Vol. 603: 147–160, 2018
https://doi.org/10.3354/meps12715

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 17

Habitat use, seasonality and demography of an apex predator: sevengill shark *Notorynchus cepedianus* in northern Patagonia

Alejo J. Irigoyen[1,*], Agustín M. De Wysiecki[1], Gastón Trobbiani[1], Nelson Bovcon[2], Cynthia A. Awruch[1,3], Federico Argemi[4], Andrés J. Jaureguizar[5,6]

[1]Centro para el Estudio de Sistemas Marinos (CESIMAR),
Consejo Nacional de Investigaciones Científicas y Técnicas (CCT CENPAT–CONICET), Puerto Madryn U9120ACD, Argentina
[2]Departamento de Pesca Deportiva, Secretaría de Pesca de la Provincia del Chubut 9020, Argentina
[3]School of Natural Sciences, University of Tasmania, Hobart, Tasmania 7001, Australia
[4]Aquarium Fundación Temaiken, Buenos Aires 1625, Argentina
[5]Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (CIC), La Plata 1900, Argentina
[6]Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata B7600EEP, Argentina

ABSTRACT: Gaining insight on how species relate to their environment and other members of the trophic community is critical for their management. We investigated habitat use, seasonal patterns of abundance and population structure of the broadnose sevengill shark *Notorynchus cepedianus* in the marine temperate environment of a northern Patagonian bay (Argentina). We expected *N. cepedianus* to exhibit strong seasonality in the bay driven by the seasonal occurrence of important marine mammal prey. However, an alternative or complementary hypothesis arose from the possibility that *N. cepedianus* uses the area seasonally as mating grounds. To explore these hypotheses, a suite of baited remote underwater video stations and catch per unit effort data indices were used to estimate the seasonal relative abundance of the species inside the bay. Reproductive hormone levels were measured to determine reproductive status and maturity stages of the population. Results indicated that *N. cepedianus* uses the bay year-round, showing a peak abundance during spring when individuals aggregate, likely for feeding and mating purposes. Male and female total lengths at maturity were 170 and 190 cm, respectively. Contrary to other studies in the Southwest Atlantic, population composition remained similar throughout the seasons, with adults dominating over juveniles, and adult females prevailing in the population at all times. Considering the historical abundance decline recently reported for the species, protection and enforcement within protected areas across the Southwest Atlantic must remain of high priority in government initiatives.

KEY WORDS: Baited remote underwater video station · BRUVS · Catch per unit effort · CPUE · Reproductive hormones · Seasonal occurrence · Caleta Valdés · Southwest Atlantic

INTRODUCTION

Understanding habitat use and seasonal dynamics of marine species and gaining insight on how they relate with their environment and other members of the community are critical for their management (Ferretti et al. 2010, Bird et al. 2018). In the case of threatened marine top predators, such as many large sharks, this type of information is important for the conservation of the marine environment because it allows us to understand their capacity to influence communities via trophic and behavior-mediated in-

---

*Corresponding author: alejo@cenpat-conicet.gob.ar

teractions (Heithaus et al. 2008, Barnett et al. 2012). However, this type of information remains deficient when assessing shark populations because of the inherent difficulty of gathering high-quality data on these animals (Heithaus et al. 2008, Heupel et al. 2015). Compared with other marine animal groups, in general large sharks occur in low densities, have elusive behavior and are distributed over large areas that are usually inaccessible by standard research methods (Heithaus et al. 2008).

The broadnose sevengill shark *Notorynchus cepedianus* Péron, 1807 belongs to a particular lineage of ancient large sharks (Hexanchiformes) that share ancestral characteristics, including a set of 7 pairs of respiratory gills from which they derive their common name (Last & Stevens 2009). The species is highly migratory and exhibits a worldwide antitropical distribution (except North Atlantic and Indian Oceans) in temperate coastal and continental shelf marine environments (Compagno 2005, Last & Stevens 2009). These sharks reach up to 300 cm in total length and consume a variety of large prey such as bony fish, other chondrichthyans and marine mammals (Ebert 1991, Crespi-Abril et al. 2003, Lucifora et al. 2005, Braccini 2008). Due to its high consumption of marine mammals, the species has been ranked as a high trophic level predator (Cortés 1999). Furthermore, Barnett et al. (2012) characterized the relevant roles of *N. cepedianus* and the other hexanchids as apex predators in marine ecosystems, since they lack sympatric shark species consuming the same prey.

N. cepedianus has been classified as Data Deficient by the IUCN Sharks Specialist Group Red List due to a general lack of information (Compagno 2005). However, the species is highly vulnerable to overfishing in many parts of the world as a consequence of exposure to intensive coastal fisheries. For example, in coastal areas of Argentina, studies using different data sources and methods reported a serious decline in *N. cepedianus* abundance over the last 4 decades (Barbini et al. 2015, Irigoyen & Trobbiani 2016). Off eastern Australia, historical catch per unit effort (CPUE) indices of sevengill shark abundance increased, suggesting a greater interaction of these animals with fisheries and shark meshing programs (Reid et al. 2011). Biological life-history traits including slow growth and long-term maturation (Compagno 2005) raise further concern about its conservation status. *N. cepedianus* grows slowly (Braccini et al. 2010) and exhibits a viviparous lecithotrophic reproductive mode (Awruch 2015), characterized by a biennial cycle, involving a 6 to 12 mo ovulation period, followed by a 1 yr gestation period (Ebert 1989, Awruch et al. 2014).

In the Southwest Atlantic, *N. cepedianus* is distributed from Cananéia, Brazil (25° S, Sadowsky 1969) to Dungeness Cape, Chile (52° S, Guzmán & Campodónico 1976). Scarce and scattered evidence suggests that *N. cepedianus* uses the coastal waters of Argentina for feeding, mating and nursing purposes between spring and early autumn (Lucifora et al. 2005, Cedrola et al. 2009, Irigoyen et al. 2015, Irigoyen & Trobbiani 2016, De Wysiecki et al. 2018). Catch and effort analyses indicate that juveniles and adults reach maximum abundance from January to April along the coastal areas of northern Patagonia (40°–42.5° S, Lucifora et al. 2005, Irigoyen et al. 2015). In southern Patagonian waters (47.5°–49.5° S), *N. cepedianus* occurs from November to March as reported from fishing tournaments and recreational fisheries data (Cedrola et al. 2009). Although large pregnant females are rarely recorded (only 1 record found in Gadig 2001), neonates were frequently reported during late spring and summer in northern areas (36.5°–40° S; Lucifora et al. 2005, Irigoyen & Trobbiani 2016), and only a few specimens were found along southern Brazilian coasts (Vooren et al. 2005). Therefore, data on the population dynamics and structure of *N. cepedianus* still remains scare in this region of the world.

Advances in the knowledge of life history, migration patterns and key habitats are priorities for the conservation and sustainability of *N. cepedianus* in the Southwest Atlantic. Theory in ecology indicates that seasonal patterns of abundance of fish are common in temperate environments because of fluctuations in environmental conditions (e.g. water temperature) and food availability (Fryxell & Sinclair 1988, Berthold 1999, Block et al. 2011). Accordingly, Barnett et al. (2010) concluded that prey abundance variations driven by water temperature fluctuations directly influence *N. cepedianus* seasonal movements in Tasmanian bays. Thus, we expected *N. cepedianus* to exhibit strong seasonality in a northern Patagonian bay (Caleta Valdés, Argentina) driven by the seasonal occurrence of important prey. Marine mammals comprise one of the most relevant groups of prey items in the diets of large sharks (Ebert 1991, Crespi-Abril et al. 2003, Lucifora et al. 2005, Braccini 2008). South American sea lions *Otaria flavescens* and southern elephant seals *Mirounga leonina* aggregate in great numbers in breeding colonies in the area during spring and summer seasons (Dans et al. 2004, Lewis et al. 2004, Ferrari et al. 2009). Therefore, a high abundance of pinniped pups is likely to be a strong driver for *N. cepedianus* abundance patterns because these are easy-to-catch, nutritious targets. In contrast, it is unlikely that the sharks use this area as a nursery ground. Neonates and nursery areas of *N. cepedianus* have been reported to occur within estuarine environments (e.g. Menni & García 1985, Lucifora et al. 2005), not in shallow marine habitats such as Caleta Valdés (Estevez & Varela 1991). Nonetheless, an alternative or complementary hypothesis could be related to the possibility that *N. cepedianus* uses the area seasonally as mating grounds. To explore these hypotheses, we aimed to determine the habitat use, seasonal pattern of abundance, demographic structure and reproductive status of *N. cepedianus* in Caleta Valdés, using a combination of fishery-independent methods over a period of 2 yr. Additionally, we include a more comprehensive estimation of length–weight relationships than the one that is currently available (Cedrola et al. 2009) to provide valuable information for this data-deficient species.

