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Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas

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Abstract The waters around Bimini (25° 43.70′ N, 79° 18.00′ W) provide an ideal nursery location for juvenile lemon sharks, *Negaprion brevirostris*, but this habitat is threatened by the development of a large resort. Since 1999 the North Sound (NS) has been subjected to intermittent periods of dredging, the most intensive of which was in March 2001. Possible effects from the development up to June 2006 were investigated by: comparing growth rates of juvenile lemon sharks in the NS, Sharkland (SL) and South Bimini (SB) nurseries between 1995-2005 using before-after, control-impact (BACI) analysis; analyzing survival of juvenile lemon sharks in the NS and SL between 1995–2006; and by comparing habitat structures in the NS and SB nurseries in 2003 and 2005. BACI analysis detected no statistically significant difference between the growth rates of juvenile lemon sharks in the three nurseries before and after the impact date of March 2001. However, a reduction in the survival rate of juvenile lemon sharks in the NS after March 2001 was statistically significant, including a 23.5% decline in first-year survival. Habitat structure of the NS in 2003 and 2005 also varied with the mean percentage cover of the seagrass *Thalassia testudinum* declining by 17.7% since 2003. Our results indicate a correlation between the development thus far and a decline in the survival rates of juvenile lemon sharks and changes in the habitat structure of the NS. To elucidate further

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information regarding potential effects of the resort development on juvenile lemon sharks in the NS nursery, we suggest several future research directions.

Keywords BACI analysis · Growth rate · Habitat structure · Lemon shark conservation · Survival rate

Introduction

Apex predators are useful indicator species with regards to environmental degradation and pollution, as species at higher trophic levels often bioaccumulate harmful substances (Fairey et al. 1997; de Pinho et al. 2002). These species can also exert strong top-down effects, and their removal can result in trophic cascades and the entire restructuring of ecosystems (Daskalov 2002; Myers et al. 2007). Within the shallow-water mangrove ecosystem of Bimini (25° 43.70′ N, 79° 18.00′ W, located on the north-western tip of the Great Bahama Bank), juvenile lemon sharks, *Negaprion brevirostris*, fulfill the apex predator role (Gruber 1982; Cortés 1999).

Lemon sharks are large coastal elasmobranchs that were once relatively abundant in the western Atlantic (Compagno 1984). Bimini provides a key nursery and essential fish habitat for this species, with adult females showing strong philopatry and returning annually to the islands for mating or parturition (Feldheim and Edrén 2002; Feldheim et al. 2002). The mean litter size produced is seven with a range of 4–18 (Feldheim and Edrén 2002), and juvenile survival rates have been estimated to be between 38% and 65% in the Bimini nurseries (Gruber et al. 2001). Neonate lemon sharks move into the mangrove habitat immediately after parturition, which for this life stage provides crucial shelter from predators such as larger conspecifics and great barracuda, *Sphyraena barracuda* (Franks 2007). They utilize the mangrove habitat almost exclusively until they reach a total length (TL) of around 85 cm, at which point they begin to venture onto the lagoon's seagrass flats and eventually out to the reefs (Morrissey and Gruber 1993; Franks 2007). With mean growth rates of juvenile lemon sharks in the Bimini nurseries varying from 6.2 cm year^{-1} (Barker et al. 2005) to 8.3 cm year^{-1} (Henningsen and Gruber 1985), this range expansion usually occurs at around 4–5 years of age (Franks 2007).

Since 1997, the construction of a large resort development (comprised of a 930-room hotel, 3,000 m^2 casino, 18-hole golf course and two large marinas) has been ongoing on North Bimini (Gruber and Parks 2002). Excavation of the seabed was initiated in 1999, with the most intensive dredging taking place in March 2001 (Gruber and Parks 2002). Dredging continued intermittently after this date, and by the end of 2006 approximately 750,000 m^3 of fill had been removed from the main lagoon, and approximately 0.8 ha or about 30% of the mangrove forest fringing the North Sound (NS) lagoon had been cleared.

