Comparison of the reproductive ecology of two sympatric blacktip sharks (*Carcharhinus limbatus* and *Carcharhinus tilstoni*) off north-eastern Australia with species identification inferred from vertebral counts

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Precaudal vertebral counts were used to distinguish between 237 morphologically similar *Carcharhinus limbatus* and *Carcharhinus tilstoni* and were congruent with differences in reproductive ecology between the species. In addition to differing lengths at maturity and adult body size, the two species had asynchronous parturition, were born at different sizes and the relative frequencies of neonates differed in two coastal nursery areas. Despite evidence that hybridization can occur, these differences suggest the species are largely reproductively isolated. © 2012 The Authors

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INTRODUCTION

Recently, Morgan *et al.* (2012) found a mismatch between species identification using mitochondrial DNA (mtDNA) and morphological characters in a pair of closely related and cryptic sharks that occur in sympatry off northern Australia: the common blacktip *Carcharhinus limbatus* (Müller & Henle 1839) and the Australian blacktip *Carcharhinus tilstoni* (Whitley 1950). The mismatch was found to be caused by hybridization and is the first reported case of two chondrichthyan species hybridizing in the wild. The finding follows two other recent molecular studies reporting dramatic shifts in the relative abundance and range of the same species pair.

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Ovenden *et al*. (2010) found that the ratio of abundance of *C. tilstoni* to *C. limbatus* was approximately equal, in stark contrast to the ratio of 300:1 previously reported by Stevens & Wiley (1986). This suggests that a rapid change in abundance of one or both species may have occurred. Additionally, Boomer *et al*. (2010) reported a southerly increase in the range of *C. tilstoni* in excess of 1000 km on the east coast of Australia, challenging the perception that this species is confined to the tropics.

Rapid changes to the relative abundance of large predatory fishes (most commonly observed due to fishing) can affect ecosystems in complex and indirect ways (Dulvy *et al*., 2000; Stevens *et al*., 2000; Myers *et al*., 2007). Blacktip sharks, assumed to be mainly *C. tilstoni*, have dominated the catch of commercial shark fisheries across northern Australia during the past 40 years (Stevens & Wiley, 1986; Harry *et al*., 2011). Management of these fisheries may need to be changed to reflect a community shift in the target species as well as the effects of hybridization (Ovenden *et al*., 2010; Morgan *et al*., 2012). The study of this species pair and its hybrids may also provide an insight into the evolutionary processes that lead to speciation in chondrichthyans (Arnold, 1992; Palumbi, 1994), and is of special interest given the apparent rarity of hybridization in this taxon.

To properly advise management and help understand the evolutionary importance of hybridization, the taxonomic boundaries between *C. limbatus* and *C. tilstoni* must be clearly defined. Although Whitley (1950) described *C. tilstoni* as a distinct species, there were no external morphological features that distinguished it from the widespread and morphologically variable *C. limbatus*. This led taxonomists to regard the two species as synonyms (Garrick, 1982; Compagno, 1988). Stevens & Wiley (1986) noted, however, the existence of two distinct groups of blacktips with divergent vertebral counts and life-history characteristics in the catch of a large-scale commercial fishery that operated off northern Australia during the 1980s. Subsequent molecular analysis supported the existence of two cryptic species (Ovenden *et al*., 2010; Morgan *et al*., 2011). Although other characteristics such as length-at-maturity appeared to differ between *C. limbatus* and *C. tilstoni* (Stevens & Wiley, 1986), there have been no studies where morphological characters have been systematically measured on specimens identified using numbers of precaudal vertebrae. Consequently, the taxonomic boundaries between these species are unclear, and there is limited understanding of how they differ ecologically.

The aim of this study was to clarify the taxonomic boundaries between *C. limbatus* and *C. tilstoni* by examining the congruence of several reproductive characteristics with precaudal vertebral counts. Precaudal vertebrae (PCV) counts were first used to distinguish between *C. limbatus* and *C. tilstoni* samples collected off north-eastern Australia. Vertebral counts were then compared with length-at-birth and timing of birth, and length at sexual maturity in males. The specific aims of this study were to compare the aspects of the reproductive ecology of the two species in a geographical area where they are sympatric, and to propose reproductive isolating mechanisms that maintain these similar species as distinct taxa.