MATERIALS AND METHODS

Study site

Sampling was conducted at Punta Bajo, Caleta Valdés, Argentina (42° 25′ S, 63° 37′ W) a northern marine bay in Patagonia, which is part of the Valdés peninsula (Fig. 1), an area recognized in 1999 by UNESCO as a World Heritage Site because of its concentration of marine mammals and birds. The bay is characterized by a narrow (between 200 and 700 m) and long water intrusion bounded by a gravel bank that is 35 km long (Fig. 1). As a result of a small mouth and shallow waters (maximum depth of 13 m at high tide) in the bay, tides produce strong currents of changing direction throughout the day. Water temperature fluctuates seasonally between a minimum value of 9°C in August and a maximum of 18°C in February (data taken in the field). Along the gravel bank and islands located at the end of the bay, elephant seals, penguins and other marine bird colonies are densely distributed (Dans et al. 2004, Lewis et al. 2004, Ferrari et al. 2009, Lisnizer et al. 2011, Pozzi et al. 2015). Adult southern elephant seals display seasonal variation in abundance with a peak during spring (September–October) when females arrive to breed and molt (Lewis et al. 2004, Ferrari et al. 2009). Weanling pups stay up until December when they move offshore for the first time. Magellanic penguins *Spheniscus magellanicus* and kelp gulls *Larus dominicanus* are also present in the area by late spring and summer to reproduce (Lisnizer et al. 2011, Pozzi et al. 2015). Furthermore, colonies of South American sea lions are located a few kilometers north and south of Caleta Valdés (Dans et al. 2004). Despite the information available regarding marine mammals and birds, baseline ecological knowledge to support marine planning in the area is very limited, especially for chondrichthyans.

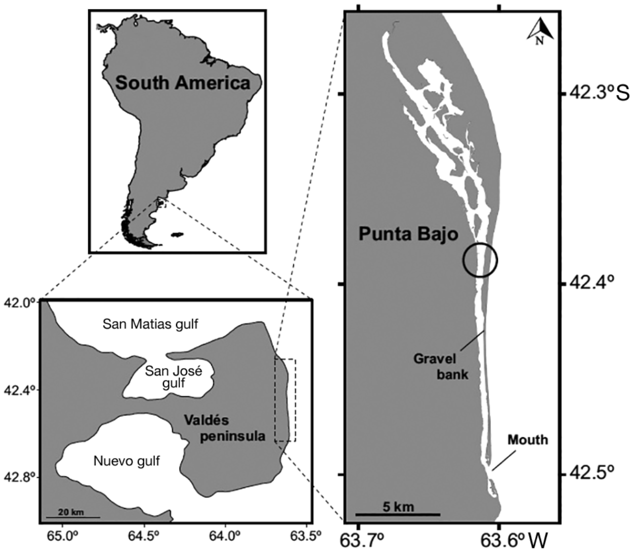

Fig. 1. Sampling location (circle) at Punta Bajo (Caleta Valdés), Argentina

Field methods and sampling design

Daily sampling trips were conducted on a bimonthly basis between June 2015 and February 2017. Site, moon phase and tide variables were fixed to avoid effects on relative abundance estimates. The sampling site (Punta Bajo) was chosen for its accessibility by land with motor vehicles. Sampling dates were set on full moon days with the high tide occurring at midday (between 11 and 14 h). Three approaches were used to collect samples, as follows.

Longline fishing

Longline fishing sessions were conducted in order to calculate a CPUE index of relative abundance. Longlines consisted of 140 m lead-core mainline with 0.8 m stainless steel snoods and 20 hooks (Mustad 2330-DT, size 1). Atlantic chub mackerel *Scomber colias* was used as bait. Lines were set from a small inflatable boat and then operated from the coast between 12 and 23 h. The total number of longline settings each day varied depending on soak time, weather and personnel availability. Soak time ranged between 30 and 120 min (average 73 min).

Rod and reel fishing

One fishing session per sampling day was performed from the coast in order to calculate an additional CPUE index of relative abundance. Fishing sessions varied between 10 and 12 h long and were conducted between 11 and 24 h using either 4 or 5 fishing rods depending on available personnel. Each rod and reel possessed 1 hook (Mustad 2330-DT, size 1) baited with *S. colias*. Fishing lines were cast close to the shore between 5 and 20 m. An additional rod and reel fishing session — not included in the sampling design — was performed on 5 November 2016 with the purpose of increasing the number of sharks tagged and sampled in this study. Data obtained on this additional sampling trip were included in the demography analysis but not included in the CPUE analysis because it was conducted at a different tide level, moon phase and site, probably influencing CPUE (see next section).

Baited remote underwater video stations (BRUVS)

BRUV deployments were conducted to calculate fishing-independent indices of relative abundance in order to corroborate those estimated by fishing methods. BRUVS consisted of iron poles and a trestle-shape frame, enclosing a GoPro® camera (models Hero 3+ and Hero 4). Detachable bait arms of 150 cm in total length (25 mm Ø plastic conduit) had a bait holder of 63 mm Ø and 20 cm long perforated conduit stuffed with 600 g of chopped *S. colias*. BRUVS were positioned between 4 and 9 m deep with 16 mm polypropylene ropes, and polystyrene surface buoys between 1 h after and 1 h before high tide. The first 60 min (approximately 30 min before and after high tide) of video imagery were analyzed to ensure the most stable physical conditions at high tide on each session. This strict deployment and video analysis procedure was based on pilot tests that determined significantly higher currents at intermediate levels of tide which modified visibility (and probably other parameters such as bait odor plume, which are difficult to measure with BRUVS) and could introduce bias for index calculations (Marsh & Sinclair 1989, Harvey et al. 2013). Deployment sites were randomly selected along a 6 km portion of the bay, northward and southward from the fishing site. The BRUVS were established at least 500 m apart from each other to ensure independence between samples. Three indices of relative abundance were calculated for each video session:

(1) Nmax: the maximum number of *Notorynchus cepedianus* observed in a single video frame;

(2) NmaxIND: the cumulative number of different *N. cepedianus* identified by spot patterns and other particular characteristics (i.e. size, sex, scar or tag). The relevance of this index in elasmobranch studies was recently described by Sherman et al. (2018). For the estimation of this index, every time a given shark entered the field of view, snapshots of the individual were taken. After visual inspection of all snapshots, the number of unique individuals were determined as NmaxIND;

(3) Nocc: the total number of occurrences of *N. cepedianus* in the field of view over the entire video record session.

Animal handling

Regardless the fishing method used, each *N. cepedianus* caught was carefully brought to the shoreline while keeping the gills underwater. Blood samples (5 ml) were taken via caudal venipuncture using pre-heparinized syringes fitted with 14- or 18-gauge needles depending on the size of the shark. Blood samples were transferred to plastic vials and placed on ice for 4–10 h, followed by centrifugation for 5 min at 1000 × *g*. The plasma was collected and stored at −20°C until it was thawed for analysis. After blood extraction, basic biological parameters were recorded, including sex, total length (L_T to the nearest cm, using a fiberglass tape), total weight (W_T to the nearest kg, using a hanging digital balance and a stretcher to hold each shark) and clasper length in males (L_C to the nearest mm, from the distal end of the metapterygium to the tip). Two additional sources of qualitative evidence were sought while handling the animals to facilitate inference regarding the use of the bay as mating or feeding grounds: (1) presence of fresh mating scars on females, and (2) prey items as a result of gastric eversion under fishing/handling stress. Lastly, all sharks were tagged on the dorsal fin with a plastic spaghetti dart tag (Floy tags) before being safely released back into the water. The whole procedure was accomplished in an average time of 4.98 min (range 2–10 min).

