Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus,* within a nursery area using telemetry data

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Abstract: A population of young blacktip sharks (*Carcharhinus limbatus*) was monitored over three years to determine their mortality rates using a series of acoustic listening stations. Based on these data it was possible to use several mortality estimators, including indirect life history based methods and direct methods such as the Kaplan-Meier and SURVIV methods, to estimate natural, fishing, and total mortality. Kaplan-Meier (61–91%) and SURVIV (62–92%) methods provided nearly identical total mortality rates during the first six months of life. This agreement suggests that these estimates are accurate for this population. All natural and fishing mortality occurred within the first 15 weeks of the study. This suggests that young sharks are most vulnerable to all types of mortality during this period. Sharks that survived beyond the first 15 weeks successfully left the nursery and were presumed to have migrated southward during fall months. These results provide critical information concerning the early life history of sharks and the importance of nursery areas to the survival of young animals.

Résumé : Un réseau de stations d'écoute nous a permis de suivre une population de jeunes requins bordés (*Carcharhinus limbatus*) pendant 3 ans pour en déterminer les taux de mortalité. Il a été possible avec ces données acoustiques d'utiliser divers estimateurs de la mortalité, en particulier des méthodes démographiques indirectes et des méthodes directes, telles que celle de Kaplan-Meier et SURVIV, pour estimer la mortalité naturelle, la mortalité due à la pêche et la mortalité totale. Les méthodes de Kaplan-Meier (61–91 %) et SURVIV (62–92 %) donnent des estimations presque identiques de la mortalité totale durant les premiers 6 mois de vie. Cet accord laisse croire que ces estimations sont exactes pour cette population. Toute la mortalité naturelle et la mortalité due à la pêche se sont produites pendant les 15 premières semaines de l'étude, ce qui fait penser que les jeunes requins sont vulnérables aux diverses causes de mortalité durant cette période. Les requins qui survivent au-delà de cette période initiale de 15 semaines quittent la zone d'alevinage et migrent sans doute vers le sud durant les mois d'automne. Ce sont là des renseignements essentiels sur les premières étapes du cycle biologique des jeunes requins et sur l'importance des zones d'alevinage pour la survie des jeunes.

[Traduit par la Rédaction]

Introduction

Estimation of mortality is a critical factor in determining the status of fished species and is typically one of the most difficult parameters to define. Many scientists have estimated the mortality of fishes, including sharks, based on life history characteristics (e.g., Pauly 1980; Vetter 1988; Simpfendorfer 1999*a*). However, as Branstetter (1990) pointed out, many of these analyses are based on the adult portion of the population. In fact, to account for the higher vulnerability of young sharks to natural mortality, researchers routinely double estimates calculated from life history methods to represent increased mortality of the first year class (e.g., Smith and Abramson 1990; Sminkey and Musick 1996; Simpfendorfer

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1999*b*). Unfortunately, this calculation is often made with no direct evidence concerning the survivorship of this portion of the population. The early life history of elasmobranchs may be a critical period for recruitment, and survival of young sharks and needs to be examined more closely.

Survival estimates in terrestrial studies are commonly calculated from telemetry data and these methods have recently been applied to aquatic populations (e.g., Bendock and Alexandersdottir 1993; Hightower et al. 2001). The use of telemetry data allows the researcher to define the fate of animals within the study site by continuously monitoring or relocating an animal. This removes the need to recapture marked individuals or to rely on tag reports from other individuals. Advancements in telemetry technology are providing opportunities to use these methodologies in aquatic systems where mortality estimates have mostly been based on life history characteristics or mark-recapture data. Mortality data have been particularly sparse in relation to juvenile stages of aquatic populations, and elasmobranchs are no exception.

Many coastal elasmobranch species are known to use nursery areas (e.g., Branstetter 1990; Castro 1993; Simpfendorfer and Milward 1993). These areas are mostly shallow-water, nearshore areas of high productivity that are thought to provide

young sharks with ample food and protection from predators. These characteristics theoretically make the use of nursery areas critical to the survival of young sharks. However, the precise benefits and costs to young sharks living in nursery areas, and in particular their rates of mortality within these areas, are largely unknown. In this paper we will describe mortality for a population of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area based on long-term acoustic telemetry data.

Materials and methods

Study site

Terra Ceia Bay, a small bay adjacent to the southeastern region of Tampa Bay along the Gulf of Mexico coast of Florida, is a nursery area for neonate and juvenile *C. limbatus*. The open water area of Terra Ceia Bay is approximately 10 km^2 with a maximum water depth of approximately 4 m. The bay is fringed by mangroves, has one major opening where it joins Tampa Bay (Fig. 1), and has a limited freshwater input in the extreme northern portion of the bay. Water quality parameters (e.g., salinity, temperature, dissolved oxygen) are similar throughout the study site (M.R. Heupel, unpublished data), which has a daily tidal range of less than 1 m.

