the Canary Islands as a suitable habitat for *S. squatina*, and may partly explain why the Canary Islands are one of the last few places globally where they can still be seen (OSPAR commission 2010).

4.2 Future research

As no accurate population estimates exist for the current distributions of *S. squatina*, this would be a logical next step in the research of *S. squatina*. Reliable population and local abundance estimates are an important aspect of research for any endangered species (Ebert et al. 2013). However, individual recognition of a number of members of the remaining population of *S. squatina* would be a highly valuable research pursuit as this would result in incredibly useful information for future conservation projects (Speed et al. 2010). Information on a number of individual's movements and habitat use could lead to a better understanding of the parameters which would be necessary if management (such as implementation of MPAs) of the species is to occur. Methods of achieving individual recognition range from simple tagging studies to identification through genetic sequencing (i.e. PCR, or even eDNA).

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Appendix 1: Dive Centre email list within the Canary Islands

Island	Dive Centre Name	email address
Lanzarote	Manta Diving	info@manta-diving-lanzarote.com
Lanzarote	Lanzarote Dive Centre	info@lanzarotedivecentre.com
Lanzarote	Saari Diving	enquiry@safaridiving.com
Lanzarote	Daivoon	daivoon@daivoon.com
Lanzarote	Island Water Sports	info@divelanzarote.com
Lanzarote	Aquasport Diving	geraldine@aquasportdiving.com
Lanzarote	Techno Diving Lanzarote	info@techno-diving.com
Lanzarote	Lanzarote Ocean Divers	info@lanzaroteoceansdivers.com
Lanzarote	Atlantis Diving Lanzarote	info@atlantislanzarote.com
Lanzarote	Lanzarote Buceo	info@lanzarote-buceo.com
Lanzarote	Bahianus Club Lanzarote	info@bahianus.com
Lanzarote	Squalo Diving	info@squalodiving.com
Lanzarote	Alisios Sub Centro de Buceo	Info@alisiosub.com
Lanzarote	Canary Island Divers	info@canaryislanddivers.com
Lanzarote	Rubicon Diving	info@rubicondiving.com
Lanzarote	Calipso Diving	calipso@arrakis.es
Lanzarote	La Santa Diving	info@lasantadiving.com
Fuerteventura	Deep Blue Diving Base	info@deep-blue-diving.com
Fuerteventura	Delphinus Diving School	info@delphinus.eu
Fuerteventura	Abyss Fuerteventura	info@abyssfuerteventura.com
Fuerteventura	Deep Blue Las Playitas Resort	playitas@deep-blue-diving.com
Fuerteventura	Jandia Divers	info@jandiadivers.com
Fuerteventura	Mar y Mas Dive Centre	info@marymas-diving.com
Fuerteventura	Fuerteventura Buceo Diving Centre	info@fuerteventurabuceo.com
Fuerteventura	Dive centre Corralejo	info@divecentercorralejo.com
Fuerteventura	Tortuga Dive Centre	info@tortugadivecentre.com
Gran Canaria	Gran Canaria Divers S.L.	info@grancanariadivers.com
Gran Canaria	Blue water Diving	info@divingingrancanaria.com
Gran Canaria	Dive Academy Gran Canaria	info@diveacademy-grancanaria.com
Gran Canaria	Davy Jones Diving	Webinfo@DavyJonesDiving.com
Gran Canaria	Let's Go Diving	info@lgdiving.com
Gran Canaria	PR Diving Puerto Rico Diving	info@prdiving.com
Gran Canaria	Top Diving Dive Centre	topdivinggc@gmail.com
Gran Canaria	Canary Diving Adventures	info@canary-diving.com
Gran Canaria	Diving Center Sun Sub	webmaster@sunsub.com
Gran Canaria	Mabaq Diving Gran Canaria	info@mabaq.com
Gran Canaria	Atlantik Diving	info@grancanariadiveresort.com
Gran Canaria	Diving Center Nautico	info@divingcenter-nautico.com
Gran Canaria	Scuba Sur Gran Canaria	info@scubasur.net

Tenerife	Blue Explorers	gc@blue-explorers.com
Tenerife	Cressi Dive Center	cressidivecenter@hotmail.com
Tenerife	Moana Diving	info@moana-diving.com
Tenerife	The Dive Shop Tenerife	tim@thediveshoptenerife.com
Tenerife	LJ Diving Tenerife	info@ljdivingtenerife.com
Tenerife	Mermaid Diving	Melissa@mermaiddiving.co
Tenerife	Teide Divers	jackie.teidedivers@gmail.com
Tenerife	Amarilla Divers	info@amarilladivers.com
Tenerife	Medanodive	info@medanodive.com
Tenerife	Island Divers	info@islanddivers.org
Tenerife	Dive and Sea Tenerife	info@diveandseatenerife.com
Tenerife	Dive Tenerife	info@divetenerife.com
Tenerife	los gigantes diving centre	divinglosgigantes@gmail.com
Tenerife	atlantik	via website
Tenerife	espíritu de buceo tenerife	via website
Tenerife	paradisedivers	info@paradisedivers.co.uk
Tenerife	12dive	info@12dive.com
Tenerife	diveria	info@diveria.net
Tenerife	blackstonedivecenter	info@blackstonedivecenter.com

Appendix 2: Survey Questions

Q1. Are you, or the dive centre, based in the Canary Islands?

Q2. Which island are you or the dive centre located?

Q3. Have you ever encountered any *Squatina squatina* (commonly known as an Angel Shark) while diving on your island?

Q4. Where and when have you personally encountered Angel Sharks (of any size) before? (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q5. Where and when have you personally encountered adult Angel Sharks (larger than 128cm in females and larger than 80cm in males) before? [If this is the same as the previous answer or you're unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q6. Where and when have you personally encountered male Angel Sharks before? [If this is the same as the previous answer or you're unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q7. Where and when have you personally encountered female Angel Sharks before? [If this is the same as the previous answer or you're unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q8. Where and when have you personally encountered juvenile/baby Angel Sharks before? (smaller than 128cm in females and smaller than 80cm in males) [If this is the same as the previous answer or you're unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q9. Have you ever seen Angel Sharks mating?

Q10. How many times have you seen them mating? [If unsure leave blank]

Q11. Where and when have you encountered Angel Shark Mating? [If unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q12. Have you ever seen any Angel Sharks with mating scars?

Q13. Where and when have you encountered Angel Sharks with mating scars? [If unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

Q14. Have you ever seen a pregnant Angel Shark?

Q15. Where and when have you encountered pregnant Angel Sharks? [If unsure please leave blank] (Please enter general location, dive site, month(s), and year(s) if known e.g. The Cathedral, Puerto Del Carmen, March, 2016)