Determination of size at maturity and reproductive stages

As has been previously done with other elasmobranch species, including *N. cepedianus* from Australian waters (Awruch et al. 2014), sex steroids were used to determine the size at maturity and address the reproductive stages for both sexes. Briefly, in viviparous elasmobranch females, the main role of 17β-estradiol (E_2) is the synthesis of hepatic vitellogenin regulating follicle development, while testosterone (T) is a precursor of E_2 and is associated with E_2 fluctuations and likely with maturational stages of follicle growth (Awruch 2013). Progesterone (P_4) plays an important role in suppressing vitellogenin production to stimulate maturational stages and ovulation of ovarian follicles that have completed their development. Circulating P_4 levels were also linked to early stages of pregnancy in previous studies on *N. cepedianus* (Awruch 2013, Awruch et al. 2014). In elasmobranch males, T seems to be the primary androgen associated with testicular development and mating, E_2 may be associated with modulating early to middle stages of spermatogenesis, and P_4 may play a role in spermiogenesis and spermiation, and/or only reflecting the rate at which it was being converted to downstream steroid metabolites such as T (Awruch 2013).

Plasma levels of T, E_2 and P_4 were measured in the laboratory by radioimmunoassay. Testosterone antiserum was purchased from Novus Biologicals©, and reconstituted by diluting 1:10 in phosphate-buffered saline assay buffer containing 0.1% gelatin and 0.01% thiomersal. The remaining assay reagents (E_2 and P_4 antiserums and tritiated T, E_2 and P_4) and assay protocol used were as described by Awruch et al. (2014).

In addition, for females, weighted averages of the predictive variables L_T, T, E_2 and P_4 were used to obtain discriminant function scores (*D*) to distinguish sexually immature juveniles from sexually mature adult sharks (Awruch et al. 2008). Briefly, *D* was calculated as follows:

$$D = B_0 + B_1X_1 + B_2X_2 + \dots + B_iX_i \tag{1}$$

where X_i is the value of each independent variable (*i*), and B_i is the coefficient estimated from the data. From *D*, it was possible to obtain the probability that a shark was either a juvenile or adult. This probability $P(Gi/D)$ was estimated by:

$$P(Gi / D) = \frac{P(D / Gi)P(Gi)}{\sum_{i=1}^{g} P(D / Gi)P(Gi)} \tag{2}$$

where $P(Gi)$ is the prior probability and is an estimate of the likelihood that a shark belongs to a specific group, *G*, where *i* = juveniles or adults. The conditional probability $P(D/Gi)$ is the probability of obtaining a particular value of *D* if the shark belongs to a specific group. Each shark was known to belong to a particular group, and the conditional probability of the observed *D* score given membership in the group was calculated. The predictive function was built using Excel and SPSS (IBM SPSS® Statistics 24).

For many elasmobranch males, an abrupt increase in L_C in relation to L_T marks the onset of sexual maturity (Conrath 2004, Awruch et al. 2014); thus, the relationship between these 2 measurements was plotted and assessed.

Population structure and seasonal variation

Catch- and BRUV-derived estimates were used to investigate *N. cepedianus* population structure and seasonal fluctuations of abundance in the study site. The CPUE was defined as the number of *N. cepedianus* caught divided by the number of hooks and soak time for each daily longline and rod and reel fishing session. Given that the 2 fishing gears are part of distinct fishing techniques with different associated fishing effort, they were analyzed separately. Juveniles and adults were differentiated by taking into account size at the onset of gonadal maturity estimated in this study. The sex ratios (female:male) of juvenile and adult stages were calculated for each season of the year. Further, analyses of similarity (ANOSIM) were used to identify any major sexual (female–male) and maturity-stage (adult–juvenile) composition differences in the catch rates between fishing gears, and between seasons for each fishing gear. The response variable (CPUE) was fourth-root-transformed to reduce variance. Values close to 1 indicate very different compositions, whereas values near 0 indicate small differences (Clarke & Warwick 2001).

Length–weight relationships

Additionally, length–weight relationships of the population were estimated with L_T and W_T values taken as part of this study plus 2 other complementary sources of data: (1) specimens captured in experimental and commercial longline fishing conducted in northern Patagonian gulfs (42°–43° S, Elías 1998) (n = 27, range = 99–244 cm L_T, mean = 132 cm L_T) and

San Clemente del Tuyú (37° S, A. Jaureguizar unpubl. data) (n = 34, range = 39–186 cm L_T, mean = 126 cm L_T), all caught between 1994 and 2005, and (2) records from recreational catches in Rawson (43° S, N. Bovcon unpubl. data) between 2010 and 2015 (n = 13, range = 148–236 cm L_T, mean = 180 cm L_T). All complementary specimens were measured to the nearest cm and weighed to the nearest 0.1 kg using electronic scales. Before fitting the models, an L_T–W_T plot was explored to detect outliers in length–weight relationships as suggested by Froese (2006). In order to decide whether a linear regression on log-transformed data or a non-linear regression on raw data described the relationship more suitably, the error distribution (additive vs. multiplicative) of the whole data set by a likelihood analysis was evaluated (see Xiao et al. 2011 for details). As the assumption of multiplicative log-normal error better supported the data (result not shown), the parameters of the length–weight relationship ($W_T = a\ L_T^{\,b}$, where a and b are growth parameters) were estimated by fitting a linear regression to the log-transformed data ($\log[W_T] = \log[a] + b\log[L_T]$) as applied by Venerus et al. (2016). All analyses were performed with R (R Core Team 2017).

RESULTS

Over the course of the study, a total of 198 sharks (145 females and 53 males, sex ratio close to 1:3) were sampled and safely released back into the water. A total of 78 individuals were captured by longline (55 females and 23 males) and 120 by rod and reel (90 females and 30 males). Females ranged from 152–253 cm L_T and males from 145–222 cm L_T. The frequency distribution presented significant differences between sexes (p = 0.02, Wilcoxon rank test) with females being larger than males (Fig. 2). No evident differences in size range were found between sharks caught through fishing or spotted on BRUVS.

Size at maturity and reproductive stages

A total of 82 (60 females, 22 males) blood samples were processed and analyzed in the study. Blood samples and L_C measurements were incorporated into the study during the last year, March 2016 to January 2017. Although most individuals had blood drawn, the priority was to release a healthy shark back into the water. Therefore, if the blood-drawing procedure took more than 5 min, the procedure was stopped and blood was not taken, although this situation only occurred in a handful of cases. In some other situations, too many sharks were caught at the same time. In those cases, we did not have enough people in the field to be able to take blood from every shark without delaying the process for more than 5 min.

Females were considered to reach sexual maturity at 190 cm L_T (Fig. 3a). Females smaller than 190 cm L_T never reached steroid levels higher than 3 ng ml^{-1} E_2, 2 ng ml^{-1} P_4 and 0.7 ng ml^{-1} T, indicating sexually immature females. Females larger than 190 cm L_T exhibited higher steroid values, likely corresponding to sexually mature females. Thus, females smaller than 190 cm L_T were categorized as sexually immature juveniles and those ≥190 cm L_T were considered sexually mature adults. Within these larger females, the 3 hormones showed a wide range of levels at a similar L_T, indicating different reproductive stages for a given length. Adult females with medium to high E_2 levels are likely experiencing the middle–late vitellogenesis stages of the ovarian cycle, while females with high P_4 levels are likely undergoing the ovulatory phase of the ovarian cycle and possibly maintaining the first stages of pregnancy. Furthermore, by using 190 cm as a cut-off point to separate sexually immature juveniles from sexually mature adult females, the linear discriminant predictive analysis showed significant differences between