Terra Ceia Bay is commonly used as a nursery area by neonate and juvenile *C. limbatus* from May to November (Heupel and Hueter 2001). Pups are born in May–June and migrate from the nursery area when water temperatures decline in the fall. Although general information about pupping time and location of nursery areas is well known (e.g., Castro 1993), the use of the nursery during the early life history of *C. limbatus* is still unclear.

Field methods

Blacktip sharks were collected by rod and reel fishing, were landed in less than one minute and fitted with 16 × 65 mm acoustic transmitters (Vemco Ltd., Nova Scotia). Transmitters were surgically implanted into the abdominal cavity of sharks using the same procedure in all years. Sharks were anesthetized prior to insertion of the transmitter, were stitched under anesthetic and were revived post-surgery in an oxygenated bath of fresh seawater (see Heupel and Hueter 2001 for detailed methods). All sharks were marked with an external dart tag (Hallprint, South Australia) for identification purposes, measured, weighed, sexed, length of handling time recorded, and condition of release assessed. Upon release, the long-term movement patterns of sharks were recorded by a series of acoustic listening stations (Heupel and Hueter 2001; Simpfendorfer et al. 2002). The acoustic array allowed sharks to be continuously monitored for the entire period they were present within the nursery area.

Animal release condition was assessed as follows (based upon a rating system developed by Hueter and Manire 1994): condition 1 (good), no revival time required when shark is returned to the water, rapid swimming upon release, usually with a vigorous splash; condition 2 (fair), no revival time required when shark is returned to the water, slow but strong swimming upon release; condition 3 (poor), short revival time (up to 30 s) required, slow but sometimes atypical swimming upon release; condition 4 (very poor), long re-

vival time (more than 30 s), limited or no swimming observed upon release but respiration functional.

Defining fates of tagged sharks

The fate of individuals in the nursery area was determined through analysis of the long-term monitoring data. Sharks were classified into three categories. (*i*) Survivals; individuals that maintained continuous movement within the study site and (or) were observed to swim out of the study site. (*ii*) Natural mortalities; individuals that ceased movement within the study site or showed movement patterns more rapid than, and inconsistent with previous or typical movements (consistent with the faster rate of movement of a large predator that had consumed the small shark). This category includes all types of natural mortality (e.g., predation, starvation, disease). (*iii*) Removals (censored); individuals removed from the study site because of factors other than natural mortality or swimming out, such as harvest by fishermen. These individuals were typified by loss of signal detection from the animal while it was within the acoustic array. Many of these instances were validated by tag and (or) transmitter returns from recreational fishermen. Although removals could include transmitter failure, it was assumed that transmitter failure would be negligible. This assumption is based on the large numbers of transmitters that functioned throughout the duration of the season and that all transmitters returned by fishermen were still functioning. The study site is a very popular location for recreational fishermen and it is more likely that these animals were harvested. The fate of each individual was assigned to one of these categories at the end of each week to construct monitoring histories.

A generalized linear model with a logistic link function was used to test if a range of release factors (shark size, shark sex, water temperature, handling time, release condition) influenced the chances of postrelease mortality. For this analysis, animals that were swimming in the study site at least 90 days after release and those that had swum out of the study site were considered to have survived. Individuals that were captured by fishermen also were considered to have survived since fishing mortality is not considered to be a source of postrelease mortality.

Mortality estimation from life history data

Natural mortality of *C. limbatus* was estimated using a range of indirect techniques based on life history data to provide a comparison to those estimated from telemetry data. Six estimators of constant lifetime mortality (Pauly 1980; Hoenig 1983; Jensen 1996) and one method of age-specific mortality (Peterson and Wroblewski 1984) were used. The Peterson and Wroblewski (1984) method uses age-specific weight to estimate natural mortality

$$M = 1.92W_a^{-0.25}$$

where W_a is the weight at age a in grams. All life history data for *C. limbatus* were taken from Killam and Parsons (1989) and Castro (1996).

Kaplan-Meier estimation

Survival of juvenile *C. limbatus* was estimated with the nonparametric Kaplan-Meier procedure (Cox and Oakes 1984; Pollock et al. 1989*a*, 1995). This approach computes

