

Aspects of the reproductive biology of the data-deficient *Mustelus minicanis* and *M. norrisi* (Chondrichthyes: Triakidae) in the southern Caribbean Sea

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Abstract Reproduction and maturation in the economically important, but data-deficient, *Mustelus minicanis* and *M. norrisi* were analysed using catches of populations exploited by a gillnet fishery during two years in the southern Caribbean Sea. In total, 691 female (mean \pm SD total length–TL of 55.3 ± 5.8 cm) and 503 male (50.4 ± 4.9 cm TL) *M. minicanis* were assessed, with $\sim 95\%$ of all specimens deemed mature. Almost 25% of females were gravid (occurring between January and October) and with variable temporal development of up to six embryos (3.3 ± 1.2), implying protracted temporal parturition. Parity in the sex ratio of embryos, but not in landed catches, suggested sexual segregation across the

fished area. The 50% sizes at maturity (M_{50}) (\pm SE) were similarly estimated at $45.11 (\pm 0.39)$ and $45.48 (\pm 0.42)$ cm TL for females and males, respectively. Relatively fewer (235) *M. norrisi* were landed, with samples comprising 150 females (82.6 ± 18.1 cm TL) and 85 males (75.5 ± 17.7 cm TL). More than 30% of both sexes were immature. Ten percent of females were gravid (up to 11 embryos) and present in catches between October and February, coinciding with the northern hemisphere autumn/winter. Female and male M_{50} s were $76.65 (\pm 1.16)$ and $69.63 (\pm 1.92)$ cm TL, respectively. The results imply variable inter-specific reproductive plasticity and the need for further life-history studies. Increasing gillnet selectivity might represent a simple precautionary management option for concurrently regulating catches of the smaller-bodied *M. minicanis* during peak abundances of gravid females and similar-sized juvenile *M. norrisi*.

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Introduction

Globally, many wild fisheries are characterised by greater-than-reported catches (due to misreporting and/or discarding) and typically show clear tendencies towards decline (Pauly and Zeller 2016). Elasmobranch fisheries often exemplify such a trend, with many species considered vulnerable to overfishing as a consequence of their life-history strategies—typified by late maturity, low

fecundity and often restricted distributions (Worm et al. 2013). Compounding the issue for elasmobranchs is their high catchability, but often limited associated biological data precluding coherent management strategies (Davis and Worm 2013; Oliver et al. 2015).

One important, cosmopolitan elasmobranch genus subjected to considerable artisanal effort is *Mustelus* Linck 1790 (Rosa and Gadig 2010; Zagaglia et al. 2011; Tagliafico et al. 2015). Considered among the most complicated elasmobranchs to taxonomically separate (Boomer et al. 2012), within this genus more than 27 species are commercially harvested (Rosa and Gadig 2010; Giresi et al. 2015; IUCN 2016). While some species are successfully managed [e.g., *M. antarcticus* (Günther, 1870), *M. lenticulatus* (Phillipps, 1932), and *M. ravidus* (White & Last, 2006)] with stable populations (Walker 2016; Francis 2003; M^cAuley 2011), many species, including *M. fasciatus* (Garman, 1913), *M. schmitti* (Springer 1939), *M. whitneyi* (Chirichigno, 1973), *M. mustelus* (Linnaeus, 1758), *M. mento* (Cope, 1877) and *M. canis* (Mitchill, 1815) have classifications ranging from ‘Near Threatened’ to ‘Critically Endangered’ by the International Union for Conservation of Nature (IUCN 2016). In nearly all cases, population declines are a consequence of minimally regulated fishing pressure (Rosa and Gadig 2010).

Artisanal fishing effort on *Mustelus* is quite intense in South America, and especially off Venezuela where at least four species [*M. higmani* (Springer and Lowe, 1963), *M. canis*, *M. norrisi* (Springer 1939) and *M. minicanis* (Heemstra 1997)] have been targeted for the past 50 years (Cervigón 1966; Heemstra 1997; Mendoza 2015). While there are few accurate data describing regional catches, it is established that owing to their high-valued meat and local demand, these four species are among the most frequently landed elasmobranchs (Cervigón and Alcalá 1999; Mendoza 2015; Tagliafico et al. 2015). Of these species, *M. canis* and *M. higmani* have had some of their life-history parameters described, including preliminary reproductive dynamics (Zagaglia et al. 2011; Tagliafico et al. 2015). However, despite their consistency among artisanal landings, comparatively few relevant data are available for either *M. minicanis* or *M. norrisi*.