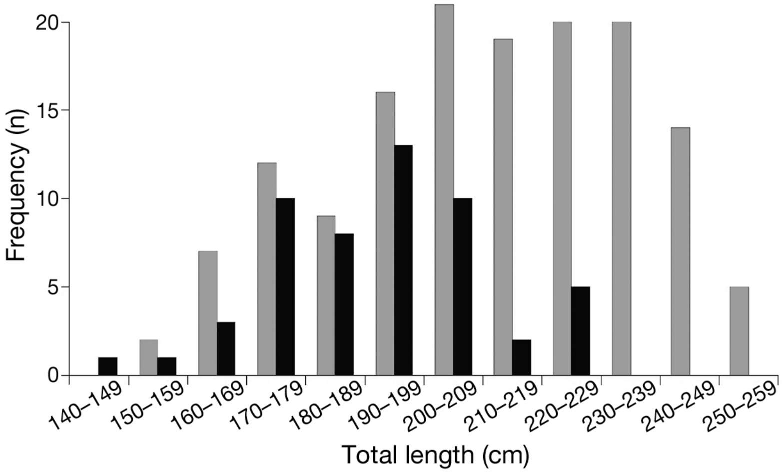

Fig. 2. Size frequency (n) distribution of *Notorynchus cepedianus* females (light bars) and males (dark bars) in Punto Bajo (Caleta Valdés)

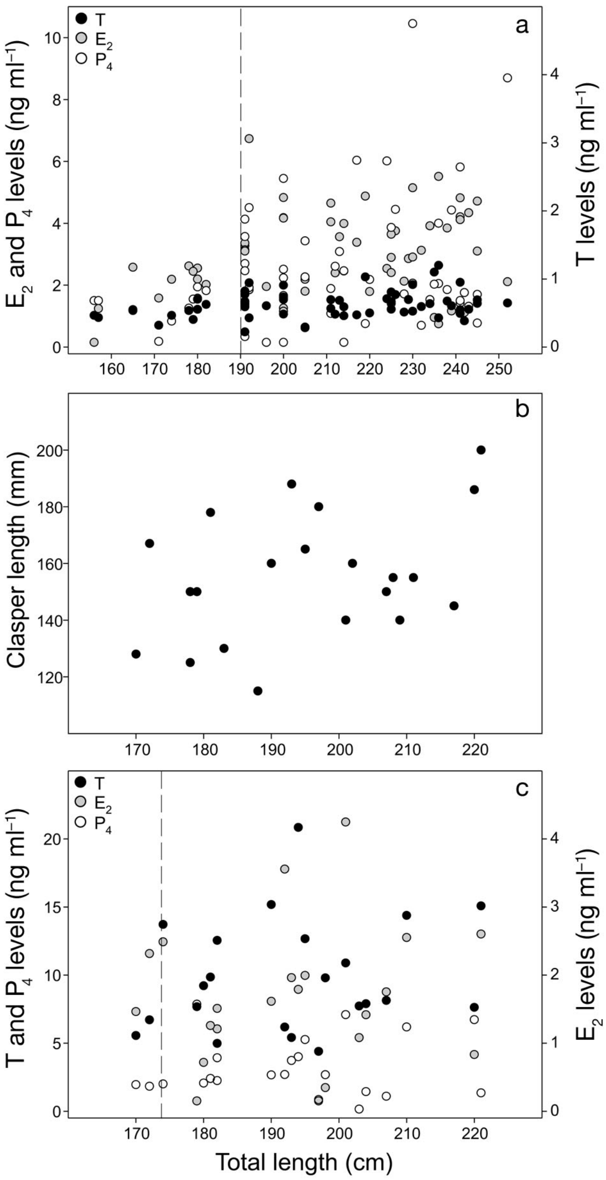

Fig. 3. Maturity stages in *Notorynchus cepedianus.* (a) Relationship between reproductive hormones and total length in females (<190 cm, n = 10; ≥190 cm, n = 50). (b) Relationship between total length and clasper length in males. (c) Relationship between reproductive hormones and total length in males (n = 22). T: testosterone, E_2: 17β-estradiol, P_4: progesterone

juvenile and adult sharks (Wilk's lambda, $\chi^2 = 0.473$, $p < 0.001$). From the *D* score generated by the predictive variables L_T, T, E_2 and P_4 ($D = -11.82 + 0.51 \times L_T + 0.63 \times [T] + 0.18 \times [E_2] + 0.086\ [P_4]$), 98.3% were correctly classified within the sexually mature stage group.

The lack of small males made it impossible to evaluate onset of maturity by looking into the L_C and L_T relationship (Fig. 3c). Furthermore, males began to show high T levels from 175 cm L_T, but only few males smaller than 175 cm L_T were caught during the sample period (Fig. 3c). Thus, it was not possible to assess the cut-off point of L_T for sexually mature males. However, similar to females, the 3 hormones, in particular T, showed a wide range of levels at a similar L_T, suggesting males undergoing different reproductive stages for a given length.

By looking into the reproductive hormones of adult females by season, although a smaller range of T, E_2 and P_4 levels were observed in winter, a wider range was displayed throughout spring to autumn indicating a multi-annual reproductive cycle within the population (Fig. 4a). Testosterone levels were the lowest of the 3 reproductive hormones (<1.2 ng ml^{-1}), showing the highest values in spring and summer. These highest levels are in concordance with the presence of females bearing fresh mating scars, suggesting a possible role of T during the mating period and/or the maturation of the ovarian follicles in preparation for ovulation. Both high and low E_2 levels were observed from spring to autumn, reaching only low values in winter; however, the sample size during the cold months was low. The wide range of circulating E_2 indicates that adult females are experiencing different stages within the ovulatory cycle. While some females with medium and high E_2 levels are actively undergoing vitellogenesis, females with low E_2 are not actively developing ovarian follicles, likely being in a resting stage of the ovulatory cycle or just at the very beginning of it. Progesterone levels slightly peaked during spring and summer, although high values were also observed in autumn and winter. One female showed an important peak in P_4 during summer, suggesting that this female was in the ovulation phase. At least 30% of adult females presented fresh mating scars on pectoral fins in spring and early summer (Fig. 5). During the other seasons, no mating scars were registered. Given that fresh mating scars were registered at the end of spring towards the beginning of summer, these slight increases in P_4 could be related to the ovulatory period, remaining elevated during autumn and winter supporting the initial stages of pregnancy.

Circulating T levels in males (5–22 ng ml^{-1}) were much higher than in females (0.2–1.1 ng ml^{-1}), also showing a wide range of values suggesting that males produce sperm in most seasons (Fig. 4b). However, apart from 1 point in autumn that could be an atypical value (twice the highest value of the season), T levels reached the highest values in spring and summer, reflecting a possible mating period and the