Fig. 1. Map of the study site, Terra Ceia Bay, and its location on the Gulf of Mexico coast of Florida. Circles represent the locations of acoustic hydrophones inside the study area, cross-hatching indicates seagrass beds.
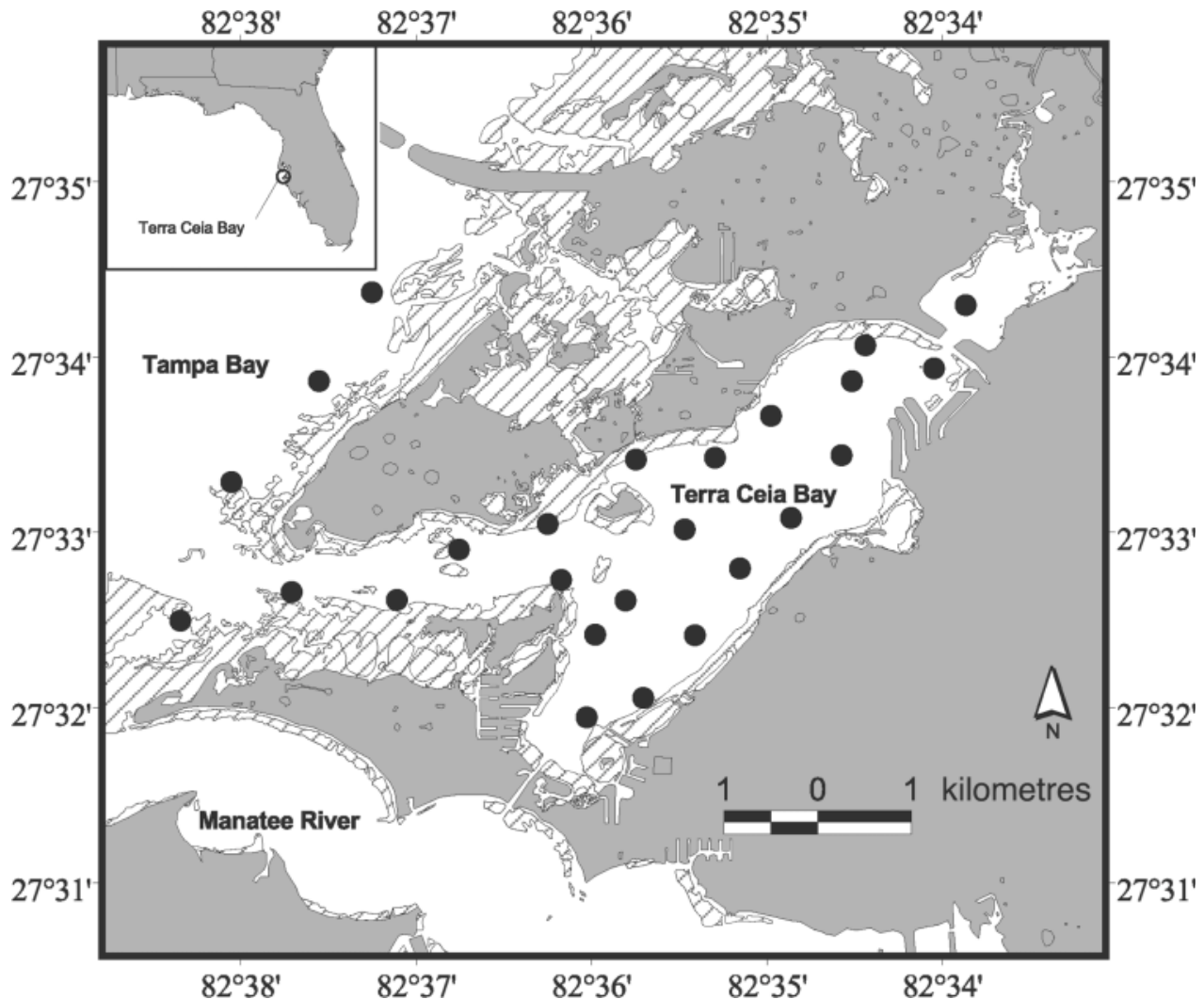
the proportion of fish that die within the study period and allows for animals that are censored from the population (Pollock et al. 1989b).

Survival estimates are based on the Kaplan-Meier staggered entry method as defined by Pollock et al. (1989b)

$$\hat{S}(t) = \prod (1 - d_j/r_j)$$

where $\hat{S}(t)$ is the survival function (the probability of an arbitrary animal in a population surviving t units of time from the beginning of the study), d_j is the number of deaths at time j, and r_j is the number of animals at risk at time j. The number of animals at risk in one time period included the number of animals present at the end of the previous period, plus the number added in the previous period, minus the number of deaths and censored animals. In this calculation the number of animals censored included those that were recorded to have swum out of the study site. Variance was calculated by

$$\mathrm{var}(\hat{S}[t]) = \frac{[\hat{S}(t)^2][1 - \hat{S}(t)]}{r(t)}$$

as discussed by Cox and Oakes (1984). Two forms of survival were calculated. The first was with the number of deaths equal to the number of animals that had died from all sources of mortality except fishing (referred to as survival from natural mortality). The second was with the number of deaths equal to those censored (removed via fishing), and was referred to as survival from fishing mortality.

Program SURVIV estimates

Natural and fishing mortality were estimated from the telemetry data using a method described by Hightower et al. (2001) for striped bass. This method considers that for R_i animals released in the study site at time t, the expected number of animals surviving at time $t + 1$ (S_{t+1}) (here t is one week) is

$$S_{t+1} = R_t e^{-F_t - M_t} p_{t+1}$$

where F_t is the instantaneous fishing mortality during period t, M_t is the instantaneous natural mortality during period t, and p_{t+1} is the probability of relocating animals at time $t + 1$. The expected number of deaths of fish relocated at time $t + 1$ (D_{t+1}) is

Fig. 2. Monitoring histories of sharks (*Carcharhinus limbatus*) for (*a*) 1999, (*b*) 2000, and (*c*) 2001. Week one is the second week of May in each year. The fate of individuals is listed at the end of the animal history where S is survival (swam out of the study site), M is natural mortality, and R is removal (fished).