As we have detailed data on the lemon shark populations of Bimini spanning two decades (including extensive environmental observations and ground-truthed Landsat images) and have also closely monitored the progress of the development (Gruber and Parks 2002), comparisons of some data pre and post-dredging can be made using before-after, control-impact (BACI) analysis. BACI analysis is a technique used to identify environmental impacts at a particular location (Underwood 1992, 1997). Data collected prior to a known environmental perturbation are compared with those collected after it, at both a control and an impact location. Growth rate data are suitable for this type of analysis (Guidetti 2001; Jacobson 2005), and the growth rate data available on juvenile lemon sharks around Bimini are from both control and putative impact locations making BACI analysis appropriate for this study.

The aim of this study was to identify potential effects from the resort development on populations of juvenile lemon sharks using three methods. The first method was a BACI analysis on the growth rates of juvenile lemon sharks in the NS, Sharkland (SL) and South Bimini (SB) nurseries before and after March 2001, as any changes in the growth rates of juveniles may indicate a broader change in the environment (Schindler et al. 2000; Gilliers et al. 2006). Secondly survival rates of juvenile sharks before and after March 2001 were analysed to determine if, following the period of intensive dredging, the survival rates differed from the earlier estimates of between 38% and 65% (Gruber et al. 2001). The third and final method used was a comparison of the habitat structure of the NS and SB nurseries in 2003 and 2005, focusing on the dominant seagrass *Thalassia testudinum*. Although work on the development began in 1997, this comparison was made to identify whether the continued dredging post-March 2001 and the increased mangrove removal in 2005 had altered the nursery habitats.

Materials and methods

Study sites

Three nurseries around Bimini were examined in this study: the NS, SL, and SB (Fig. 1). The NS is a shallow, semi-enclosed lagoon (0–2 m deep) with an area of approximately 3 km^2 (Jacobsen 1987; Newman 2003), situated at the northern tip of North Bimini. SL is an open area of mangrove fringed shoreline approximately 3 km in length and located just outside of the NS, with a similar depth. The SB nursery, which runs for almost the entire length of the southern coast of the island for approximately 4 km, differs from the NS and SL in that it is entirely open to the sea.

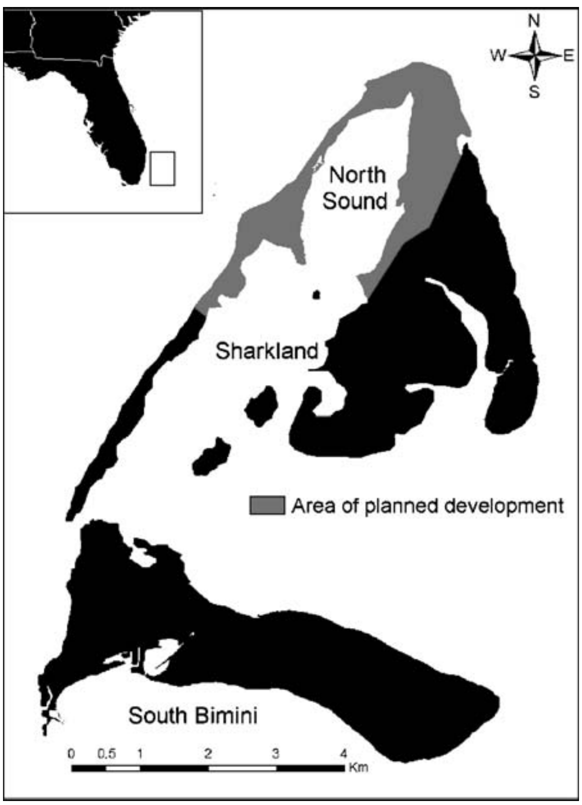

Fig. 1 Map of Bimini, showing the location of the three nurseries studied and the Bimini Bay Resort