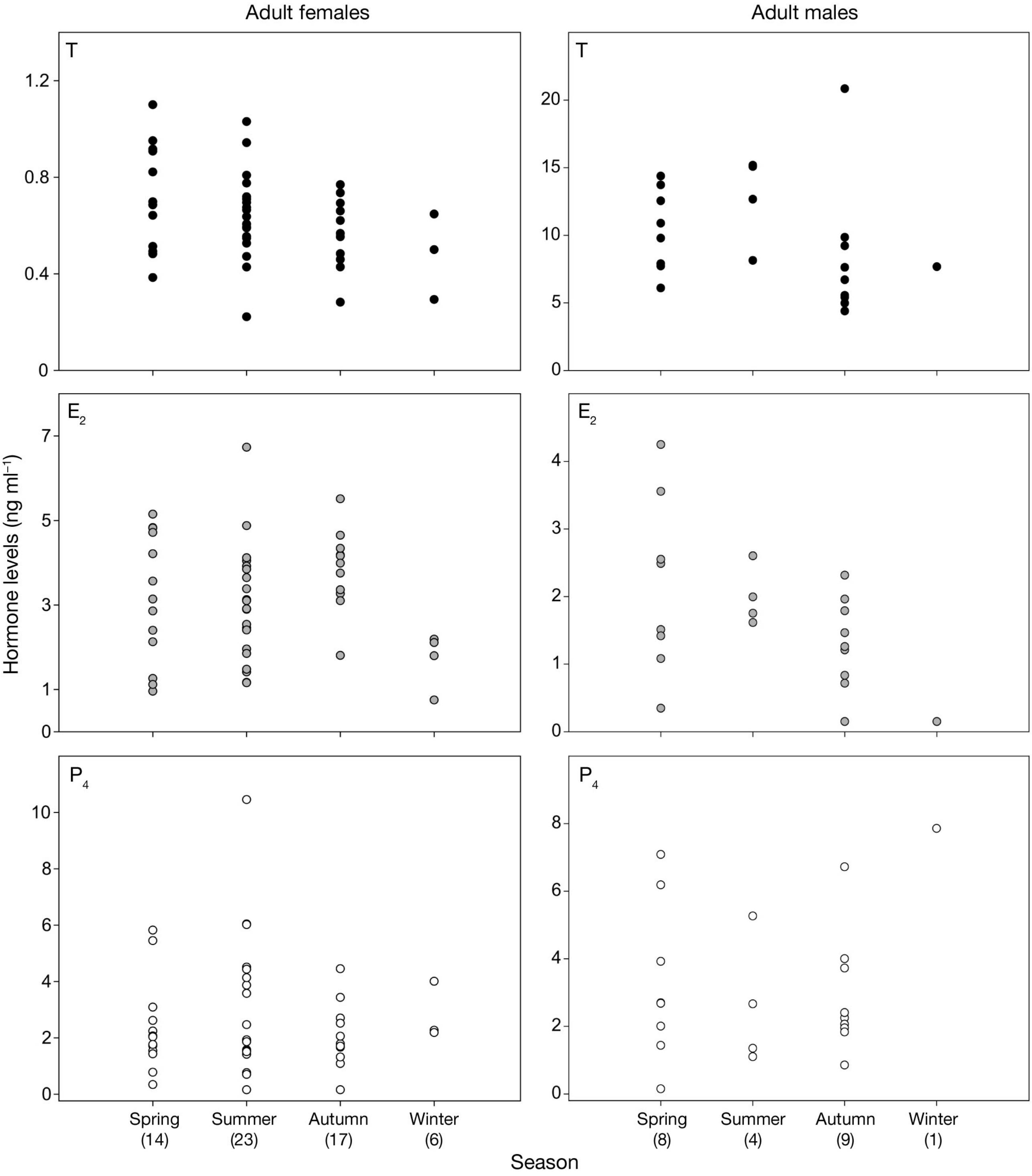

Fig. 4. Seasonal variations of reproductive hormones in *Notorynchus cepedianus* throughout the study period in adult females and males. Numbers in parentheses indicate sample sizes. T: testosterone, E_2: 17β-estradiol, P_4: progesterone

role of T triggering the copulatory behavior in males. Plasma E_2 and P_4 levels also showed a wide range of values throughout spring to autumn. The highest E_2 levels were observed in spring, and the very high P_4 level found in winter could be linked to the antagonistic effect between E_2 and P_4, which is evident in winter by the low level of E_2 and very high level of P_4.

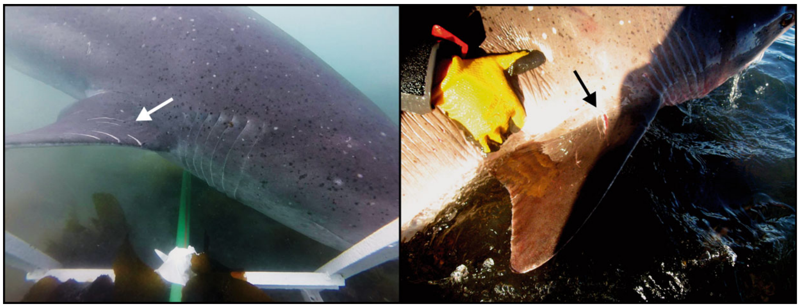

Fig. 5. Female *Notorynchus cepedianus* observed during the study showing fresh mating scars on pectoral fins (arrows). The image on the left is from a baited remote underwater video record, and the image on the right was taken during a longline operation

Population structure and seasonal variation

N. cepedianus CPUEs (longline and rod and reel fishing) and BRUV-derived relative abundance indices showed a strong seasonal pattern over the 2 seasonal cycles of the study (Fig. 6). Maximum CPUEs, Nmax, NmaxIND and Nocc values occurred in spring, as opposed to autumn when minimum relative abundances were registered. Longline and rod and reel CPUEs showed similar patterns, ranging from 0.02 to 0.22, and 0.05 to 0.46 sharks hook^{-1} h^{-1}, respectively. Sharks were not observed at BRUVS between March and May 2016. In the other seasons (winter and summer), relative abundances showed intermediate values.

Besides sevengill sharks observed at BRUVS, schools of silversides *Odontesthes smitti* and *O. argentinensis* were usually abundant and were registered in all video sessions, whereas solitary individuals of papamoscas *Nemadactylus bergi*, Brazilian sandperch *Pinguipes brasilianus* and Patagonian blennie *Eleginops maclovinus* were registered only on a few occasions.

Sharks showed no significant differences in the maturity-stage composition in any of the fishing gears (longline, rod and reel), either throughout the year (ANOSIM, R = 0.009, p = 0.351) or by season (longline ANOSIM, R = 0.088, p = 0.32; rod and reel ANOSIM, R = 0.27, p = 0.071). Overall, catches were dominated by adults (56.2–92.6%) and females (56–81%) (Fig. 7). The sex ratios (female:male) of juvenile and adult stages were >1 for most seasons (spring = 13 and 3, summer = 6.5 and 5.2, autumn = 3 and 1.6, respectively); male juveniles were equally as abundant as female juveniles only in winter (juvenile = 1, adult = 2.5). Most sex-stage categories showed the highest CPUE in spring and the lowest in winter, in accordance with Fig. 6.

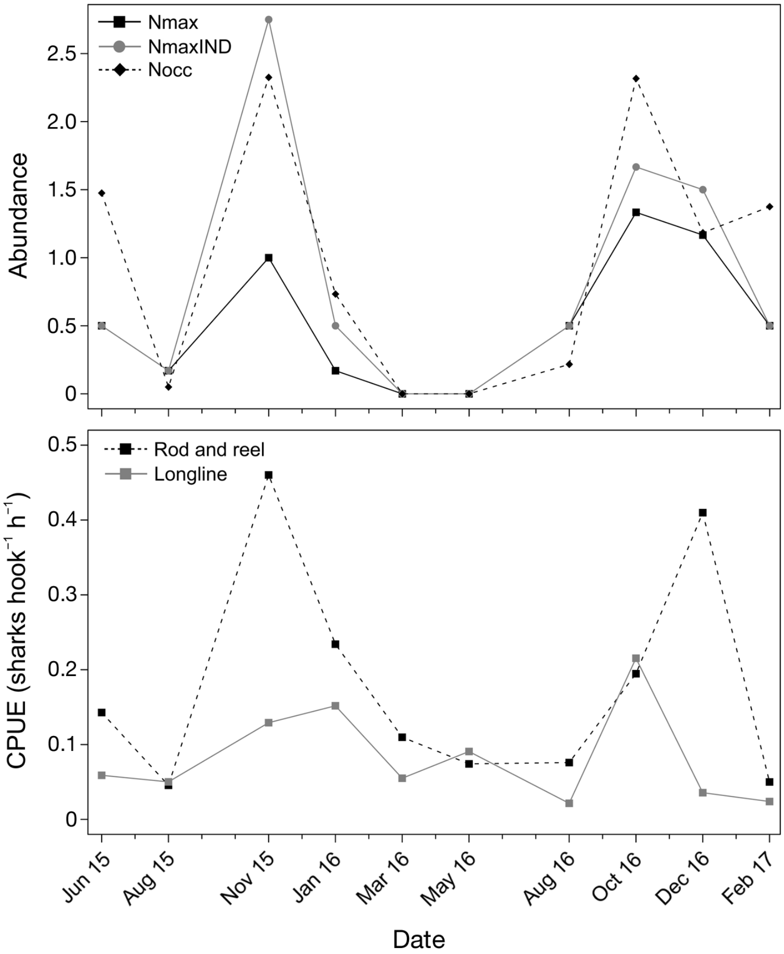

Fig. 6. Seasonal variation in *Notorynchus cepedianus* relative abundance indices in Punta Bajo (Caleta Valdés) from June 2015 to February 2017. Indices derive from baited remote underwater video deployments (see 'Materials and methods: Field methods and sampling design' for detailed definitions of Nmax, NmaxIND and Nocc) and catch per unit effort (CPUE) data (longline and rod and reel). Note that the Nocc index was divided by 10 to match the scale of the other 2 indices; the factor 'hook' in CPUE relates to different effort in each fishing method; sampling occurred mostly on a bimonthly basis