Mustelus minicanis was only recently described (Heemstra 1997), and appears to be endemic to the southern Caribbean Sea (Navia et al. 2016). Statistics describing historical landings are non-existent, and the species has been assessed by the IUCN as Data

Deficient (Leandro and Caldas 2006). *Mustelus norrisi* is also classified as Data Deficient (Jones et al. 2009), but has a broader distribution across several territorial waters (i.e. from the USA to Brazil; Cervigón and Alcalá 1999). The taxonomy of *M. norrisi* often is confused with the very similar *M. canis*; a characteristic that contributes towards most of the *Mustelus* species being collectively grouped in landings data, confounding assessments of inter-specific exploitation and biology (Rosa and Gadig 2010).

Like some of their South American congeners, both *M. minicanis* and *M. norrisi* might be characterised by various biological factors that render them susceptible to overfishing, especially in the absence of adequate management. Sufficient information describing life-history traits, and particularly reproduction and maturation, is essential for effective stock management and conservation. Our primary aim here was to contribute towards providing some of the required baseline life-history data for *M. minicanis* and *M. norrisi* and, more specifically, via a first assessment of their reproductive characteristics with a focus on maturation. A secondary aim was to use this information to propose precautionary management measures.

Methods

This study was done using specimens opportunistically collected during weekly sampling of the catches landed by up to ~20 artisanal vessels (7–12 m and 59–110 kw) at La Pared (11° 3' 36" N, 64° 18' 47" W) and Juan Griego (11° 5' 2" N, 63° 58' 21" W), and also at two local fish markets, Los Cocos (10° 56' 59" N, 63° 51' 16" W) and Conejeros (10° 57' 45" N, 63° 52' 2" W) on Margarita Island, Venezuela, between January 2006 and December 2007. Each vessel fished a single, bottom-set gillnet comprising polyamide monofilament (~0.5 mm diameter twine) mesh (~75 mm stretched mesh opening) and measuring ~2.4–3.2 m deep and 400–1500 m long. The nets typically were deployed between 16:00 and 18:00 h in depths of ~60–300 m off north Margarita Island (~11° 8' 39" N; 64° 28' 41" W) and retrieved between 05:30 and 08:00 on the following day.

All specimens were identified using established taxonomic keys. *Mustelus minicanis* was identified following Heemstra (1997) and separated based on its uniform brown colour and smaller adult sizes than congeners, and its unique characteristic of being the only *Mustelus*

with an orbit diameter greater than the internostril distance. On the contrary, *M. norrisi* is very similar to *M. canis*, with morphometric characteristics that strongly overlap throughout several taxonomic keys (Compagno 1984; Heemstra 1997; Rosa and Gadig 2010; Robertson and Allen 2016). We subsequently used three criteria to separate these latter two species, the: (i) maturity of small male specimens, with *M. canis* only mature at >80 cm TL (Giresi et al. 2015); (ii) shape of the caudal fin, with the lower lobe more pointed in *M. norrisi* than in *M. canis* (Giresi et al. 2013, 2015) and (iii) internarinal or internostril space (proportional to TL), which is one measure with minimal overlapping range (Heemstra 1997; Rosa and Gadig 2010).

Each specimen was measured for TL and sexed based on the presence or absence of claspers. The extent of subsequent sampling mostly depended on the willingness of fishers and/or wholesalers to release specimens. Nevertheless, for many males, their claspers were measured (from tip to the junction of the pelvic fin) and the stage of calcification noted, as described below. Wherever possible, females were dissected and their reproductive organs were removed and visually assessed *in situ*. Uteri were dissected and, if possible, embryos were measured for TL, counted and sexed. All measures were recorded to the nearest 0.1 mm, and one specimen of each sex was deposited in the ichthyology collection at the *Universidad de Oriente*, in Boca de Río, Venezuela.

Maturation was determined according to definitions provided in previous studies (e.g., Conrath 2004; Zagaglia et al. 2011). Depending on ovarian and uterine development, females were assigned into four stages: juvenile (undeveloped ovary with translucent oocytes); ovulating (fully developed yellow