Table 1. Effect of release factors on time of mortality of neonate *Carcharhinus limbatus*.

Effect	Degrees of freedom	Wald statistic	p
Intercept	1	1.6277	0.2020
Size (fork length)	1	1.0502	0.3055
Handling time	1	0.4047	0.5247
Water temperature	1	0.7026	0.4019
Sex	1	1.0949	0.2954
Release condition	1	3.1892	0.0741
Sex * release condition	1	1.4137	0.2344

Note: Results of a generalized linear model with a binomial error distribution and a logit link function.

$$D_{t+1} = R_t M_t \frac{1 - e^{-F_t - M_t}}{F_t + M_t} p_{t+1}$$

Animals that survive to time $t + 1$ are then considered releases for the next time period and were added to new releases in that period.

Since the acoustic system used in the current study provided practically total coverage in the study site on a continuous basis we assumed that $p = 1$. Thus, unlike Hightower et al. (2001), it was not necessary to consider the possibility that an animal had died during one period, but was not detected until a few periods later. This made specification of the model simpler. The computer program SURVIV (White 1983) was used to estimate the model parameters (F_t and M_t). To arrange the monitoring history data into the appropriate form for input to SURVIV, it was first converted to a full-m array (a summary table of relocations for each release period) using the computer program RELEASE (Burnham et al. 1987). Each year of data was considered separately, with two different models run for each. The first model assumed that mortality rates were constant across all periods within a year, and the second allowed mortality rates to vary between time periods.

Results

A total of 92 *C. limbatus* were collected and fitted with transmitters over the course of three years. The sample size in 1999 was 18 (11 male, 7 female), in 2000 was 33 (20 male, 13 female), and in 2001 was 41 (14 male, 27 female). All individuals collected were neonates with open umbilical scars (mean total length 62 cm) and were monitored within the study site from 1 to 167 days. All sharks were assessed as being in condition 2 or 3 upon release. Owing to the need to resuscitate animals on board after surgery none could be classified as condition 1, but all sharks were swimming well at the time of release. Handling time for surgical procedures and revival ranged from 8 to 43 min with a mean of 14 min and a median of 13 min. One individual was revived, but would not swim, so this individual was revived longer than most (43 min) to ensure it swam away in good condition.

Monitoring histories were defined for all sharks in each year (Fig. 2). During the three years, 23 sharks (25.3%) were censored, or removed from the study site (5 in 1999, 7 in 2000, 11 in 2001). Eight tagged shark recaptures were reported (34.8% of censored animals) from local anglers during this period with five transmitters returned. Twenty-eight (30.8%) cases of natural mortality occurred during the course of the study (7 in 1999, 9 in 2000, and 12 in 2001). Five sharks died within 24 h of release, with at least two of these animals appearing to have been consumed by a predator (see below). These five individuals were excluded from mortality estimates since it is likely that their deaths were a direct result of the surgical procedure and (or) handling. Most natural mortalities occurred within the first month of the study (mean = 12 days) but there were two animals that died after 55 and 66 days at liberty. Forty-one (42.9%) sharks were observed to have swum out of the study site and were considered survivals (6 in 1999, 17 in 2000, and 18 in 2001). Logistic regression analysis showed no significant relationship between survival and shark size, sex, environmental variables, handling time, or release condition (Table 1).

Two individuals appeared to have been consumed by the same large predator a few hours after release. Both animals simultaneously exited the study site at a faster rate than normally exhibited by juvenile *C. limbatus*. The next day both sharks were recorded to return, swim to identical locations simultaneously, and rapidly leave together. Neither individual was recorded by the monitoring system after this time. This behavior is very uncharacteristic of the other juvenile *C. limbatus* monitored and suggests that both transmitters were recorded returning to the study site within the stomach of a predator. Great hammerhead (*Sphyrna mokarran*) and bull (*Carcharhinus leucas*) sharks have both been observed in Terra Ceia Bay and are potential predators on young *C. limbatus*.

Results of mortality estimates based on life history characteristics were calculated for *C. limbatus* (Table 2). Constant mortality estimates varied slightly between males and females, but were generally within the range of 0.35–0.45·year⁻¹. The age-specific mortality estimates from the Peterson and Wroblewski (1984) method declined from 0.30·year⁻¹ for newborn individuals to 0.14·year⁻¹ at maximum age (10 years).