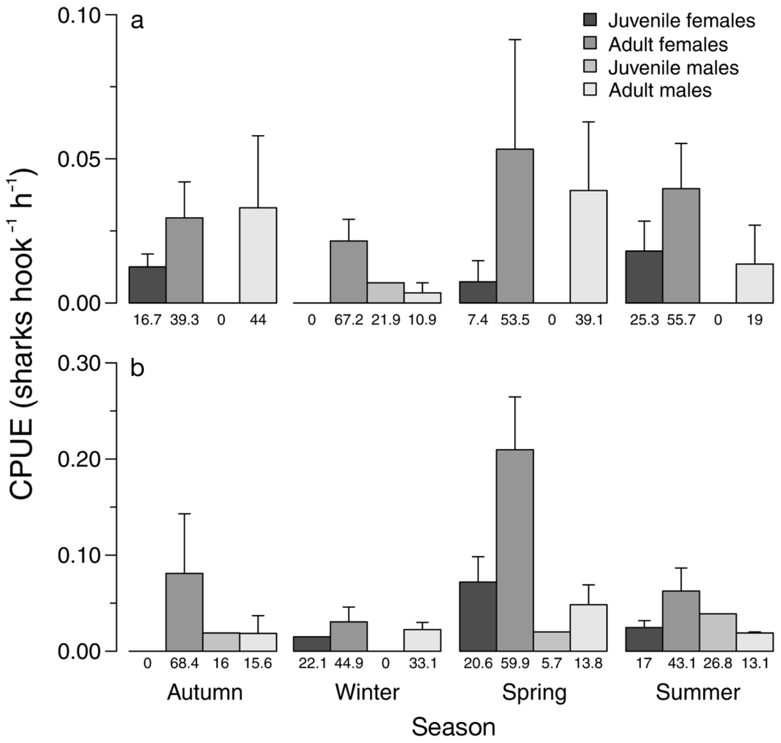

Fig. 7. Seasonal variation in *Notorynchus cepedianus* mean (±SE) catch per unit effort (CPUE) derived from (a) longline fishing and (b) rod and reel fishing by sex-maturity-stage categories. Maturity was determined by the onset at sexual maturity estimated in this study. Numbers below bars indicate percentage of each category relative to each particular season. Note that the factor 'hook' relates to different effort in each fishing method

Qualitative prey data

In total, 30 (15.2%) individuals regurgitated stomach contents as a result of gastric eversion during handling on the shore. Only in spring and early summer, 24 individuals regurgitated chunks of southern elephant seals. At different times of the year, 6 individuals regurgitated whole fish or pieces (2 were identified as plownose chimaera *Callorhinchus callorynchus*, 1 as *Eleginops maclovinus*, 2 as non-identified bony fishes, and 1 as a non-identified skate). It is important to note that the regurgitation rate was probably underestimated because it may have occurred before sharks were being carried to the coast.

Length–weight relationships

The length–weight relationship was constructed from a total of 151 *N. cepedianus* specimens ranging from 39 to 252 cm L_T and 0.3 to 90 kg W_T (Table 1). The comparison between analysis of covariance (ANCOVA) models suggested the occurrence of sexual dimorphism in the length–weight relationship (difference in Akaike's information criterion [ΔAIC] = $\text{AIC}_{\text{min}} - \text{AIC}_{\text{max}} = 5.24$), with females being heavier and showing wider length range compared to males (Table 1).

Recaptures

During the study, 15 sharks were recaptured at the same tagging site, for a total recapture rate of 7.58%. Seven recaptures occurred at short time scales, i.e. within 4 mo after tagging (average = 2.2 mo). Eight occurred at longer time scales between spring and early summer sampling periods, i.e. from 6 to 13 mo (average = 8 mo). The 7 individuals recaptured at short time scales were all females (4 adults and 3 juveniles). The 8 individuals recaptured at longer time scales were adults (3 males and 5 females). To date, no recaptures by fishermen have been reported.

DISCUSSION

This study suggests that *Notorynchus cepedianus* uses Caleta Valdés year-round and aggregates in spring for feeding and mating purposes. The 3

Table 1. Length–weight relationships for females, males and all individuals of sevengill sharks *Notorynchus cepedianus* from Argentina, Southwest Atlantic. Samples were collected between 1994 and 2016. L_T: total length, W_T: total weight

Sex	n	L_T (cm)	W_T (kg)	Regression parameters (95% CI) *a*	*b*	R^2
Female	100	39–252	0.3–90	0.0023 (0.0015–0.0035)	3.127 (3.043–3.211)	0.982
Male	51	81–221	2.3–42	0.0034 (0.0016–0.0075)	3.032 (2.879–3.184)	0.970
All	151	39–252	0.3–90	0.0023 (0.0016–0.0035)	3.116 (3.041–3.190)	0.979

methodologies used to estimate relative abundance during the study period showed a consistent and strong seasonal pattern of abundance of sevengill sharks inside the bay. The peak of abundance in late spring coincides with the occurrence of regurgitated pieces of southern elephant seal, supporting the hypothesis that fluctuations in prey availability drive *N. cepedianus* seasonal patterns of abundance. At this time of the year, elephant seals arrive at Valdés peninsula to breed and molt, and by late spring pups enter the sea for the first time (Lewis et al. 2004, Ferrari et al. 2009) and hence are vulnerable to predation by sharks. In addition to using the area as a feeding ground, the presence of mating scars registered on large females supports the complementary hypothesis that *N. cepedianus* also uses the bay for mating.

The seasonal aggregation of *N. cepedianus* in bay environments was also described at Humboldt and San Francisco Bays in California, USA (Gotshall et al. 1980, Ebert 1989), Willapa Bay and Grays Harbor in Washington, USA (Williams et al. 2012), Norfolk Bay in Tasmania, Australia (Barnett et al. 2010, Barnett & Semmens 2012), False Bay in South Africa (de Necker 2017) and Anegada Bay, Ria Deseado and Río de la Plata in Argentina (Lucifora et al. 2005, Cedrola et al. 2009). These studies all agreed that spring appearances or species aggregations in coastal areas are related to feeding and mating activities driven by seasonal fluctuations in prey abundance. Prey abundance is believed to be among the main factors determining distribution of sharks (Speed et al. 2010, Schlaff et al. 2014). This conclusion is consistent with our results, as *N. cepedianus*, despite having been registered year-round in the study site, was more abundant in late spring, which coincides with the mating season and maximum prey availability (i.e. elephant seal pups). This is further supported by the fact that during the summer–autumn period, *N. cepedianus* presented intermediate abundances, probably as a result of sharks leaving Caleta Valdés to feed on other seasonally abundant prey outside the bay, including sea lions (Dans et al. 2004), plownose chimaera (Di Giácomo 1992) and migratory bony fish (e.g. *Scomber colias*, A. Irigoyen pers. obs.).

The wide range of the 3 reproductive hormone levels from spring to autumn indicates a simultaneous occurrence of adult females at different reproductive stages, suggesting a trend in temporal periodicity of the reproductive cycle. The high hormone values distinguish those females ready to ovulate from females with very low hormone levels that are likely in the resting stages or beginning of the ovulatory cycle. It can then be suggested that *N. cepedianus* females exhibit an annual ovulatory cycle followed by a pregnancy period and subsequent rest, although the length of these 2 periods remains unknown. The higher androgen levels found in adult males during spring and summer would indicate a reproductive synchrony in female and male cycles, with males actively producing sperm and prepared for mating during spring and summer. It is therefore likely that the warm and shallow waters of the Caleta Valdés provide a prime habitat for feeding but also for mating in sexually active individuals.

Although strong seasonal fluctuations of *N. cepedianus* abundance were found in Caleta Valdés, population structure remained constant throughout the seasons, with no evident differences in sex-stage composition. Females outnumbered males year-round in the area, as also observed during warm months in northward (Lucifora et al. 2005) and southward locations (Cedrola et al. 2009). Conversely to these studies, however, adult individuals outnumbered juveniles in the bay, probably as a consequence of intraspecific exclusion for food resources (Ebert 2002), or due to an artefact of the methods used in the study. Furthermore, no young-of-the-year or neonates were registered in the catches, observed at BRUVS or reported by fishermen during informal interviews (A. Irigoyen unpubl. data). Further sampling along the entire study area is necessary to reinforce this conclusion.