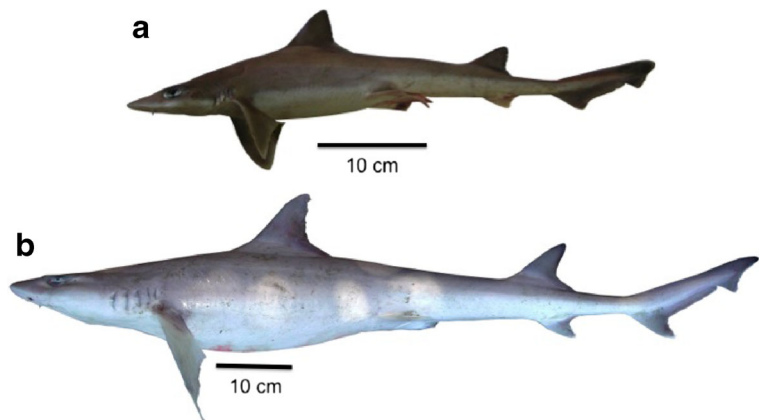
oocytes in the ovaries with well-defined uteri); gravid (embryos present in the uteri); and post-partum (highly vascularized, developed, flaccid and empty uteri). Males were classified as juvenile, maturing or adult if their claspers were soft (and relatively small), calcifying or completely calcified, respectively.

Data were analysed separately for each species. The hypotheses of equal sex (i) ratios and (ii) size-frequency distributions were tested using chi-squared goodness-of-fit and two-sample Kolmogorov-Smirnov tests, respectively. Where there were sufficient data, linear regression analyses were used to examine the relationship between gravid female TL and litter size. Sex-specific 50% sizes at maturity (M_{50}) were estimated by fitting logistic curves to the size frequencies (1-cm TL intervals) of confirmed immature (juvenile and maturing males, and juvenile females) and mature individuals using maximum likelihood. The logistic equation is $M_f = 1/1 + \exp -a(1-b)$, where M_f is the proportion of mature individuals and a and b are the parameters to be estimated (confidence intervals of 2.5 and 97.5% were calculated). All analyses were implemented in R (R Development Core T 2011) and the null hypothesis rejected at $p = 0.05$.

Results

A total of 1429 sharks were assessed during all sampling. Of these specimens, 1194 and 235 were identified as *M. minicanis* and *M. norrisi*, respectively. Considering there are few published images of either species, we provide photographs in Fig. 1.

Fig. 1 Photographs of **a** *Mustelus minicanis* and **b** *M. norrisi*



Mustelus minicanis

A two-sample Kolmogorov-Smirnov test detected a significant difference between the size-frequency distributions of females ($n = 691$; range of 22.7–72.2 cm TL; mean \pm SD of 55.3 ± 5.8 cm TL) and males ($n = 503$; 22.4–71.2; 50.4 ± 4.9 cm TL) sampled, with considerably more females >60 cm TL than males in catches ($p < 0.01$). The pooled sex ratio (1:0.7) was significantly biased toward females ($\chi^2 = 29.6$; $p < 0.05$), but the null hypothesis of parity was maintained for embryos (0.9:1, $n = 230$) ($\chi^2 = 0.64$; $p > 0.05$).

Specimens of both sexes were sampled in all months except April and May, which coincided with a seasonal

change in the fishery to target pelagic teleosts. Owing to the small number of specimens sampled per year, and because preliminary data exploration revealed few temporal differences in reproductive stages between the two years, data were pooled.

Female maturation

Of 691 females assessed, 36 were separated as juvenile (22.7–48.6 cm TL) and characterised by small ovaries and translucent oocytes. By comparison, mature ovulating females represented the largest sample size ($n = 471$) and were 45.6–72.2 cm TL. Gravid females were the second largest group ($n = 164$;

Fig. 2 a Linear regression between total length (cm) of gravid *Mustelus minicanis* and the number of embryos, and **b** mean total length (cm) of embryos by month from *M. minicanis*. SD = standard deviation

