SHORT COMMUNICATION

The conservation implications of spatial and temporal variability in the diurnal use of Bahamian tidal mangrove creeks by transient predatory fishes

ALASTAIR R. HARBORNEa,*, BRENDAN TALWARb and EDWARD J. BROOKSB

aMarine Spatial Ecology Laboratory and Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, Brisbane, Australia
bShark Research and Conservation Program, Cape Eleuthera Institute, Eleuthera, The Bahamas

ABSTRACT

1. Mangrove creeks have a range of functional roles in tropical seascapes, but their use as feeding and refuge areas for commercially and ecologically important transient predators is poorly understood.

2. This study used video cameras to investigate the diurnal use of three Bahamian mangrove creeks by transient predators during a 2-month period. More than 500 fishes from 10 species were recorded, including elasmobranchs, reef-associated fishes, and nearshore specialists. A multivariate analysis indicated that movement of the transient predator assemblage was not significantly linked to any abiotic variable and did not vary among creeks.

3. Generalized linear mixed-effects models of the four most abundant transient predators demonstrated species-specific variations in creek use. Sightings of Caranx ruber and Negaprion brevirostris varied significantly among the three creeks. Furthermore, C. ruber was seen most frequently close to high tide, while N. brevirostris was seen more frequently with increasing time since sunrise and during higher tidal ranges. Sphyraena barracuda and Tylosurus crocodilus were seen most frequently just after low tide. All three creeks appear to be functionally important for transient predators, but these species exhibit considerable spatio-temporal variability in how they use this habitat.

4. Mangrove creeks are threatened by a range of anthropogenic stressors, and are frequently a target of conservation initiatives. The species-specific spatial variability in creek use demonstrates that simply including representative creeks in marine protected areas could exclude functionally important areas. Furthermore, development that alters tidal cycles in creeks is likely to have significant impacts on transient predators, and underscores the need for restoration and conservation of hydrological flow.

Received 20 January 2014; Revised 01 September 2014; Accepted 1 October 2014

KEY WORDS: coral reef; barracuda; generalized linear models; habitat fragmentation; lemon shark; The Bahamas; video surveys

*Correspondence to: A.R. Harborne, School of Biological Sciences, Goddard Building, The University of Queensland, Brisbane, QLD 4072, Australia. E-mail: a.harborne@uq.edu.au
INTRODUCTION

Caribbean mangroves, along with adjacent soft-bottom habitats, are recognized as important nurseries for a range of fish species (Mumby et al., 2004). Typically, research on the nursery function of tidal mangrove creeks has focused on their use by juvenile fishes, and how the presence of nursery habitats alters fish assemblages on nearby reefs (Eggleston, 1995; Nagelkerken et al., 2000; Mumby et al., 2004). In contrast, there are limited data on larger, transient species that may be predators of these juvenile fishes. These species, subsequently referred to as ‘transient predators’ move into mangrove areas on rising tides to feed and find refuge from their own predators, but leave these areas at low tide when the water is too shallow (Valentine-Rose and Layman, 2011). This lack of data for transient predators is surprising given that many of these species are ecologically and commercially important. A key role of nursery habitats is providing a refuge from predators (Beck et al., 2001), and transient predators may be important piscivores in mangrove creeks and contribute to prey mortality often being closely correlated with increasing water depth (Rypel et al., 2007). Consequently, a better understanding of the behaviour of transient predators is critical for assessing whether mangrove creeks increase the survival of juvenile fishes, which, as previously stated, is a key functional role of nursery habitats (Beck et al., 2001). In addition, transient fishes provide an important trophic linkage between estuarine areas and the nearshore marine environment (Deegan, 1993).