Shark collecting

Tag-recapture is a method widely used in the study of fish biology and ecology, and has produced reliable estimates for growth (Simpfendorfer 2000) and survival rates (Gruber et al. 2001) of sharks. The tag–recapture method does not discriminate between natural mortality, anthropogenic-induced mortality or emigration however, which limits the inferences that can be made from the results. For the present study neonate and juvenile lemon sharks were captured using monofilament, 50 mm^2 mesh gill-nets 180 m long and 2 m deep. Between 1995 and 2005, a total of 721 gill-net sets (including those from an annual tagging project) were carried out in the three nurseries (NS, SL and SB). The gill-nets were set at different times of day (and at different times of year) for up to a 12 h period, generally on a rising or a falling tide. Three different length measurements of captured sharks were taken to the nearest mm: pre-caudal length (PCL), fork length and TL. For a more detailed description of the basic shark collecting techniques employed in this study, see Henningsen and Gruber (1985), Manire and Gruber (1991), Gruber et al. (2001) or Barker et al. (2005).

The shark collecting techniques employed for the annual tagging project undertaken in the NS and SL between 1995 and 2006 differed slightly from the basic shark collecting techniques described above. For the annual tagging project, the gill-netting campaign was always conducted from late May to mid June. Three nets were set simultaneously for a 12 h period over six nights in one nursery before moving on to the other, to ensure that fishing effort remained constant throughout the multi-year study (36 gill-nets set per year).

BACI analysis on growth rates

For the present BACI analysis, the NS and SL were selected as the putative impact locations due to their proximity to the development. The SB nursery formed the control location as it was located approximately 6 km from the impact sites, thereby avoiding any direct impacts from the development. The impact date was set at March 2001, coinciding with the date of the most intensive dredging period. Daily growth rates of each shark were calculated and then extrapolated to give an estimation of the annual growth rate following DiBattista et al. (2007). Juvenile lemon sharks were classified as individuals with a PCL of <85 cm. Once the sharks reach this length they start to extend their home-range outside of the mangroves and potentially into other nurseries (Franks 2007).

Survival analysis

Differences in survival of juvenile lemon sharks were analysed before (1995–2000) and after (2001–2006) major dredging occurred, using data from the annual tagging projects in the NS and SL nurseries. Neonates were identified either by open umbilical scars (1997-2006) or by PCL (1995–1996); neonate lemon sharks have a PCL of between 40–53 cm (Gruber et al. 2001). We calculated the minimum number of years alive for each shark which was initially captured as a neonate (years from initial capture to final capture). We omitted sharks for 2001–2006 whose capture dates fell before 2001 and cut off shark ages at 2000 for 1995–2000, eliminating data overlap between the two time periods. An uncensored survival regression analysis on these age estimates was then conducted to test for a relative difference in survival between the two time periods. We blocked for the effect of the year of initial capture (controlling for the expectation that sharks caught earlier in each time period can be expected to have longer capture histories) and tested for effects of sex and location. We used a Gaussian error distribution, which fit the data better than the exponential, extreme or Weibull distributions (lowest Akaike's Information Criterion). Uncensored survival analysis assumes that sharks not recaptured were dead, rather than alive but unobserved or permanently emigrated, though these assumptions are not necessary to test for relative differences in survival/emigration. In any event these assumptions seem to hold for our dataset, with recapture rates for approaching 99% (Gruber et al. 2001) and no apparent permanent migration between the two nurseries (Gruber et al. 1988; Morrissey and Gruber 1993; Gruber et al. 2001; DiBattista et al. 2007; Franks 2007).

Habitat sampling

To compare habitat structure, ten sites in the NS nursery and ten sites in the SB nursery were randomly selected and sampled in 2003 and 2005. Sample sites were identified using Wide Area Augmentation System–Global Positioning System (Garmin Inc.) co-ordinates. For the sampling procedure, a 1×1 m quadrat was randomly placed over the substrate at the specified location. The percentage cover of *T. testudinum*, *H. wrightii*, *Batophora* sp., *Laurencia* sp., leaf litter and bare substrate within the quadrat were recorded. Four quadrats were carried out at each location, giving a total of 80 quadrat surveys for the NS and SB (40 in each nursery).