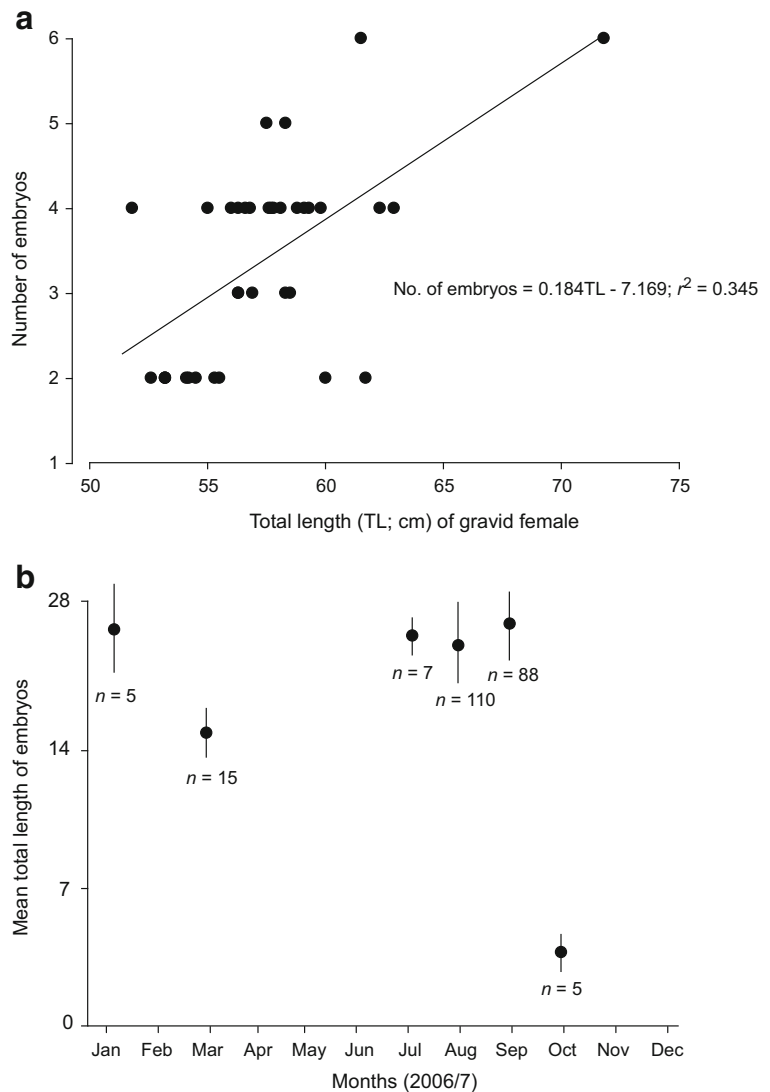


Table 1 Estimated 50% lengths at maturity (M_{50}), standard errors (SE) and confidence intervals (CI; 2.5–97.5%) for female (F) and male (M) *Mustelus minicanis* and *M. norrisi* caught in the southern Caribbean Sea during 2006/07

	Sex	M_{50}	SE	CI
<i>M. minicanis</i>	F	45.11	0.39	44.21–45.95
	M	45.48	0.42	44.60–46.40
<i>M. norrisi</i>	F	76.65	1.16	74.13–79.55
	M	69.63	1.92	65.25–73.92

50.6–65.7 cm TL), and presented placental viviparity, containing between two and six embryos (mean number \pm SD of 3.3 ± 1.2). A significant linear regression was observed between uterine fecundity and the size of the mother, although the latter explained only 35% of the variation ($p < 0.01$; Fig. 2a).

Only 20 post-partum females (52.7–65.0 cm TL) were recorded; all with flaccid abdomens and highly vascularized empty uteri. Considering the above proportions of juvenile and mature (all other stages) females, a logistic maturation curve was converged with an M_{50} (\pm SE) estimated at 45.11 (\pm 0.39) cm TL (Table 1).

Logistics precluded identifying the mother of every embryo (i.e. because these were rapidly removed and stored together) during all sampling trips, but the largest observed embryo was 29.5 cm TL (vs the smallest free-swimming

specimens of 22.4 cm TL) recorded in January, while the smallest embryo (3.4 cm TL) was observed in October (Fig. 2b). Embryos were always observed in similar numbers in both uteri, and near-term pups had their caudal fin bent.

The temporal abundances of females in each of the four stages of reproduction were fairly broad. However, in general: (i) juveniles mostly occurred in catches in March, September and October; (ii) post-partum and gravid females were present from January to October (but especially March to September for the latter); and (iii) ovulating females were caught throughout all sampled months (Fig. 3).

Male maturation

Notwithstanding considerable variability among TLs within reproductive stages, 20 sampled males were separated as juvenile (37.3–53.5 cm TL) with flexible claspers all < 4 cm TL (Fig. 4a). Maturing males ($n = 27$) had less variable TLs (42.3–55.0 cm TL) and typically larger but semi-calcified or soft claspers, while the assessed adults ($n = 241$) showed greater variability among TLs (43.4–59.2 cm TL) and had obviously calcified claspers (that were 3.0–4.9 cm long) (Fig. 4a). A logistic regression was converged with an M_{50} of 45.48 (\pm 0.42) cm TL (Table 1). Like for females, juvenile males mostly were present in catches between March and October (Fig. 4b). Maturing

Fig. 3 Monthly relative abundance of female *Mustelus minicanis* in landings (during 2006 and 2007) according to their stage of maturation