Individual transient species in tidal creeks, such as Sphyraena barracuda and Albula spp., also have significant non-extractive commercial value to sport fishers and divers, and use mangrove habitats as both a nursery and adult feeding area (Danylchuk et al., 2007; O’Toole et al., 2011). However, because the foraging behaviour of many transient species is poorly known, managers have a limited understanding of how to protect this commercial value. A notable exception to the lack of knowledge about transient predators is Negaprion brevirostris, which exemplifies many of the reasons why predators use mangrove creeks. Negaprion brevirostris uses mangrove creeks as a nursery and refuge because juvenile sharks are at risk from cannibalistic feeding by larger animals (Guttridge et al., 2012). Consequently N. brevirostris juveniles have a high fidelity towards shallow, mangrove-fringed habitats at high tide because these areas are inaccessible to larger sub-adults (Guttridge et al., 2012). However, while avoiding predators of their own, juvenile N. brevirostris use mangrove creeks to find their preferred fish prey (Newman et al., 2012). Finally, shallow water is often significantly warmer than deeper areas, so movements into mangrove creeks may have some metabolic benefits for sharks (Hight and Lowe, 2007).

This study aimed to provide further insights into the identity of diurnal transient predators entering mangrove creeks, and how their use of this habitat is affected by water depth, flow rate, tidal range, and time of day. Such an understanding of the factors affecting the movement of transient predators in creeks is critical for predicting the impacts of anthropogenic disturbance. Mangroves are threatened by a range of human activities, which has led to rates of loss that are comparable with terrestrial tropical forests (2.1% per year, Valiela et al., 2001). Additional evidence of the functional role provided by mangroves strengthens the justification for their conservation. Furthermore, the functioning of mangrove creeks is threatened by fragmentation, such as that caused by road building, which reduces species density, the abundance of marine species, and the secondary production of commercially important fishes, and may destabilize remnant food webs by homogenizing energy flow pathways to top predators (Layman et al., 2004, 2007; Valentine-Rose et al., 2007). Increased knowledge of the factors influencing the ecology of transient predators would assist predicting the effects of fragmentation and reduced hydrologic connectivity (sensu Pringle, 2001), and planning effective restoration.

By studying three adjacent creeks in the same biophysical environment, this study also aimed to assess the degree of intra-habitat variability in creek use by transient predators. Mangrove stands are frequently highlighted as important conservation targets, and their inclusion in initiatives such as marine protected areas is often recommended (Roberts et al., 2003). However, like most habitats within a seascape, mangroves exhibit significant...
intra-habitat variability in the fish assemblages that they support (Faunce and Serafy, 2008; Harborne et al., 2008). Such variability is problematic to coastal managers: if all mangroves are considered equal, it is possible that the amount of essential fish habitat will be overestimated and protected areas may be sited ineffectively (Faunce and Serafy, 2008). By quantifying variability in creek use by transient predators, this study aimed to demonstrate an additional component of intra-habitat variability that should be considered during conservation planning.

**METHODS**

**Study sites**

Data were collected from three tidal mangrove creeks (Page, Kemps, and Broad) within 4 km of each other in Cape Eleuthera, The Bahamas (Figure 1). Each creek contains extensive tracts of *Rhizophora mangle*, and the benthos is a mosaic of hardbottom, seagrass, and sand. The creeks vary in their geomorphology. Page Creek is ~25 m wide at the mouth, and then narrows to <10 m wide before opening out into a large area of mangroves and soft-sediment habitats that are extremely shallow at low tide (subsequently referred to as ‘wetlands’). The Page Creek system is separated from Kemps Creek by a roadway. The entrance to Kemps Creek is ~60 m wide at the mouth, and then immediately opens out into a large area of wetland divided by numerous branches of the creek. Broad Creek has two entrances: a western entrance that is ~180 m wide and an eastern entrance that is ~90 m wide and is divided into two parts by small rocky islands. Broad Creek is a large area of wetlands with the creek continuing in an easterly direction. The area has a semi-diurnal tidal regime with a maximum range of ~80 cm (Murchie et al., 2010).