Calculation of Kaplan-Meier survival estimates varied among years (Fig. 3). Survival estimates were lower for year 1 than those for years 2 and 3, probably owing to small sample sizes in year 1 (Table 3). Similarly, animals tagged early in year 2 had to be excluded because small sample sizes caused exaggerated mortality for that year. Natural mortality was greatest within the first 15 weeks of the study period in each year before leveling off at zero. Rates of fishing mortality also varied among years (Fig. 4), but appeared to be greatest early in the season (May–July). After this point, fishing mortality leveled off at zero for the remainder of the summer months. Pooling data from all years to estimate survival from natural mortality revealed that survival initially decreases, followed by a leveling off at approximately 0.5 (Fig. 5). Survival from fishing mortality also showed a decline early in the season, followed by a level period at a rate of approximately 0.5 (Fig. 5). The combined effects of fishing and natural mortality resulted in total mortality estimates ranging from 0.61 to 0.91 (Table 3).

Natural and fishing mortality rates were calculated by week based on the output of the program SURVIV (Fig. 6). Natural mortality estimates ranged from 0 to 0.69·week⁻¹ and fishing mortality estimates ranged from 0 to 0.79·week⁻¹, but both

Table 2. Methods used to calculate mortality rates (M, natural mortality; Z, total mortality) for *Carcharhinus limbatus* based on life history parameters.

Method	Relationship	Male	Female
Hoenig (1983) (fish)	$\ln(Z) = 1.46 - 1.01 \ln(t_{max})$	0.47	0.42
Hoenig (1983) (cetacean)	$\ln(Z) = 0.941 - 0.873 \ln(t_{max})$	0.38	0.34
Pauly (1980)	$\ln(M) = -0.0066 - 0.279 \log(L_\infty) + 0.6543 \log(K) + 0.4634 \log(T)$	0.46	0.35
Jensen (1996) (age)	$M = 1.65/x_m$	0.37	0.25
Jensen (1996) (growth)	$M = 1.5K$ (theoretical)	0.42	0.30
Jensen (1996) (Pauly)	$M = 1.6K$	0.44	0.32

Note: K, Brody growth coefficient (males = 0.276·year^{-1}, females = 0.197·year^{-1}); L_∞, maximum length (males = 166.5 cm, females = 195 cm); T, mean temperature (25°C); t_{max}, maximum age (males = 9 years, females = 10 years); x_m, age at maturity (males = 4.5 years, females = 6.5 years).

Fig. 3. Kaplan-Meier estimation of survival from natural mortality for juvenile *Carcharhinus limbatus* in Terra Ceia Bay during (*a*) 1999, (*b*) 2000, and (*c*) 2001. Dashed lines indicate 95% confidence intervals. All graphs use the second week of May as week 1.
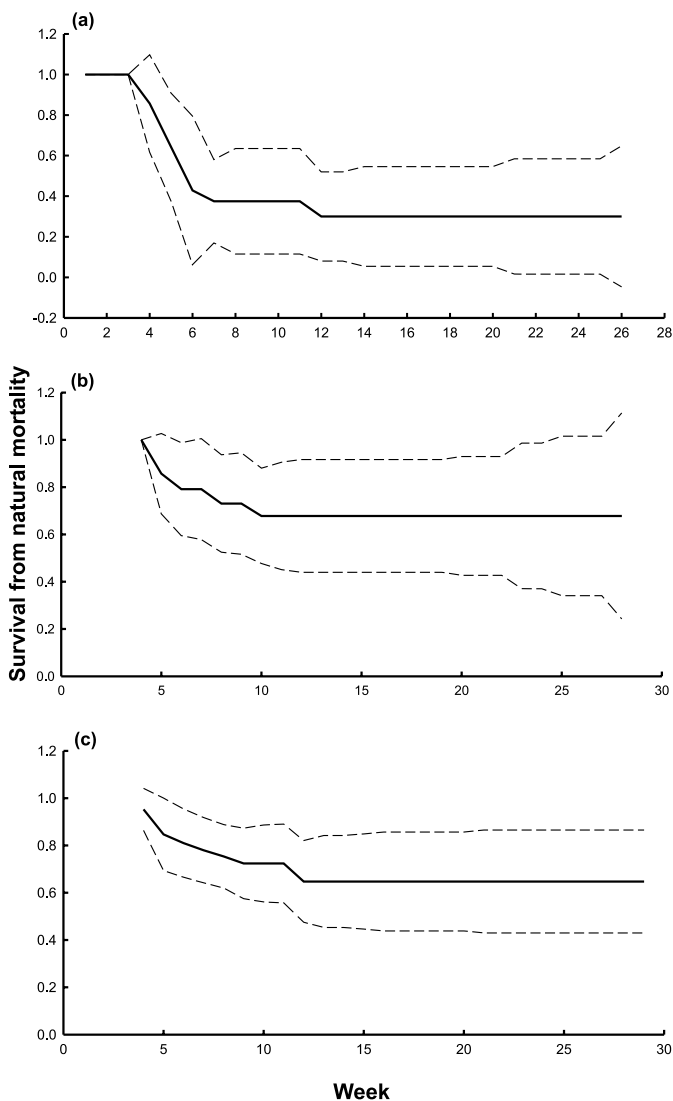
Discussion