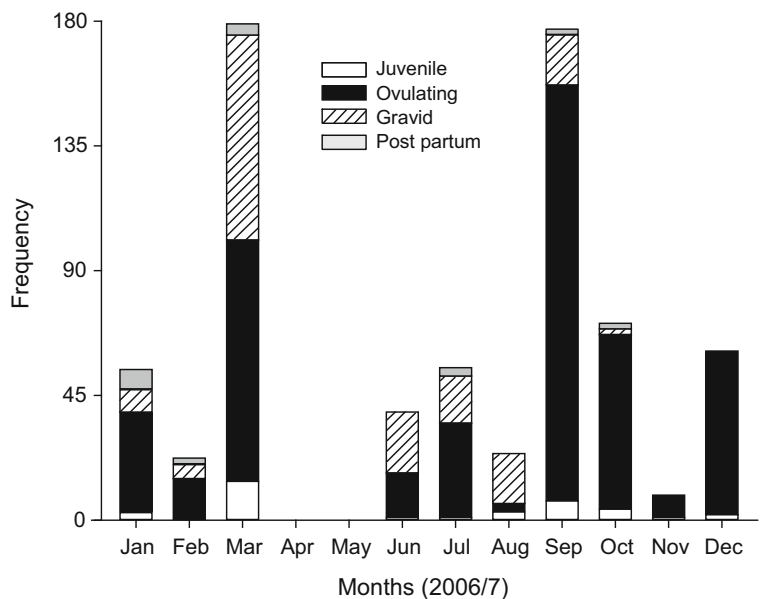
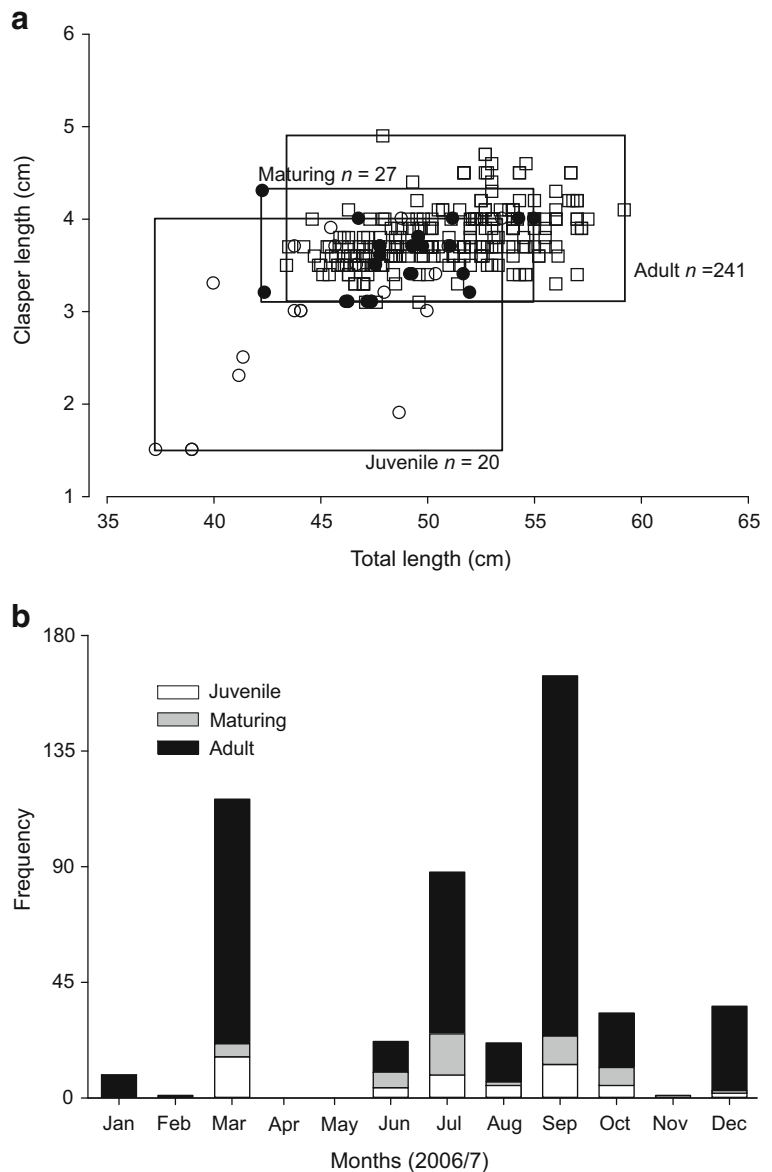


Fig. 4 Relationship between (a) total length and the length of claspers (cm) and (b) maturity stage and monthly relative abundance for male *Mustelus minicanis*. The boxes define the boundaries between maturity stages: white circles = juveniles; black circles = maturing; and white squares = adults



males showed a similar trend, while adults were present in all sampled months (Fig. 4b).