**Data collection**

Fish entering the creeks were recorded diurnally using GoPro video cameras in September and October 2012. Using video cameras has a number of benefits over visual surveys, including not scaring fish in shallow water, a permanent record of each fish seen, and the ability to simultaneously collect data for multiple hours at multiple locations. The mouth of Page Creek was monitored by a single video camera, but two cameras (with non-overlapping fields of view) were required at Kemps and Broad Creeks. Only the eastern mouth of Broad Creek was monitored because it is functionally more important; fish cannot enter or exit the wetland area from the western entrance around low tide because of an aerially exposed sand bar. Cameras started recording within 3 h after low tide on nine different days during the study period in order to record fish entering the creeks as they flooded, and typically ran for approximately 4 h (mean = 244 min, SD = 43 min). Because of the duration of the study and starting cameras around low tide, data were automatically collected at different times of day. All transient predators entering the creeks were identified from the video and each record was associated with the time of day, which was subsequently used to calculate the time since the previous low tide (a proxy for water depth). The life phase of *N. brevirostris* (either juveniles <1 m or larger sub-adults, Guttridge et al., 2012) and size class (<30 cm, 30–60 cm, or >60 cm) of each *S. barracuda* were also estimated, but quantifiable size differences could not be ascertained for any other species.

**Data analysis**

For each daily camera deployment, individual fish counts were combined to calculate the number of fish per species entering each creek during each hour surveyed after low tide (subsequently ‘time segment’; first time segment = from low tide to 1 h post-low tide, second time segment = from 1 to 2 h post-low tide and so on). Each hour-long segment was associated with a time since sunrise by calculating the time from sunrise to the mid-point of each time segment (i.e. from sunrise to 30 mins after low tide for the time segment representing 1 h post-low tide). Time segments were only included in the data set if the camera captured >30 min of the 1 h period, and the number of fish per time segment was standardized as the number of fish per min. These abundance per min data were first used to assess whether there was any
evidence of the transient predator assemblage varying among creeks or being significantly influenced by abiotic factors. This assessment used a permutational multivariate analysis of variance carried out in the PERMANOVA package in PRIMER 6 (Anderson, 2001), with a Type I model following log transformation of the data to downweight the influence of the most abundant species and using Euclidean distance as the resemblance measure in order to include joint absences of fishes. Explanatory variables were creek identity (categorical), and the continuous variables hours since low tide, minutes since sunrise, and the published low-tide depth during each tidal cycle. This latter variable was included to examine whether larger tidal cycles affected creek use by fishes. Finally, a quadratic term for the number of hours since low tide was included to examine the effects of tidal flow as opposed to water depth: water depth increases continually from low to high tidal states, but flow is highest midway through the tidal cycle. Since data from individual time segments were nested within daily camera deployments (i.e. each day’s camera deployment generated data for multiple time segments), a random variable representing camera deployment was included within the analysis.

Univariate, species-specific analyses were then conducted. For even the most common transient species, fishes were recorded during less than 45% of the time segments, leading to left-skewed data distributions. Therefore, the data were transformed...
from number of fish seen per minute to presence/absence per time segment and analysed using generalized linear models with binomial error structures and the logit link function. The explanatory variables were the same as for the multivariate analysis, including the random variable for camera deployment. Therefore, generalized linear mixed-effects models were performed using the lme4 package (Bates et al., 2014) in R (R Development Core Team, 2008). Models were fitted using the procedure outlined by Crawley (2007). Briefly, a maximal model was fitted including all factors, and then least significant terms were removed in turn. After each term was removed, models were compared to ensure that term removal did not lead to a significant increase in deviance or an increase in AIC. Terms were removed until the model contained only significant terms or removal of any non-significant terms caused a significant increase in deviance or AIC (minimal adequate model).