All recaptures occurred inside the bay, suggesting both long- and short-term site fidelity in the timescale covered by the study (i.e. between field trips, and seasons). Similar results were obtained for *N. cepedianus* conventional tagging conducted in Tasmania, with a 15% recapture rate occurring almost exclusively in the original tagging location (Barnett et al. 2010). In South Africa, the recapture rate of *N. cepedianus* was lower (4.2%) and did not show evidence that site fidelity was occurring, probably because individuals were tagged in open coasts (Ebert 1996). Furthermore, large migrations (>1000 km) were also reported associated with the exit from coastal areas in winter towards warmer areas (Barnett et al. 2011). At a finer scale, the different movement pattern found for males and females in Tasmanian bays is explained by adult females using coastal habitats earlier and for longer periods of time than males (Barnett et al. 2011). The prevalence of females inside Caleta Valdés at all times may be a result of fine-scale sex-specific differences in habitat use, as found in Tasmanian bays. Satellite tracking studies should be conducted in Caleta Valdés to address this hypothesis and gather information of potential migration routes.

Visual census based on BRUVS imagery showed that sevengill sharks and silversides dominated the fish assemblage in Caleta Valdés. No other chondrichthyan species was registered in 50 h of video imagery, and few other bony fishes were observed. Despite the fact that the single-camera BRUV method used in this study could not be used to measure fish length (as opposed to stereo-BRUV systems; Harvey et al. 2002), *N. cepedianus* individuals observed were visually estimated to fall within the range of lengths of sharks caught by fishing, suggesting that smaller or larger individuals were not present. The constraining dimensions of the bay and the high concentration of large sevengill sharks likely caused the exclusion of other species by predation pressure (e.g. Papastamatiou et al. 2006), including young *N. cepedianus*.

The maximum L_T reported here (253 cm) is smaller than previously reported in North American (283 cm, Williams et al. 2011), Tasmanian (296 cm, Barnett et al. 2010) and South African waters (280 cm, Ebert 1996). Despite a lower sample size in the present study (particularly in males), previous maximum total length registered for Argentinian waters from scientific surveys (253 cm, Lucifora et al. 2005) and expert fishermen records (250 cm, A. Irigoyen unpubl. data) suggest that *N. cepedianus* individuals grow to smaller sizes in the Southwest Atlantic. In concordance, it is not surprising to observe that the size at sexual maturity in females also seems to be smaller than previously reported for *N. cepedianus* from other regions. In the present study, females reached sexual maturity at 190 cm L_T, compared to 210 cm L_T reported from Tasmania (Awruch et al. 2014), 230–250 cm L_T from North America (Ebert 1989, Williams et al. 2011) and 220 cm L_T from South Africa (Ebert 1996). It is interesting to note the differences in size at sexual maturity between the far north end of Patagonia (224 cm L_T with the largest immature female of 220 mm L_T and the smallest adult female of 214 mm L_T, Lucifora et al. 2005) and the present study, considering that both areas reported similar maximum L_T. As reproductive hormones regulate all processes of reproduction (Awruch 2013), it has been suggested that physiological reproductive parameters may provide a more accurate estimate of sexual maturity than morphological reproductive characteristics, as has also been suggested for *N. cepedianus* from Tasmanian waters (Awruch et al. 2014). It was not possible to determine the onset at sexual maturity in males because of the lack of small-sized individuals during the last year of the sampling period. However, all males at 170–175 cm L_T presented a wide range of hormones, suggesting that these males were sexually mature. This would be in agreement with the L_{T50} reported for *N. cepedianus* from North Patagonia (Lucifora et al. 2005).

Length–weight relationships showed significant sexual differences, as previously reported in *N. cepedianus* populations. It is important to note that some bias may have been introduced in the regression estimates, as a high number of sharks everted stomach contents prior to being weighed, and some pregnant mature females (>220 cm L_T) may have been inadvertently included in the database, causing data dispersion among larger individuals. However, since sharks were not examined internally, these factors were not evaluated. In southern Patagonia, such sexual dimorphism in growth was not observed for *N. cepedianus*, which is likely caused by a narrower size range biased towards immature individuals (Cedrola et al. 2009). As discussed by Cedrola et al. (2009), Ria Deseado and San Julián peninsula may act as secondary nursery grounds for *N. cepedianus*, which makes the area prone to bias while estimating growth parameters. In this sense, the *a* and *b* growth parameters — used to calculate the length–weight relationship of fish species — that were estimated in the present study include female and male individuals from several locations in the Southwest Atlantic, describing a broader population with more applicable results.

Based on data and qualitative evidence found in this work, we conclude that sevengill sharks inhabit Caleta Valdés year round with a peak in abundance during late spring and early summer probably for feeding and mating purposes. Further work is necessary to understand the magnitude of this aggregation site, the role of the species within the region and the degree of connectivity with other sites along its southwestern distribution range. Considering the vulnerability of sevengill sharks and their historical abundance decline in the Southwest Atlantic, protection and enforcement within protected areas such as the Valdés peninsula must remain of high priority in government initiatives.

Acknowledgements. We thank the 3 anonymous reviewers for their very constructive revisions. We especially thank anglers G. Zamora, M. Cuestas, M. Lupiano, M. De Francesco, O. Trobbiani, and colleagues N. Sanchez-Carnero, M. Funes, F. Rios, M. Rossi, D. Galván, I. Rojo, J. M. Pereñíguez, R. Hernández, M. Pucheta and N. Demergassi for invaluable field support and A. Barnett for scientific advice. Funding was provided by the Save Our Seas Foundation (project number 359/2016) and the Temaiken Foundation. Field work included sampling within a World Natural Heritage Site and was authorized by the Secretaría de Turismo y Áreas Protegidas del Chubut.

LITERATURE CITED

Awruch CA (2013) Reproductive endocrinology in chondrichthyans: the present and the future. Gen Comp Endocrinol 192:60–70

Awruch CA (2015) Reproduction strategies. In: Shadwick RE, Farrell AP, Brauner CJ (eds) Physiology of elasmobranch fishes: structure and interaction with environment. Vol 34A. Elsevier, London, p 255–310

Awruch CA, Frusher SD, Pankhurst NW, Stevens JD (2008) Non-lethal assessment of reproductive characteristics for management and conservation of sharks. Mar Ecol Prog Ser 355:277–285

Awruch CA, Jones SM, Asorey MG, Barnett A (2014) Non-lethal assessment of the reproductive status of broadnose sevengill sharks (*Notorynchus cepedianus*) to determine the significance of habitat use in coastal areas. Conserv Physiol 2:cou013

Barbini SA, Lucifora LO, Figueroa DE (2015) Using opportunistic records from a recreational fishing magazine to assess population trends of sharks. Can J Fish Aquat Sci 72:1853–1859

Barnett A, Semmens JM (2012) Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. Oikos 121:882–890

Barnett A, Stevens JD, Frusher SD, Semmens JM (2010) Seasonal occurrence and population structure of the broadnose sevengill shark *Notorynchus cepedianus* in coastal habitats of south-east Tasmania. J Fish Biol 77: 1688–1701

Barnett A, Abrantes KG, Stevens JD, Semmens JM (2011) Site fidelity and sex-specific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. Anim Behav 81:1039–1048

Barnett A, Braccini JM, Awruch CA, Ebert DA (2012) An overview on the role of Hexanchiformes in marine ecosystems: biology, ecology and conservation status of a primitive order of modern sharks. J Fish Biol 80:966–990

Berthold P (1999) A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70: 1–11

Bird CS, Veríssimo A, Magozzi S, Abrantes KG and others (2018) A global perspective on the trophic geography of sharks. Nat Ecol Evol 2:299–305

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Braccini JM (2008) Feeding ecology of two high-order predators from south-eastern Australia: the coastal broadnose and the deepwater sharpnose sevengill sharks. Mar Ecol Prog Ser 371:273–284

Braccini JM, Troynikov VS, Walker TI, Mollet HF, Ebert DA, Barnett A, Kirby N (2010) Incorporating heterogeneity into growth analyses of wild and captive broadnose sevengill sharks *Notorynchus cepedianus*. Aquat Biol 9: 131–138