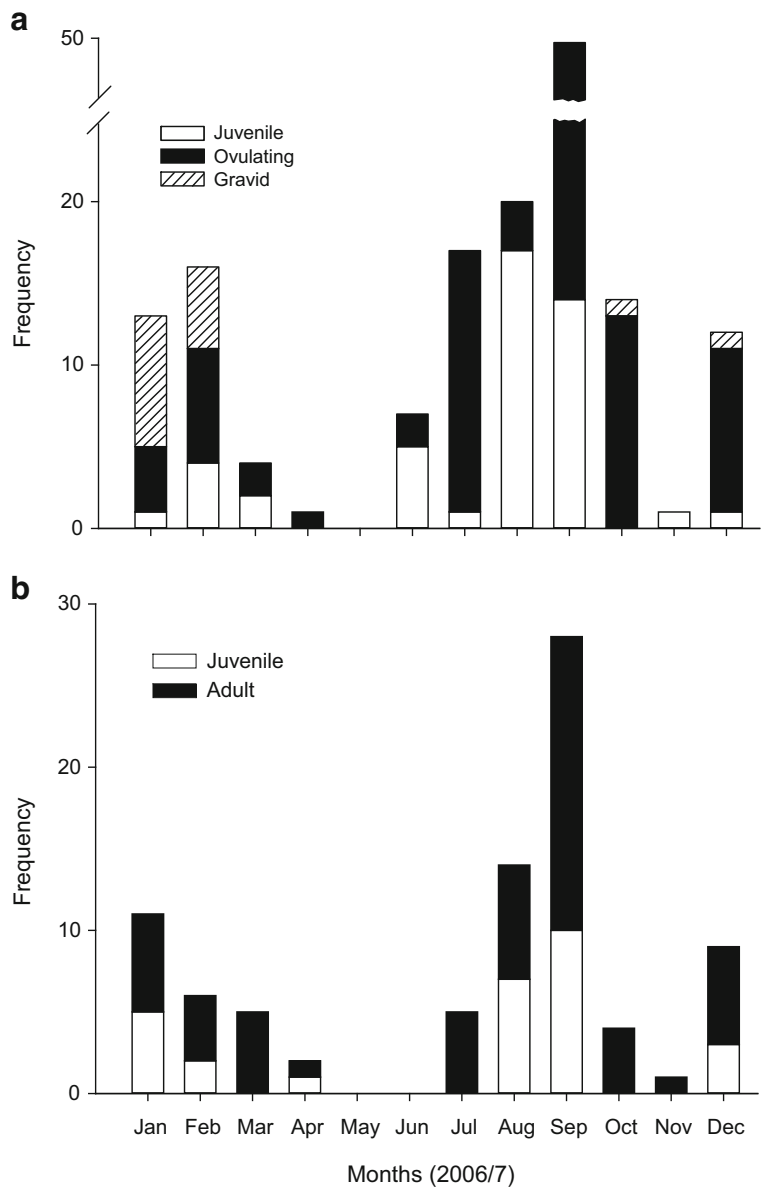
Mustelus norrisi

There was no significant difference between the size-frequency distributions of females ($n = 150$; 47.4–139.7; 82.6 ± 18.1 cm TL) and males ($n = 85$; 43.3–121.8; 75.5 ± 17.7 cm TL) sampled (Kolmogorov-Smirnov test; $p > 0.05$). However, the pooled sex ratio (1:0.6) was significantly biased toward females ($\chi^2 = 18.0$; $p < 0.05$).

Female maturation

We were able to separate the 150 females into juvenile, ovulating and gravid stages (Fig. 5a). Juveniles ($n = 46$; 47.4–93.4 cm TL) had obviously underdeveloped gonads and most were smaller than the clearly ovulating specimens ($n = 89$; 77.5–139.7 cm TL) (Fig. 5a). The gravid females ($n = 15$; 85.5–126 cm TL) all had embryos ($n = 1$ –11) in their uteri and, while few data describing embryos were collected (i.e. for eight females and four males), the largest measured was 41.0 cm TL recorded in October. Using the immature and mature

Fig. 5 Monthly relative abundances of (a) female and (b) male *Mustelus norrisi* in landings according to their stage of maturation



stages above, M_{50} was estimated at 76.65 (\pm 1.16) cm TL (Table 1).

The temporal abundance of females revealed juveniles and ovulating specimens in virtually all months (no specimens were sampled in May owing to the stated shift in fishing effort), except April for juveniles and November for ovulating individuals (Fig. 5a). By comparison, the few gravid females were restricted mostly to January and February, but with one recorded in each of October and December (Fig. 5a).