Experimental design and statistical analyses

A 2×3 factorial design was used for the BACI analysis (before or after March 2001 crossed with nursery) and a 2×2 factorial design was used for the habitat structure analysis (year crossed with nursery). Two-way analyses of variance (ANOVA) followed by Bonferroni post-hoc tests were used to test for statistical significance in the BACI analysis, and two-way ANOVA followed by Holm–Sidak post-hoc tests were used for the habitat structure analyses. Statistical significance of survival was analysed using χ^2 tests. Normality of all the data was tested for using the Kolomogorov–Smirnov test. If data failed to fit the normal distribution, they were $\log_{10}(N+1)$ transformed and tested again for normality using the Kolmogorov–Smirnov test. BACI and habitat structure analyses were carried out using SigmaStat 3.0 (SPSS Inc.), and the survival analysis was carried out using package Survreg in R 2.6 (R Development Core Team 2007).

Results

BACI analysis

A total of 1,034 annual growth rate calculations were obtained from juvenile lemon sharks collected between 1995 and 2005. Of these 1,034 calculations, 485 were from the NS, 367 were from SL and 182 were from SB. 437 of these estimations predated March 2001 and 597 were from after this date. Table 1 shows the growth rates for juveniles in all three nurseries. We found considerable individual and inter-annual variation in the data. In the NS, the mean PCL growth rate decreased from 6.4 to 6.3 cm year^{-1} after March 2001, while in SL the growth rate decreased from 7.7 to 6.3 cm year^{-1}. The growth rate of juveniles in SB remained constant at 8.7 cm year^{-1} before and after March 2001.

Table 1 Mean growth rates in centimeter (±1SE) each year for different nurseries

Year	Nursery		
	NS—major dredging	SL—major dredging	SB—control
1996	4.82±0.43 (23)	8.93±0.60 (24)	5.61±2.57 (2)
1997	4.62±0.35 (33)	6.84±0.52 (26)	9.03±1.59 (7)
1998	4.86±0.31 (38)	7.75±0.38 (51)	8.58±0.69 (4)
1999	7.44±0.54 (28)	8.53±0.41 (34)	13.06±0.56 (2)
2000	7.71±0.60 (99)	6.82±0.34 (43)	8.52±0.87 (20)
Major dredging			
2001	7.48±0.47 (101)	5.40±0.31 (45)	7.71±0.80 (42)
2002	3.88±0.42 (55)	6.82±0.50 (27)	6.88±0.93 (36)
2003	6.85±0.55 (45)	7.17±0.40 (42)	9.54±1.14 (25)
2004	5.95±0.76 (31)	6.54±0.33 (39)	10.67±1.13 (26)
2005	6.06±0.46 (32)	5.60±0.36 (36)	10.72±1.27 (18)

Number of sharks in parentheses

Statistical significance was only found for the growth rates (cm per year) of juveniles between nurseries (two-way ANOVA $F_{2,\ 29}$=9.1, P<0.001). Growth rates did not differ significantly before and after the impact ($F_{1,\ 29}$=0.4, P>0.05) and the interaction term between nursery and before/after impact was also non-significant ($F_{2,\ 29}$=0.8, P>0.05).

Survival analysis

Between 1995 and 2006, 955 juvenile lemon sharks were caught and tagged (450 between 1995 and 2000, and 505 between 2001 and 2006). Survival was significantly lower in the 2001–2006 time period (Table 2), driven by a decrease in survival at the NS, where juveniles had consistently lower survival rates after March 2001 (Fig. 2). For example, first-year survival in the NS decreased from 60.6% before March 2001 to 37.1% after, representing a 23.5% decline. Second-year survival of juveniles in the NS experienced a similar decrease, falling from 45.4% before March 2001 to 21.4% after. However, there was also a significant interaction between location and time period, showing that the change in survival was not consistent between nurseries (Table 2). In contrast to the NS, SL showed no apparent change in survival after March 2001 (Fig. 2). There was no main effect of location or sex and no other statistically significant interactions between any of the four variables (all P>0.2).