MATERIALS AND METHODS

Samples were collected from January 2006 to December 2011 between Princess Charlotte Bay (14° 15′ S) and Moreton Bay (27° 12′ S), on the north-east coast of Queensland, Australia. Fishes were obtained from a fishery-dependent observer programme of a

gillnet fishery (Harry *et al.*, 2011). Although sampling occurred year-round, the majority of individuals were collected between the months of September and January. The fishes described in this study are a sub-set of a larger sample (*c.* 1000 individuals), on which vertebral counts were opportunistically undertaken. Specimen collection was supplemented by direct purchase of fishes from commercial fishers, and through fishery-independent sampling using gillnet and multi-hook drop lines. All samples were collected from water depths <25m, with the exception of a single individual caught from an unknown depth by a prawn trawler.

The stretched total length, L_{ST}, of individuals was measured in mm and outer clasper length, $L_{Clasper}$, of males was measured as the distance from the tip of the clasper to the pelvic fin (Compagno *et al.*, 2005). Length-at-birth, $L_{STbirth}$, and timing of birth were inferred from neonates that were prolific in nearshore habitats during spring and early summer. Neonates were defined as individuals that had recently been born and could be identified as such by the presence of an unhealed umbilical scar during their first few weeks of life (Duncan & Holland, 2006). Precaudal vertebrae counts were taken from the first complete centrum posterior to the chondrocranial occipital centrum, to the centrum anterior to the precaudal pit (Compagno, 1988). This was done by dissection. Eight pregnant females were also identified by PCV counts of their embryos, as this trait was assumed to be inherited and not affected by environment. Embryos were assumed not to be hybrids.

RESULTS

PCV counts were obtained from 212 post-natal individuals (568–1588 mm L_{ST}) and 25 embryos (179–644 mm L_{ST}). PCV values displayed two modal peaks of 83–89 and 96–102 (Fig. 1). Three outlying individuals had counts between 89 and 94, and five outlying individuals had counts >102 (Fig. 1). In general, these ranges were consistent with previous studies that suggested *C. limbatus* had >93 PCV and *C. tilstoni* had <92 PCV (Garrick, 1982; Stevens & Wiley, 1986). Adopting this definition, the mean ± S.D. PCV of 125 *C. limbatus* (PCV > 93) was 99·28 ± 2·35, while the mode was 98. The size range of post-natal males and females identified using vertebral counts was 650–1380 and 651–1588 mm L_{ST}. The mean ± S.D. PCV of 109 *C. tilstoni* (PCV < 92) was 86·09 ± 1·30, while the mode was 86. The length range of post-natal males and females identified using vertebral counts was 568–1480 and 586–1800 mm L_{ST}. This included all eight pregnant females (1553–1800 mm L_{ST})
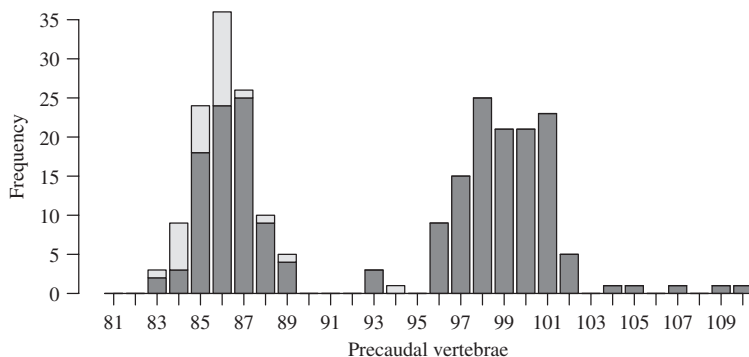

FIG. 1. Distribution of precaudal vertebrae counts undertaken on 212 post-natal (■) and 25 embryonic (□) *Carcharhinus* spp.
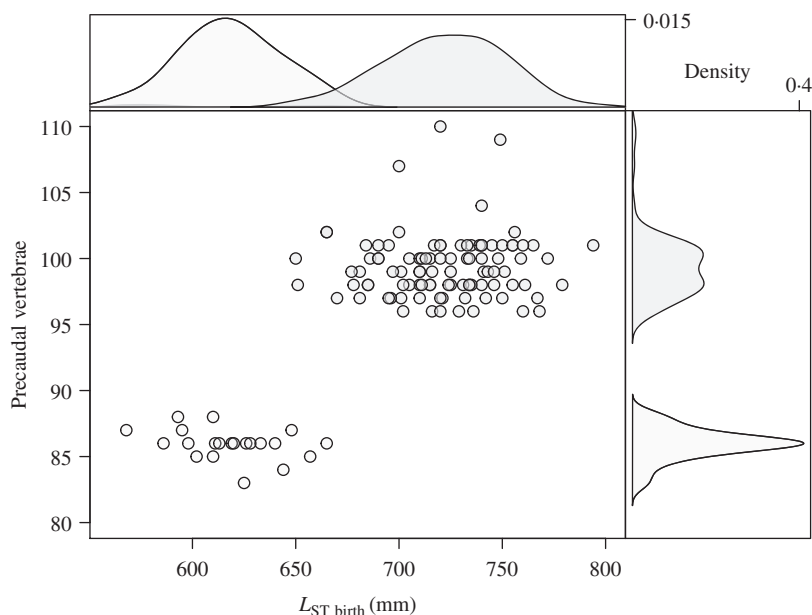
FIG. 2. Comparison of differences in stretched total length-at-birth ($L_{STbirth}$) and number of precaudal vertebrae in 97 *Carcharhinus limbatus* (O, PCV > 93) and 23 *Carcharhinus tilstoni* (O, PCV < 92), including both raw data and kernel density estimates.