Male maturation

Based on clearly flaccid or calcified claspers, the 85 males were separated into 28 juveniles (43.4–83.5 cm TL) and 57 adults (49.3–121.8 cm TL)—although insufficient data were collected on clasper lengths to facilitate plots. Following these classifications, M_{50} was estimated at 69.63 (\pm 1.92) cm TL (Table 1).

The temporal abundances were sporadic for both stages of males. Juveniles were present in January,

February, April, August, September and December (Fig. 5b). Adults were also present during these months and all others (no data were collected for May; Fig. 5b).

Discussion

This study provides the first detailed descriptions of reproduction in *M. minicanis* and *M. norrisi* and, in doing so, contributes towards the very limited information collected during earlier taxonomic descriptions (Springer 1939; Compagno 1984; Heemstra 1997; Cervigón and Alcalá 1999; Rosa and Gadig 2010). The key observations here were that each species presented both similar and divergent reproductive aspects, which can be discussed in terms of possible regional environmental influences, and then used to propose precautionary management strategies—although first our sampling methodology warrants consideration.

The observed patterns of catches and reproductive stages can be considered appropriate indices of abundances among the broader populations. Nevertheless, like all fishing gears, the sampled gillnets would have had defined selectivity, which might be expected to present as a uni- or multimodal bell-shaped curves for each species (Kirkwood and Walker 1986). However, considering *M. norrisi* up to 139.7 cm TL and *M. minicanis* as small as 22.0 cm TL were retained, it seems plausible that the selectivity curves were quite wide, and that most individuals in each population should have been available for capture (Weigmann 2016). In support of this hypothesis, the same mesh size has been shown to retain elasmobranchs across an even wider range of sizes in other fisheries (Carlson and Cortés 2003).

The apparent broad selectivity of the gear used here might explain why our observed maximum lengths for *M. minicanis* (72.2 cm TL) and *M. norrisi* (139.7 cm TL) were considerably greater than those previously reported (57 and 120 cm TL, respectively; Heemstra 1997; Weigmann 2016)—although the latter were based on few specimens (e.g., $n = 9$ for *M. minicanis*). Similar biases might also explain our different mean sizes at maturity compared to earlier estimates. Specifically, previous reports suggested that female and male *M. norrisi* mature at ~65.0 and 57.0–61.0 cm TL, respectively (Springer 1939; Heemstra 1997). In contrast, we estimated considerably larger and less variable $M_{50\%}$ at 76.7 and 69.6 cm TL for females and males,

respectively. Conversely, for *M. minicanis*, previous estimates of $M_{50\%}$ (~57 and 47 cm TL; Heemstra 1997) were larger than our estimated ~45 cm TL for both sexes. Beyond the likely importance of relative sample sizes, intraspecific differences in size at maturity among studies might also at least partially reflect other factors, including different fishing pressures, biogeographic barriers, sampling methodologies and seasons (Mendonça et al. 2011; Tagliafico et al. 2015).

Assuming no sex-specific effects on gillnet selectivity, the significant bias towards females of both species in catches might imply some sexual segregation and/or differential mortality or growth. The potential for such effects was reinforced for *M. minicanis*, with parity in the sex ratio of embryos. Other studies have identified similar sex-specific patterns among *Mustelus* (Pereyra et al. 2010; Rigby et al. 2016), although Springer (1939) reported a bias among males for *M. norrisi*.

For *Mustelus* in general, sexual segregation is often attributed to area, depth, seasonality and/or behaviour (Heemstra 1997; Hozbor et al. 2004; Cortés et al. 2011). Often, females tend to have a relatively greater investment in reproduction (large ova, long gestation times and fidelity to coastal nursery grounds), whereas males contribute less energy to reproduction and tend to exhibit promiscuity (Zeh and Zeh 2000). Such differences can manifest as sex-specific dispersion patterns (Zeh and Zeh 2000; Neff and Pitcher 2005; Daly-Engel et al. 2012). Additional data across broader areas are required to confirm and/or explain the sexual segregation observed here.

The relative proportions of individuals in the different reproductive stages were also comparable between species, with the greater (albeit variable) component of catches comprising adults. Similarities also extended to the temporal distribution of males according to their reproductive stages. Although their absolute sizes differed considerably, consistent relative proportions of adults and juvenile/maturing individuals throughout the year were observed for both species. Such results contrast with other regional *Mustelus* fisheries, where catches predominantly comprise juveniles (Zagaglia et al. 2011; Tagliafico et al. 2015), which may indicate segregation or differential fishing pressure.