Cedrola PV, Caille GM, Chiaramonte GE, Pettovello AD (2009) Demographic structure of broadnose seven-gill shark, *Notorynchus cepedianus*, caught by anglers in southern Patagonia, Argentina. Mar Biodivers Rec 2: e138

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Compagno LJV (2005) *Notorynchus cepedianus*. The IUCN Red List of Threatened Species 2005:e.T39324A10200310

Conrath CL (2004) Reproductive biology. In: Musick AJ, Bonfil R (eds) Elasmobranch fisheries management techniques. APEC, Singapore, p 133–134

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717

Crespi-Abril AC, García NA, Crespo EA, Coscarella MA (2003) Consumption of marine mammals by broadnose sevengill shark *Notorynchus cepedianus* in the northern and central Patagonian shelf. Lat Am J Aquat Mamm 2: 101–107

Dans SL, Crespo EA, Pedraza SN, Alonso MK (2004) Recovery of the South American sea lion (*Otaria flavescens*) population in northern Patagonia. Can J Fish Aquat Sci 61:1681–1690

de Necker L (2017) The trophic dynamics of the broadnose sevengill shark (*Notorynchus cepedianus*) in False Bay, South Africa, using multiple tissue stable isotope analysis. MSc dissertation, University of Cape Town

De Wysiecki AM, Milessi AC, Wiff R, Jaureguizar AJ (2018) Highest catch of the vulnerable broadnose sevengill shark *Notorynchus cepedianus* in the south-west Atlantic. J Fish Biol 92:543–548

Di Giácomo EE (1992) Distribución de la población del pez gallo (*Callorhynchus* [sic] *callorhynchus* [sic]) en el Golfo de San Matías, Argentina. Frente Marít 12:113–118

Ebert DA (1989) Life history of the sevengill shark, *Notorynchus cepedianus* Peron, in two northern California bays. Calif Fish Game 75:102–112

Ebert DA (1991) Diet of the sevengill shark *Notorynchus cepedianus* in the temperate coastal waters of southern Africa. S Afr J Mar Sci 11:565–572

Ebert DA (1996) Biology of the sevengill shark *Notorynchus cepedianus* (Péron, 1807) in the temperate coastal waters of southern Africa. S Afr J Mar Sci 17:93–103

Ebert DA (2002) Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). Mar Freshw Res 53:517–523

Elías I (1998) Alternativas de explotación pesquera en áreas costeras norpatagónicas ecológicamente sensibles. PhD dissertation, Universidad Nacional de La Plata, Buenos Aires

Estevez JL, Varela DE (1991) Dynamics of nutrient cycling of the Valdes Bay-Punta Cero pond system (Peninsula Valdes, Patagonia) Argentine [sic]. Oceanol Acta 14: 51–58. http://archimer.ifremer.fr/doc/00101/21273/

Ferrari MA, Lewis MN, Pascual MA, Campagna C (2009) Interdependence of social structure and demography in the southern elephant seal colony of Península Valdés, Argentina. Mar Mamm Sci 25:681–692

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071

Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J Appl Ichthyol 22:241–253

Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. Trends Ecol Evol 3:237–241

Gadig OBF (2001) Tubarões da costa brasileira. PhD dissertation. Instituto de Biociências de Rio Claro da Universidade Estadual Paulista, São Paulo

Gotshall DW, Allen GH, Barnhart RA (1980) An annotated checklist of fishes from Humboldt Bay, California. Calif Fish Game 66:220–232

Guzmán L, Campodónico I (1976) *Notorynchus cepedianus* (Peron, 1807) en la entrada oriental del Estrecho de Magallanes (Elasmobranchii, Hexanchiidae). An Inst Patagon 7:207–210

Harvey E, Shortis M, Stadler M, Cappo M (2002) A comparison of the accuracy and precision of measurements from single and stereo-video systems. Mar Technol Soc J 36: 38–49

Harvey ES, McLean D, Frusher S, Haywood MD, Newman SJ, Williams A (2013) The use of BRUVs as a tool for assessing marine fisheries and ecosystems: a review of the hurdles and potential. University of Western Australia, Perth

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210

Heupel MR, Simpfendorfer CA, Espinoza M, Smoothey AF, Tobin A, Peddemors V (2015) Conservation challenges of sharks with continental scale migrations. Front Mar Sci 2:12

Irigoyen AJ, Trobbiani G (2016) Depletion of trophy large-sized sharks populations of the Argentinean coast, southwestern Atlantic: insights from fishers' knowledge. Neotrop Ichthyol 14:e150081

Irigoyen AJ, Sibbald C, Cuestas M, Cristiani F, Trobbiani G (2015) Patrones estacionales de abundancia en el Golfo Nuevo y migración a lo largo de la plataforma Argentina de cazones (*Galeorhinus galeus* [Linnaeus 1758]) y gatopardos (*Notorynchus cepedianus* [Péron 1807]) (Argentina). Ecol Austral 25:144–148

Last PR, Stevens JD (2009) Sharks and rays of Australia, 2nd edn. CSIRO Publishing, Collingwood

Lewis M, Campagna C, Zavatti J (2004) Annual cycle and inter-annual variation in the haul-out pattern of a growing southern elephant seal colony. Antarct Sci 16: 219–226

Lisnizer N, Garcia-Borboroglu P, Yorio P (2011) Spatial and temporal variation in population trends of kelp gulls in northern Patagonia, Argentina. Emu 111:259–267

Lucifora LO, Menni RC, Escalante AH (2005) Reproduction, abundance and feeding habits of the broadnose sevengill shark *Notorynchus cepedianus* in north Patagonia, Argentina. Mar Ecol Prog Ser 289:237–244

Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. J Wildl Manag 53:1017–1024

Menni RC, García ML (1985) Juveniles de *Notorynchus pectorosus* (Hexanchidae) y *Sphyrna zygaena* (Sphyrnidae) frente a la boca del Río de la Plata (Chondrichthyes). Hist Nat 5:1–10

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar Ecol Prog Ser 320:239–251

Pozzi LM, Borboroglu PG, Boersma PD, Pascual MA (2015) Population regulation in Magellanic penguins: What determines changes in colony size? PLOS ONE 10: e0119002

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reid DD, Robbins WD, Peddemors VM (2011) Decadal trends in shark catches and effort from the New South Wales, Australia, Shark Meshing Program 1950–2010. Mar Freshw Res 62:676–693

Sadowsky V (1969) First record of broad-snouted sevengilled shark from the Cananéia, Brazil. Bol Inst Paul Oceanogr 18:33–35

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24:1089–1103

Sherman CS, Chin A, Heupel MR, Simpfendorfer CA (2018) Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? J Exp Mar Biol Ecol 503:80–85

Speed CW, Field IC, Meekan MG, Bradshaw CJA (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408: 275–293

Venerus LA, Villanueva-Gomila GL, Sueiro MC, Bovcon ND (2016) Length–weight relationships for two abundant rocky reef fishes from northern Patagonia, Argentina: *Sebastes oculatus* Valenciennes, 1833 and *Pinguipes brasilianus* Cuvier, 1829. J Appl Ichthyology 32:1347–1349

Vooren CM, Klippel S, Galina AB (2005) Os elasmobrânquios das águas costeiras da Plataforma Sul. In: Vooren CM, Klippel S (eds) Ações para a conservação de tubarões e raias no sul do Brasil. Igaré, Porto Alegre, p 113–120

Williams GD, Andrews KS, Farrer DA, Bargmann GG, Levin PS (2011) Occurrence and biological characteristics of broadnose sevengill sharks (*Notorynchus cepedianus*) in Pacific Northwest coastal estuaries. Environ Biol Fishes 91:379–388

Williams GD, Andrews KS, Katz SL, Moser ML, Tolimieri N, Farrer DA, Levin PS (2012) Scale and pattern of broadnose sevengill shark *Notorynchus cepedianus* movement in estuarine embayments. J Fish Biol 80:1380–1400

Xiao X, White EP, Hooten MB, Durham SL (2011) On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. Ecology 92:1887–1894

Editorial responsibility: Konstantinos Stergiou, Thessaloniki, Greece

Submitted: February 15, 2018; Accepted: July 29, 2018
Proofs received from author(s): August 27, 2018