that were identified by PCV counts of one or more embryos. Miscounting cannot be ruled out as an explanation for the outlying PCV counts including a 186 mm L_{ST} embryo with 94 PCV whose siblings had 86, 86 and 84 PCV.

Of the 237 individuals identified using vertebral counts, 120 were neonates. Ninety-seven *C. limbatus* (PCV > 93) had a mean ± S.D. $L_{STbirth}$ of 721·8 ± 29·4 mm while 23 *C. tilstoni* (PCV < 92) had a mean ± S.D. $L_{STbirth}$ of 619·7 ± 23·4 mm (Fig. 2). There was little overlap between length-at-birth distributions (Fig. 2) and *C. limbatus*, were born, on average, *c*. 102 mm or 16% longer than *C. tilstoni*. The longer *C. limbatus* were also, on average, 54% heavier than *C. tilstoni* (2·10 kg compared to 1·37 kg). Differences in length-at-birth were consistent with the differences in PCV counts.

In addition to clear interspecific differences in length-at-birth, there were also differences in timing and location of birth. The majority of neonates were collected within two spatially discrete coastal nurseries: Cleveland Bay (19° 13′ S) and Moreton Bay (27° 12′ S). Within Cleveland Bay, *C. limbatus* made up 36% of 33 neonates compared to 100% of 83 neonates in the Moreton Bay sample. This is consistent with the observations that *C. tilstoni* is more common in tropical waters (a single *C. tilstoni* was recorded from Moreton Bay but it was not a neonate) (Last & Stevens, 2009). Timing of parturition was also observed to be asynchronous between the two species, and more protracted in *C. limbatus* than *C. tilstoni* (Fig. 3). *Carcharhinus limbatus* neonates were recorded from early October (day 280) to early January (day 8), and the peak in parturition occurred during late November (Moreton Bay samples were collected on day 334). In contrast, *C. tilstoni* neonates were
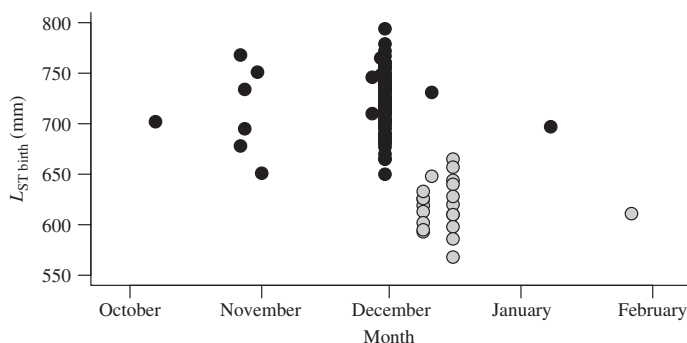
FIG. 3. Comparison of date of capture (used to infer timing of parturition) of 96 neonate *Carcharhinus limbatus* (●, precaudal vertebrae count, PCV > 93) and 21 neonate *Carcharhinus tilstoni* (◯, PCV < 92) and stretched total length-at-birth ($L_{STbirth}$).

not recorded until December (days 343–350), by which time the umbilical scar of most *C. limbatus* neonates had healed. While the timing of parturition probably varies among individuals and from year to year (and the observation of it is partly an artefact of when sampling occurred), there was a consistent tendency for neonate *C. limbatus* to be observed earlier than *C. tilstoni* across the 5 year sampling period (Fig. 3).