Unlike for males, the temporal distributions of female reproductive stages were less comparable between species, with gravid *M. minicanis* observed throughout nearly all months, while gravid *M. norrisi* only were present in catches between October and February, which

corresponds to the northern hemisphere late autumn and winter. These differences might reflect the different sample sizes and/or spatial segregation, although when considered with the other stages of maturation, it is clear there was contrasting reproductive development between these two species.

Specifically, *M. minicanis* had a maximum uterine fecundity of six, which was comparable to that observed by Heemstra (1997), while the increasing litter size with maternal TL was consistent with other *Mustelus* (Saidi et al. 2009; Zagaglia et al. 2011). The largest embryo (~30 cm TL) was recorded in January and also was considerably larger than the smallest juvenile (~22 cm TL recorded in August) and the maximum embryo size previously reported for the species (20–21 cm TL; Heemstra 1997). Other large embryos were recorded between July and September, and the smallest in October. Collectively, these observations imply a protracted parturition (supported by the bent caudal fins which would maximise space in the uterus) but a lack of synchronicity between females. The same characteristic previously has been reported for *Mustelus higmani* and other Caribbean elasmobranchs (Tagliafico et al. 2013, 2015) and might reflect the steady, warm temperatures and abundant resources characteristic of the tropics, which facilitate such reproduction (Vila-Gispert et al. 2002). The large size of offspring might increase their survival probability (Cortés 1998).

In contrast, the maximum fecundity of 11 embryos observed for *M. norrisi* was greater than noted previously for specimens collected off Florida ($n = 6$) (Springer 1939), Brazil ($n = 4–6$) (Rosa and Gadig 2010), and locally ($n = 8$) (Cervigón and Alcalá 1999), but within the range (7–14) reported by Heemstra (1997)—who also suggested a minimum size at birth of 29–30 cm TL. Considering the sizes of the largest embryos and the smallest free-living specimens observed here, an estimated birth size of 41–43 cm TL might be more appropriate. Such differences between studies might imply a latitudinal gradient in fecundity, although the small sample sizes preclude any definitive conclusions.

Irrespective of uterine fecundity and size at birth, and unlike for *M. minicanis*, the data here support the supposition that *M. norrisi* has reproductive behaviour similar to several other *Mustelus* in the northern hemisphere, and is characterised by a synchronized, seasonal parturition (Conrath and Musick 2002). One hypothesis to explain such conformity is that *M. norrisi* off Venezuela might align their reproduction with conspecifics off North

America, and possibly even migrate along the western Atlantic. Migratory behaviour previously has been suggested for *M. norrisi* in the Gulf of Mexico (Heemstra 1997) and tagging studies with other *Mustelus* have revealed high dispersal capabilities (>1000 km), with females typically traveling more than males (Francis 1988). The potential for such behaviour warrants investigation, especially considering there are varying levels of fishing effort transcending territorial boundaries.

The presence of variable regional fishing effort highlights that while our study has provided definitive and valuable information describing the reproductive biology of exploited populations of *M. minicanis* and *M. norrisi*, clearly additional data are required to rigorously assess the effects of harvesting on populations. Although relatively few juveniles were caught here (especially for *M. minicanis*), gravid females consistently appeared in catches. Excessive fishing mortality among gravid females potentially could represent a long-term threat to the reproductive success of the species. This statement is supported by severe population declines among *Mustelus* caught in other unmanaged South American artisanal fisheries (Massa et al. 2006; Hozbor et al. 2004).

One method of reducing fishing mortality among defined sizes and/or reproductive stages of *Mustelus* might involve applied gear modifications (along with controlled effort). In particular, the apparent broad selectivity of the existing mesh size and other important technical factors should be formally quantified and understood. Such variables include, but are not limited to: net length (Rudstam et al. 1984); soak time (Minns and Hurley 1988); hanging ratio (Acosta and Appeldoorn 1995); and twine size and material (Jensen 1995). Coherent, key factors might then be identified and regulated across appropriate spatio-temporal scales to control selectivity and, as one example, perhaps minimise catches of juvenile *M. norrisi* (i.e. ~30% of the total catch), while concurrently limiting catches of some similar-sized gravid *M. minicanis* (i.e. ~25% of females).

Appropriate gear restrictions can be an effective method for limiting fishing mortality (Uhlmann and Broadhurst 2015) but the considerable intra-specific (for *M. norrisi*) and inter-specific variation in sizes at maturity and overlapping spatial and temporal distributions means any modifications will require careful consideration. Such work should be considered a priority given the local importance and likely restricted ranges of both species, but especially the endemic *M. minicanis*.

The need for such actions is even more poignant considering the Caribbean region has been catalogued as an irreplaceable hotspot for endemic, threatened marine chondrichthyans (Dulvy et al. 2014).

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