RESULTS

In total, 13 camera deployments were conducted, consisting of five in Page Creek, four in Kemps Creek, and four in Broad Creek (details of deployments in Supplementary Material). These deployments represented 55 one-hour time segments. Video footage from these time segments recorded 10 species that were categorized as transient creek visitors (502 individuals; 245, 166, and 91 in Page, Kemps, and Broad Creeks, respectively). These species were: Aetobatus narinari (five individuals seen; mean of 0.002 fish per min across all 55 time segments; seen in 3.6% of time segments), Albula vulpes (20; 0.006; 5.5%), Caranx ruber (108; 0.034; 38.2%), Carcharhinus limbatus (3; 0.001; 5.5%), Ginglymostoma cirratum (3; 0.001; 5.5%), Mugil spp. (155; 0.047; 9.1%), N. brevirostris (38; 0.014; 27.3%), Ocyurus chrysurus (40; 0.013; 10.9), S. barracuda (71; 0.025; 43.6%; <30cm =40; 0.013; 25.5%; 30–60 cm =23; 0.007; 23.6%; >60 cm =8; 0.003; 9.1%), and Tylosurus crocodilus (59; 0.021; 38.2%). Sphyraena barracuda and T. crocodilus were seen in all three creeks, N. brevirostris was not seen in Kemps Creek, C. limbatus and C. ruber were not seen in Page Creek, and A. vulpes was not seen in Broad Creek. Mugil spp. were seen only in Page Creek, A. narinari and G. cirratum were seen only in Kemps Creek, and O. chrysurus was seen only in Broad Creek.

None of the fixed factors were significant (P > 0.075) in the PERMANOVA model, indicating that the transient predator assemblage did not vary systematically among creeks or was responding to any of the abiotic explanatory variables (full model results provided in the Supplementary material). Of the 10 transient species, only four were sufficiently abundant (seen in >25% of time segments) for detailed analyses (Table 1, Figure 2, Supplementary material). Two size classes (<30 cm and 30–60 cm) of S. barracuda were also sufficiently abundant for detailed analyses (seen in >20% of time segments; Table 1). The timings of the visits by all four species were correlated with at least one of the abiotic variables, and the frequency of visits by two of the species also varied among creeks. Caranx ruber was seen significantly more frequently in Kemps Creek than Broad Creek, and was absent from Page Creek (which precluded obtaining a statistical significance). This species was also seen increasingly more frequently as the tidal cycle approached high tide, meaning water depth in the creek mouth was at its highest (Figure 2(a)). The majority of N. brevirostris individuals seen were juveniles (only one sub-adult was observed), and were more abundant in Page Creek than Broad Creek, with no individuals recorded in the mouth of Kemps Creek. Negaprion brevirostris was seen more frequently later in the day (Figure 2(b)), and was more abundant during tidal cycles with a shallower low tide (larger total range). There was no difference in the frequency of sightings of either S. barracuda or T. crocodilus among creeks, but both were seen more frequently just after low tide. The frequency of sightings then decreased linearly with time after low tide as depth in the creek mouths increased (Figure 2(c), (d)). Models for small (<30 cm) and medium-sized (30–60 cm) S. barracuda were qualitatively similar to the model for all individuals combined (Table 1).
DISCUSSION

This study demonstrated that transient predators using the mangrove creeks of Cape Eleuthera include sharks, rays, reef-associated fishes, and nearshore specialists, although the data cannot explain whether foraging, predator refuge, or some other use is the predominant reason why transient species enter this habitat. Within this assemblage, four species were particularly common and their use of the creeks demonstrated that the drivers of habitat use were species specific. *Sphyraena barracuda* and *T. crocodilus* were most frequently seen just after low tide, and appeared to be...

Table 1. Minimal adequate generalized linear mixed-effects models (fixed effects only) for the presence/absence of the most frequently observed fishes transiently visiting the study creeks. Analyses for *Sphyraena barracuda* were conducted for all individuals and two size classes. Values are model coefficients with P-values in parentheses. ns: non-significant term (P > 0.05). Hour = number of hours since low tide. Hour$^2$ = quadratic term for number of hours since low tide. Removal of non-significant terms led to a significant increase in model deviance and AIC.