Natural and fishing mortality rates of elasmobranch populations have traditionally been difficult to estimate and analyses have generally relied on life history parameters. However, results of the current study have gone beyond previously available methods to provide a temporally explicit definition of mortality in a population of juvenile sharks. There are few available data with which to compare mortality estimates for neonate *C. limbatus*. Manire and Gruber (1993) provided the most comparable data by conducting a census of a closed population of neonate lemon sharks (*Negaprion brevirostris*) in Bimini, Bahamas, for which they estimated that 44 to 61% of sharks die in the first year of life. The total mortality estimate for lemon sharks was lower than for neonate blacktip sharks, in part because there was little or no fishing mortality for the lemon shark population (Manire and Gruber 1993). The natural mortality estimate for neonate blacktip sharks for the period from May to November was similar to that for neonate lemon sharks for their entire first year. This suggests that the natural mortality of blacktip sharks in their first full year of life in Terra Ceia Bay is higher than for lemon sharks in Bimini, Bahamas.

Natural mortality estimates for other elasmobranch species have come mostly from indirect life history methods (e.g., Waring 1984; Smith and Abramson 1990; Cortes and Parsons 1996). These indirect methods have resulted in a range of estimates, from 0.14·year^{-1} for leopard sharks, *Triakis semifasciata* (Smith and Abramson 1990), to 0.35–0.70·year^{-1} for bonnethead sharks, *Sphyrna tiburo* (Cortes and Parsons 1996), and 0.56·year^{-1} for Australian sharpnose sharks, *Rhizoprionodon taylori* (Simpfendorfer 1999a). Applying similar life history methods to *C. limbatus* resulted in estimates of natural mortality lower than those from direct estimation methods. The technique of doubling natural mortality rates for the first year of life increased these mortality estimates but they are still lower than those estimated by direct methods (40–60% dying in the first year). The limitation of most life history methods is that it is necessary to assume that the mortality rate is constant across all year classes. Results of the current study clearly show that this assumption cannot be met within the first year of life and therefore is unlikely to hold for the duration of a lifetime. While the Peterson and Wroblewski (1984) method provided age-specific mortality estimates, this method also produced mortality estimates lower than direct methods.

The direct methods applied to *C. limbatus* in this study as-

were generally below 0.2·week^{-1}. While mortality rates varied among years, all years showed a consistent pattern where both natural and fishing mortality occurred within the first 15 weeks of the season (Fig. 6).

Table 3. Kaplan-Meier estimates of mortality for young of the year *Carcharhinus limbatus* based on natural, fishing, and total mortality rates.

	1999	2000	2001	Pooled data
Natural mortality	0.70 (0.032)	0.32 (0.049)	0.44 (0.011)	0.52 (0.010)
Fishing mortality	0.60 (0.048)	0.41 (0.047)	0.42 (0.012)	0.51 (0.010)
Total mortality	0.91 (0.004)	0.61 (0.031)	0.66 (0.006)	0.75 (0.003)

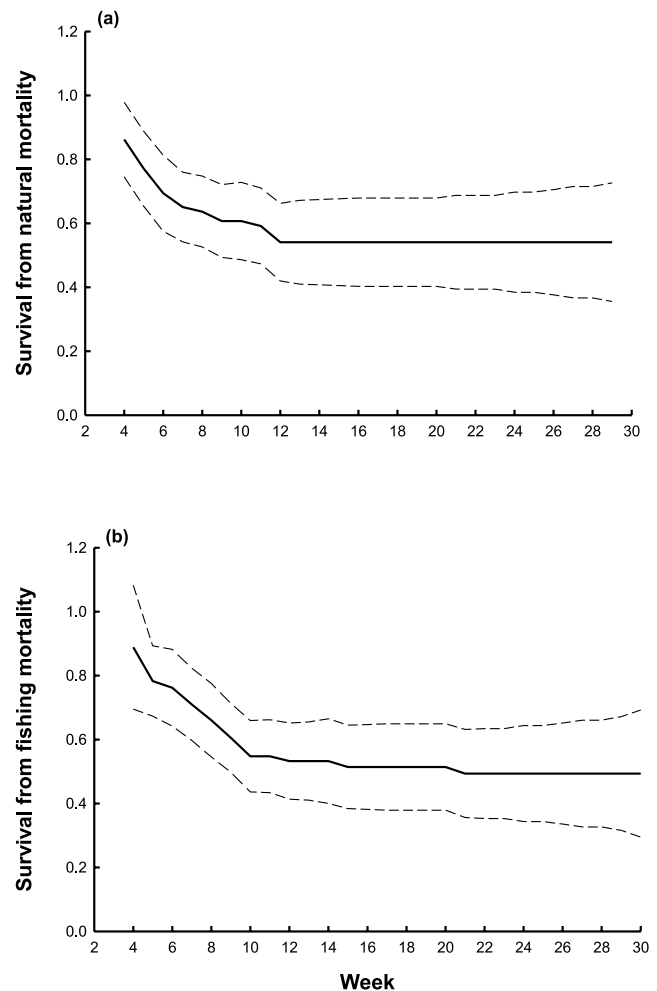**Note:** Values in parentheses are variance estimates.