A previous study of *Carcharhinus* spp. off northern Australia showed two partially overlapping, but divergent groupings of males based on clasper morphology (Stevens & Wiley, 1986). A similar pattern was observed among 366 male blacktips (595–1620 mm L_{ST}) sampled in this study (Fig. 4). Vertebral counts on 26 male *C. tilstoni* (PCV < 92, 613–1480 mm L_{ST}) confirmed that they matured at the smaller length (Fig. 4), and that vertebral counts were congruent with the two distinct groups. Based on these 26 males, L_{ST} could be used to predict clasper length in the following four-parameter logistic model (White, 2007): $L_{Clasper} = 14 \cdot 02 +$
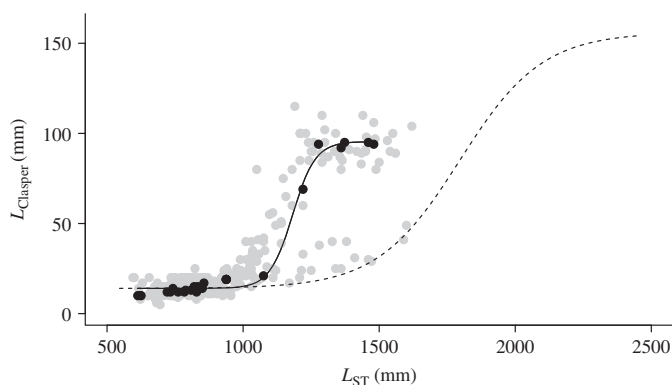

FIG. 4. Clasper length ($L_{Clasper}$) as a function of stretched total length (L_{ST}) in 26 male *Carcharhinus tilstoni* (precaudal vertebrae count, PCV < 92) (●), plotted over data from 366 males (◯) for which vertebral counts were not available. A four parameter logistic function fitted to the 26 *Carcharhinus tilstoni* (——) is compared to the same function fitted to *C. limbatus* from Indonesia waters (– – –) by White (2007), and highlights the large difference in size between these species.

$(95\cdot46 - 14\cdot02)[1 + e^{(- \ln(19)(L_{ST}-1182)(1306-1182)^{-1})}]^{-1}$, where 1182 and 1306 are fitted parameters that indicate the L_{ST} in mm when claspers have attained 50 and 95% of their maximum size, respectively. A similar relationship could not be derived for *C. limbatus* due to a lack of adult males, but White (2007) provides this relationship for the species in Indonesia (Fig. 4). This relationship provides compelling evidence that the individuals maturing at the larger size are, indeed, *C. limbatus* and that they have similar maturity characteristics to the Indonesian population.

DISCUSSION

This study confirms that there is congruence between vertebral counts and several aspects of reproductive ecology in *C. tilstoni* and *C. limbatus.* This demonstrates that, in addition to internal morphology (PCV counts) and molecular characteristics, this species pair can be distinguished based on life-history characteristics, providing further evidence that they are distinct species. This finding is important since hybridization between these species can lead to misidentifications using mtDNA-based molecular identification techniques (Morgan *et al.*, 2012). This study also demonstrates the broad ecological differences between *C. limbatus* and *C. tilstoni* and provides preliminary evidence of the reproductive isolating mechanisms between these species.

One of the most obvious differences between the two species is body size. Based on vertebral counts of embryos from pregnant female *C. tilstoni*, the maximum length of this species appears to rarely exceed 1600–1800 mm L_{ST}. Since male *C. limbatus* are immature at this length, it is likely that they grow much larger. Reports of *C. limbatus* off eastern Australia up to 2650 mm L_{ST} suggest a difference in maximum length of *c*. 800 mm (Stevens, 1984; Macbeth *et al.*, 2009). Body size is an important mechanism for maintaining reproductive isolation between sympatric species (Nagel & Schluter, 1998), and the large length difference between adult *C. limbatus* and *C. tilstoni* could be a barrier to interspecies reproduction between many individuals. The magnitude of this difference is more apparent when expressed as mass. For example, the heaviest female *C. tilstoni* in this study was 34·15 kg (1660 mm L_{ST}). In comparison, a 2600 mm L_{ST} female *C. limbatus* measured in South Africa was 114 kg (Dudley & Cliff, 1993), and Australian *C. limbatus* of this length would probably be of a similar mass.

Size differences may also reflect specialization for different habitats. Although *C. limbatus* is often reported to occur close inshore in water depths <30 m (Compagno *et al.*, 2005), no adult *C. limbatus* were captured in this study (water depths <25 m), despite extensive sampling with a range of gear types. Although adult females must come inshore to give birth, it seems likely that they prefer deeper waters (to at least 130 m depth) and range much further into temperate waters than *C. tilstoni* (Stevens, 1984; Macbeth *et al.*, 2009; Reid *et al.*, 2011). Therefore, although juvenile *C. limbatus* do occur sympatrically with *C. tilstoni*, the absence of adult *C. limbatus* in the study area suggests that geographic separation also acts as a barrier to interbreeding.