Table 2 Results from survival analysis χ^2 tests

Variable	*df*	χ^2	*P*
Nursery	1	0.0	0.914 n.s.
Sex	1	1.0	0.313 n.s.
Year	5	287.3	0.000***
Impact	1	14.7	0.000***
Nursery × impact	1	5.9	0.015*

df Degrees of freedom; *n.s.* Not significant

*P<0.05; **P<0.01; ***P<0.001

Habitat sampling

Two-way ANOVA found a statistically significant difference for *T. testudinum* coverage between nurseries ($F_{1,\ 39}$=4.6, P<0.05), but no significance was found for the year ($F_{1,\ 39}$=0.8, P>0.05) or the interaction term between year and nursery ($F_{1,\ 39}$= 0.7, P>0.05). Between 2003 and 2005, the percentage cover of *T. testudinum* in the NS decreased by 17.7% (Fig. 3). At the sample site closest to the dredging and recent mangrove removal in the NS, the percentage cover of *T. testudinum* had decreased by 46.5% since 2003—a highly significant decline (one-way ANOVA $F_{1,\ 7}$=72.2, P<0.001). The percentage cover of bare substrate increased by 20.6% between 2003 and 2005, and the percentage cover of *Halodule wrightii* and *Laurencia* sp. showed smaller increases between 2003 and 2005 (3.2% and 2.8% respectively). In contrast the percentage cover of *T. testudinum* in the SB nursery varied little between 2003 and 2005 with a reduction of 0.1% (Fig. 4). Small reductions in percentage cover were also recorded for *H. wrightii* (1.5%), *Batophora* sp. (2.5%), *Laurencia* sp. (0.8%) and leaf litter (1.2%).

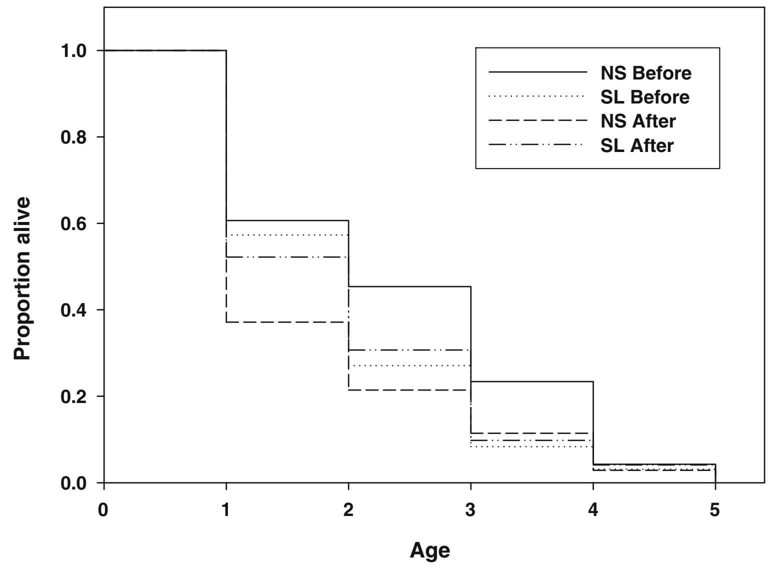

Fig. 2 Graph showing the proportion of surviving juvenile lemon sharks from age 0 to age 5 before and after March 2001 in the NS and SL

Discussion

Since March 2001 there has been a statistically significant reduction in the survival rates of juvenile lemon sharks in North Bimini, which correlates with the increased dredging activity. Possible explanations for reduced survival rates include liberation of toxins and bound nutrients into the water column (Parsons 2004), and increased intraspecific and interspecific competition for limited resources as the habitat became degraded. It is also possible that other factors such as increased predation or emigration may have