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>Caranx ruber</em></th>
<th><em>Negaprion brevirostris</em></th>
<th><em>Sphyraena barracuda</em></th>
<th><em>Tylosurus crocodilus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.906 (0.392)</td>
<td>3.564 (0.263)</td>
<td>1.810 (0.035)</td>
<td>5.535 (0.001)</td>
</tr>
<tr>
<td>Creek</td>
<td>Kemps &gt; Broad (0.012)$^a$</td>
<td>Page &gt; Broad (0.003)$^b$</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Hour</td>
<td>0.581 (0.041)</td>
<td>ns</td>
<td>-0.576 (0.011)</td>
<td>-1.821 (&lt;0.001)</td>
</tr>
<tr>
<td>Hour$^2$</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Time since sunrise</td>
<td>ns</td>
<td>0.014 (0.053)</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Tidal height</td>
<td>ns</td>
<td>-16.593 (0.100)</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

$^a$No fish seen in Page Creek
$^b$No fish seen in Kemps Creek
entering the creeks as soon as they began to flood. In contrast, *C. ruber* was most frequently seen in the creek mouths at times close to high tide. A third pattern of creek use was seen in *N. brevirostris*, which appeared to enter the creeks more frequently later in the day and during larger tidal cycles. Furthermore, creeks were used equally by *S. barracuda* and *T. crocodilus*, but significant spatial variability in creek usage was exhibited by *C. ruber* and *N. brevirostris*. This variation among transient predatory species was reflected in the multivariate analysis where the detections of all species combined into a single assemblage were not significantly correlated with any variable, and extends earlier findings of spatially and temporally variable use of intertidal mangroves by resident and juvenile fishes (Ellis and Bell, 2008).

The ecology of *N. brevirostris* is well studied in The Bahamas (Sundström et al., 2001), and previous work in Cape Eleuthera has demonstrated that the creeks are important nursery habitats for juvenile animals (Murchie et al., 2010). More generally, juvenile *N. brevirostris* elsewhere in the Caribbean are found exclusively in shallow, mangrove-fringed seagrass habitats (DeAngelis et al., 2008), presumably because these creeks represent refuges from larger sharks, potentially provide metabolic benefits because of increased water temperatures, and contain abundant prey. For example, *Gerres cinereus* were ubiquitous on the video footage from each creek, and they represent the major prey item for *N. brevirostris* (Newman et al., 2010). Activity patterns of *N. brevirostris* are equivocal, but juveniles are thought to feed most actively in crepuscular or nocturnal time periods (Sundström et al., 2001), and may also be most at risk of predation during these periods. Therefore, the increased number of sightings later in the day in this study, although marginally non-significant, may represent animals entering feeding and refuge grounds in preparation for these time periods. Tidal range was also included in the minimal adequate model, although it was not significant, and may represent the need of small sharks to use shallow refugia more frequently when bigger tidal ranges allow larger sharks to hunt closer to shore, as seen elsewhere in The Bahamas (Guttridge et al., 2012).

The lack of a tidal signal in the frequency of observations of *N. brevirostris* was unexpected, but may reflect the physiological and behavioural adaptations that allow them to remain within water so shallow that their dorsal fins are aerially exposed (Morrissey and Gruber, 1993). Consequently, *N. brevirostris* can leave and enter tidal creeks almost independently of water depth. Indeed, sharks may have greater hunting success in shallow water because prey have less three-dimensional space into which they can escape (Heithaus et al., 2009), and this could be an additional reason why other transient predators have to leave creeks at low tide, since many of the species seen in this study are potential prey items for *N. brevirostris* (Newman et al., 2012). The ability to remain in creeks at low tide may also explain why some of the results of this study contrast with those of Murchie et al. (2010). The present study did not observe any *N. brevirostris* individuals entering Kemps Creek, but acoustic tracking has highlighted this creek as being highly utilized (Murchie et al., 2010). The entrance of Kemps Creek has a deeper section than found at Page or Broad Creek (Murchie et al., 2010), perhaps allowing juvenile *N. brevirostris* to remain resident within Kemps at all times and not be recorded on cameras positioned at the mouth. Among the shallower creeks, it seems that Page Creek is utilized more frequently than Broad Creek, although elucidating the drivers of this pattern requires further research. However, the only sub-adult shark observed in this study was seen entering Broad Creek, and other sub-adults have regularly been observed in the creek (EJB, pers. obs.), perhaps suggesting that this creek may not provide a shallow refuge for juvenile animals.