Fig. 4. Kaplan-Meier estimation of survival from fishing mortality for juvenile *Carcharhinus limbatus* in Terra Ceia Bay during (*a*) 1999, (*b*) 2000, and (*c*) 2001. Dashed lines indicate 95% confidence intervals. All graphs use the second week of May as week 1.

Fig. 5. Kaplan-Meier estimates of survival from (*a*) natural mortality and (*b*) fishing mortality for juvenile *Carcharhinus limbatus* combined from all three years. Dashed lines indicate 95% confidence intervals. Graphs use the second week of May as week 1.
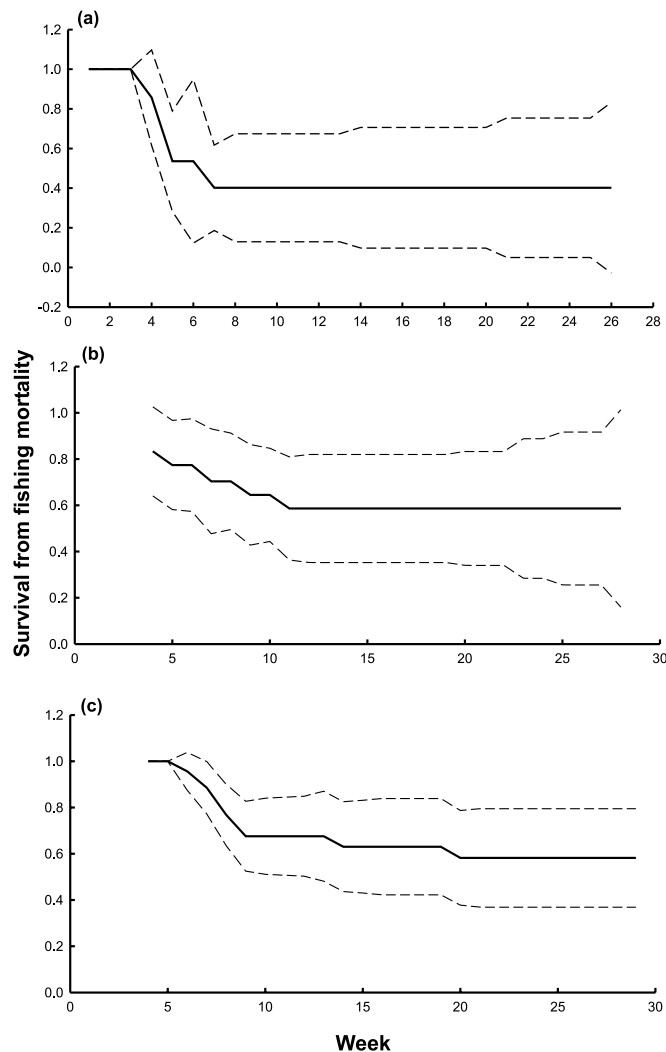
sume that all animals in the study have an equal chance of survival. The results of the generalized linear model for release factors showed no differences in survival between sex, size, and environmental conditions, suggesting that this assumption was met. However, it was not possible to determine if survival is different between tagged and untagged individuals.

Analysis of telemetry data in the present study provided the ability to directly estimate mortality for neonate *C. limbatus*. The Kaplan-Meier method estimated that over the course of a summer between 61 and 91% of neonates died, with all mor-

tality occurring prior to week 15. The upper end of this range was based on the fewest data and is likely to overestimate mortality, as deaths among a small number of animals released early in the season heavily weighted the estimates. SURVIV results provided estimates of weekly natural and fishing mortality rates that were generally less than 0.2·week^{-1} for the first 12 to 15 weeks in each year. However, these results are independent weekly estimates that are not directly comparable to Kaplan-Meier results. If the total mortality rates estimated by the SURVIV method are applied to a population equivalent to the total number of tags released in each year of the current study, a comparable estimate is obtained.