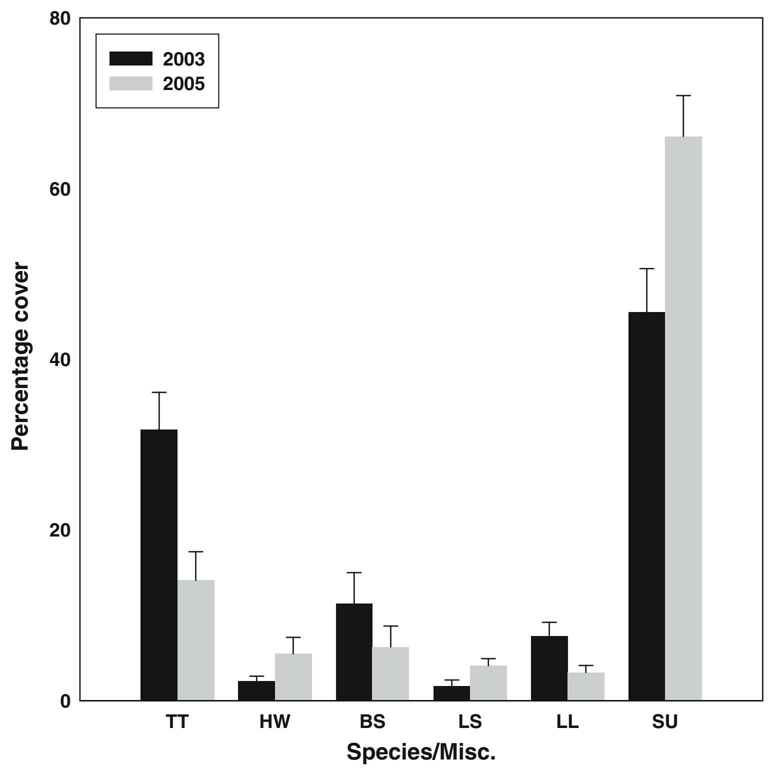

Fig. 3 The percentage cover of different seagrass and algae species (also leaf litter and bare substrate) in the NS in 2003 and 2005, with *error bars* indicating ±1SE (TT = *T. testudinum*; HW = *H. wrightii*; BS = *Batophora* sp.; LS = *Laurencia* sp.; LL = leaf litter; SU = substrate)

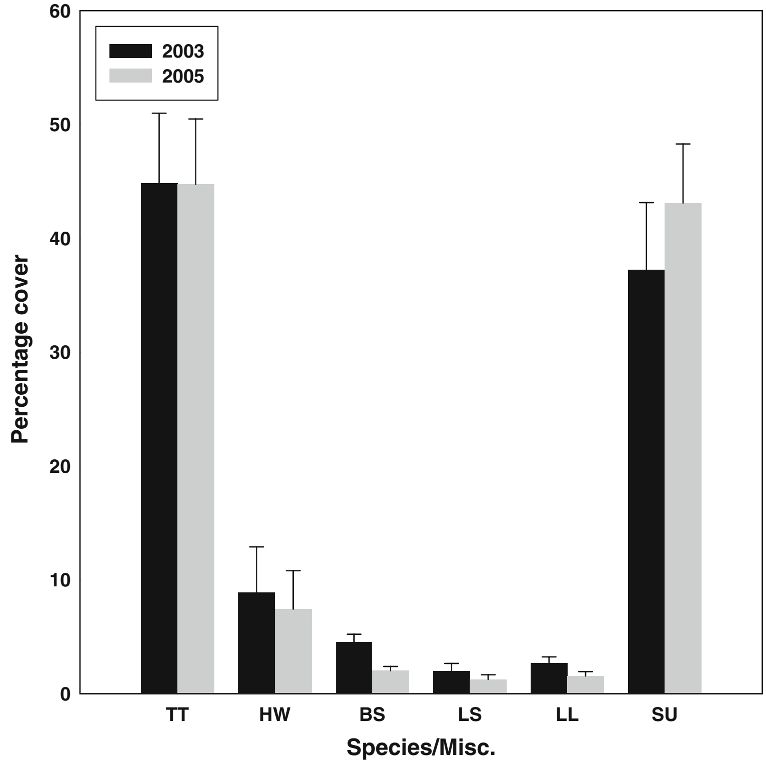

Fig. 4 The percentage cover of different seagrass and algae species (also leaf litter and bare substrate) in the SB nursery in 2003 and 2005, with *error bars* indicating ±1SE (see Fig. 3 for abbreviations)