Niche partitioning may also occur for neonates. Although both species use coastal nurseries, <5% of neonates of the two species had overlapping lengths (Fig. 2). Birth size in *C. limbatus* is a trait that exhibits a high degree of plasticity (Fig. 5); where
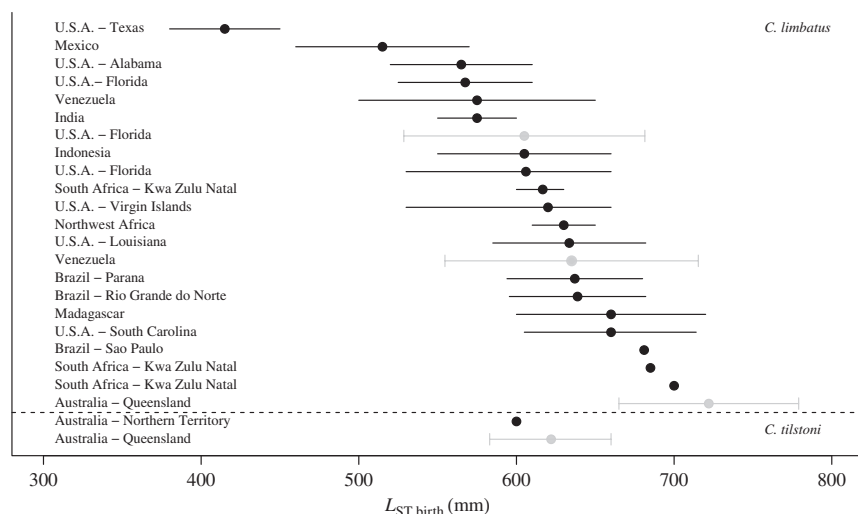
FIG. 5. Comparison of stretched total length-at-birth ($L_{STbirth}$) reported from 22 global studies of *Carcharhinus limbatus* and two studies of *Carcharhinus tilstoni*, found through a search of Web of Science. ● is the mean or mid-point of the reported range of birth sizes ——. |—●—| indicate that the values are the mean ±1·96 S.D. for studies that also reported an S.E.

C. limbatus occurs in sympatry with *C. tilstoni* it has a larger length-at-birth than any other documented population (721·8 mm L_{ST} compared to the global average of 616 mm L_{ST}). It is unclear whether the larger length-at-birth of *C. limbatus* in Australia is related to the coexistence of *C. tilstoni*, which are born at *c*. 619 mm L_{ST}. In Indonesia, however, where *C. tilstoni* is absent, *C. limbatus* are born close to the global average between 550 and 660 mm L_{ST} (White, 2007). Natural mortality of neonate *C. limbatus* is highest during the first few weeks of life (Heupel & Simpfendorfer, 2002), and survival of neonates is likely to decrease as population density increases (Gruber *et al.*, 2001; Gedamke *et al.*, 2007). Any mechanism that reduces competition between neonates of the two species in sympatric nursery areas could therefore be an advantage. Alternatively, geographical differences in life-history traits may explain the larger birth size of *C. limbatus* in Australian waters.

These findings suggest that although *C. limbatus* and *C. tilstoni* may hybridize, the species pair are largely reproductively isolated. Putative evidence of reproductive isolation includes large differences in adult body size, length-at-maturity, geographical separation of adults, as well as asynchronous parturition and differing relative abundance of neonates in two spatially discrete coastal nursery areas. Since samples were taken on the eastern Australian coast where hybridization has been reported (Morgan *et al.*, 2012), it is reasonable to expect that some individuals in this study may have had hybrid ancestry; however, there were insufficient resources to test for this in this study. Given that there was little evidence of any intermediate types, it is unclear whether vertebral counts and life-history traits can be used to distinguish hybrids, and future studies should attempt to understand the effect of hybridization on phenotypic traits in this species pair. This study highlights the ongoing importance of using multiple lines of evidence (ecological, morphological and molecular) to distinguish

between groups of closely related and cryptic species such as these (Corrigan *et al.*, 2008; Ebert *et al.*, 2010). A clearer definition of taxonomic boundaries can be used to improve management. In this case, the large differences in reproductive ecology between *C. limbatus* and *C. tilstoni* reinforce the need for species-specific management of *Carcharhinus* spp. in Australian waters (Lavery & Shaklee, 1991). While *C. tilstoni* is perceived to be a relatively fast growing species (Last & Stevens, 2009), the larger maximum length and length-at-maturity of *C. limbatus*, as well as a likely biennial or longer reproductive cycle (Dudley & Cliff, 1993; Castro, 1996), may mean *C. limbatus* is less resilient to fishing. This highlights the need for detailed study of the life history of *C. limbatus* in Australian waters.

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