Fig. 6. Weekly estimates of instantaneous (*a*) natural mortality and (*b*) fishing mortality based on program SURVIV calculations for juvenile *Carcharhinus limbatus* during 1999 (solid line), 2000 (dotted line), and 2001 (dashed line). Graphs use the second week of May as week 1.
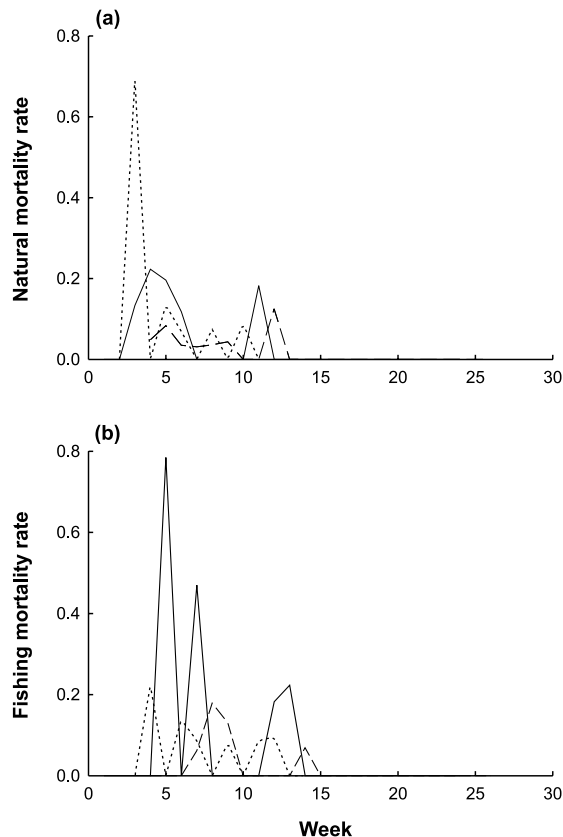
This technique resulted in an estimate where 62–92% of neonate *C. limbatus* died. This result is almost identical to that estimated by the Kaplan-Meier method. The agreement between these two models suggests that the calculated natural and fishing mortality estimates are accurate for the population within Terra Ceia Bay.

The magnitude of the mortality rates for *C. limbatus* in Terra Ceia Bay (61–91%) probably represents a conservative estimate. Terra Ceia Bay is part of an aquatic buffer preserve and does not suffer from high pollution loads. Although this area is not the most pristine estuary in Florida waters, it is a relatively healthy habitat with thick mangrove stands fringing most of the shoreline. As such, the bay represents a good model of continental nursery areas for blacktip sharks. In addition, predation levels appear to be relatively low, probably due to the semi-enclosed nature of the bay (M.R. Heupel, unpublished data). Comparison of the mortality estimates from Terra Ceia Bay to other nursery areas with lower environmental quality and (or) higher predation will provide an understanding of the range of mortality rates possible for young-of-the-year *C. limbatus*.

The results of the Kaplan-Meier and SURVIV methods at times estimated high levels of mortality in individual weeks. In all cases these were the result of animals dying or being removed while there were small numbers of tagged animals in the population. This occurred in both 1999 and 2000

when small numbers of animals were released over time, but did not occur in 2001 when relatively large numbers of animals were released over a short period. It is thus possible that mortality was overestimated in 1999 and 2000. Future studies employing this technique may wish to avoid the situation where estimates are based on small numbers of animals initially released.

The results of this study demonstrate that natural and fishing mortality of neonate *C. limbatus* in Terra Ceia Bay occurs in the first 12–15 weeks of life. If an animal survives this period, it has a high likelihood of surviving until leaving the nursery area in the fall. All of the animals released in the study were less than a month old, and many were only a few days old. Anecdotal evidence suggests that one cause of early mortality may be inexperience. When fishing within the study site early in the summer it was not uncommon to have several sharks around the boat within 5–15 min of putting bait in the water. Sharks were caught in quick succession with a new shark caught almost immediately upon release of the previous animal. This suggests that these young animals are hungry and will bite at any potential prey. This tendency has obvious consequences when considering fishing mortality and the number of sharks removed from the nursery early in the year. This is supported by the fact that during this study sharks became increasingly difficult to capture and by August were rarely captured, although monitoring data indicate that sharks were still present in the area. Another learning experience these young sharks had to contend with is predator avoidance. While fishing in the northern portion of Terra Ceia Bay in June 2001 a hammerhead (approximately 2 m in length) was observed chasing a juvenile *C. limbatus*. Although some of these observations are anecdotal, they are consistent with the results of the mortality estimation that suggests that if sharks can survive beyond 15 weeks they will have a good chance of surviving the rest of the summer. This 15-week period is obviously critical to the learning, development, and survival of these animals, even within what is defined as a protected nursery area.

Estimation of natural mortality within elasmobranch populations is a common problem that has limited efforts to define the dynamics of species and design appropriate fishery management plans (Cortes 1998). Previous authors have suggested that mortality rates for juvenile sharks are highest in the first year of life (e.g., Hoenig and Gruber 1990; Manire and Gruber 1993; Simpfendorfer 1999*b*). The results presented here support those conclusions. In fact, the first few months of life appear to be the most critical time for survival of neonate *C. limbatus* in Terra Ceia Bay. Therefore, the protection of nursery areas would be of significant value to animals in the first few months of life when mortality rates appear to be highest. The added impact of fishing pressure on this young portion of the population increases total mortality and future management plans may consider closing fishing for these young animals during the first few months of life.

Acknowledgements

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