been responsible for the reduction found. However, it is unlikely that increased emigration was responsible as a recent spatial ecology study found no permanent migration of juveniles between the NS and SL, and no migration at all between those two nurseries and SB (Franks 2007). Several other studies have also found similar results with respect to migration between Bimini nurseries (Gruber et al. 1988; Morrissey and Gruber 1993; Gruber et al. 2001; DiBattista et al. 2007).

Between 2003 and 2005, the SB habitat exhibited little sign of change, while over the same period statistically significant changes in the habitat structure occurred in the NS. Although juvenile lemon sharks generally avoid seagrass beds (Morrissey and Gruber 1993), the decrease in *T. testudinum* habitat may result in a reduction in the abundance of their main prey species, the yellowfin mojarra, *Gerres cireneus* (Newman 2003). The correlation of reduced seagrass cover with increased anthropogenic development is consistent with observations made by Sealey (2004) at other coastal sites in the Bahamas. As relatively large predatory fish may take several decades to recover from large declines in population size (Russ and Alcala 2004), these effects could result in a long-term reduction of the carrying capacity of the NS for the juvenile lemon sharks.

BACI analysis showed no significant difference between growth rates of juvenile lemon sharks before and after the dredging in 2001. However, sharks in general and the juvenile lemon shark in particular can have extremely variable growth rates (Lombardi-Carlson et al. 2003; Barker et al. 2005; Goldman and Musick 2006), and accurately measuring length to mm can be difficult to achieve consistently. The analysis was also constrained by small *n* for some years in the SB nursery.

The extent of mangrove habitat around Bimini makes the islands one of the most important lemon shark nurseries in the north-west Bahamas. Removing the mangroves around the NS may lead to juvenile lemon sharks experiencing increased exposure to predators, as well as reducing the habitat for their prey species. The abundance of prey has been shown to affect the distribution of predatory sharks in coastal ecosystems (Heithaus et al. 2002; Torres et al. 2006), and thus a reduction in prey habitat and abundance may also displace juvenile lemon sharks from the NS. In addition to the importance of mangroves, juvenile lemon sharks preferentially select shallower, warmer areas of the lagoon to inhabit (Morrissey and Gruber 1993). It is unlikely that the development currently planned will have an effect on water temperatures within the NS, but if the entrance to the lagoon was further restricted then more extreme temperatures could be observed. Any future dredging taking place within the NS would obviously alter depth levels too, creating deep channels and reducing the amount of suitable shallow, warm-water habitat for juvenile lemon sharks.

Summary

In conclusion, a decrease in the survival of juvenile lemon sharks in the NS and a reduction in the percentage cover of seagrass in the NS, were correlated with increased dredging activity. To elucidate further information regarding potential effects of the resort development on juvenile lemon sharks in the NS nursery we recommend: (1) implementing further research to investigate the habitat use of juvenile lemon sharks in the NS post-mangrove removal—such investigations should assess if their spatial ecology has changed and these data will provide a base-line to compare with future potential impacts; (2) expanding toxicological studies on the sharks and their environment to determine possible causes for altered trends and behaviour observed over recent years; (3) executing a systematic annual tagging project in the SB nursery in a manner similar to those in the NS and SL, to allow for more appropriate growth rate comparisons; (4) monitoring lemon shark demography around Bimini for at least another decade—as the sharks in the current study were juveniles, the full effects of the development may not be seen until those sharks reach maturity.

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