Fewer previous data are available for the other focal species, meaning that this study represents the first demonstration of the timing of *S. barracuda* and *T. crocodilus* entering mangrove creeks. It seems likely that mangrove creeks represent important feeding and refuge areas for these species. Consequently, fishes re-enter the creeks as soon as possible after exclusion at low tide and presumably move further into the wetlands as the flood tide inundates additional areas. Furthermore, water depth appears to be the main abiotic driver of the behaviour of these
fishes, as opposed to using high water flow during mid-tide periods to reduce the energetic cost of entering creeks. There was no evidence of ontogenetic changes when *S. barracuda* enter the creeks, as the patterns of sightings of small and medium-sized individuals were similar. However, a full exploration of how creek use changes with age in this species requires a consideration of both transient and any resident individuals. The lack of changes in creek use by *S. barracuda* depending on the time of day is consistent with insignificant differences in diel activity during biotelemetry studies in the area (O’Toole et al., 2010). In contrast to *S. barracuda* and *T. crocodilus*, *C. ruber* entered the creeks more frequently as high tide approached. Presumably the creeks are less important feeding grounds for this species, and foraging activities are restricted to short periods around high tide when the maximum area of wetlands is available to transient predators. *Caranx ruber* also appears to favour Kemps and Broad Creeks, perhaps because of the different biophysical environment in the smaller Page Creek. The influx of additional predatory species into mangrove areas at high tide may explain the reduced abundance of some juvenile fishes at this time compared with during flood and ebb tides (Ellis and Bell, 2008).

The duration of the study meant that it was not possible to address quantitatively the question of temporal variation in creek use. For example, seasonal changes in creek use may be driven by factors such as fluctuating abundances of prey fishes caused by variable recruitment (Eggleston, 1995), or the spring parturition of *N. brevirostris* (Feldheim et al., 2002). However, it seems likely that the variation in behaviour among species occurs to some extent throughout the year, and that the creeks are continually functionally important. The study was also limited by the use of video cameras to observe fishes. Cameras have a range of benefits in marine survey work, but are typically limited to diurnal studies because of the challenges of filming at night. Although there are potential solutions to this problem (Holmes et al., 2012), acoustic tracking may be better for quantifying nocturnal movement, but this technique is limited to monitoring only those species and individuals invasively implanted with tags. Similarly, routinely deriving fish sizes from video surveys is difficult, even with complex stereo-camera systems (Holmes et al., 2013). Consequently, this study was only able to distinguish broad size categories for two species, and detailed analyses of any ontogenetic changes in behaviour both at the creek mouth and within the creek itself were not possible.

While there is a need for additional research, the range of transient predators recorded during this study highlights the importance of mangrove creeks to these ecologically and commercially important species. In addition to the other functions provided by mangroves and associated shallow-water benthic habitats that makes their conservation important (Harborne et al., 2006), the use of creeks by these transient species represents an additional, currently underestimated functional role for creeks. Coastal zone areas are in high demand for tourism development in Caribbean countries such as The Bahamas (Murchie et al., 2010), and the threat to inshore fauna from urbanization has been clearly demonstrated elsewhere (Jennings et al., 2008). Furthermore, conservation of mangroves must target the functionally most important creeks, rather than just attempting to include a representative creek within a protected area. This study highlights the variable use of different creeks by *N. brevirostris*, *C. ruber* and other transient predators. For example, although only seen infrequently, *C. limbatus* and *A. narinari* were recorded only in Kemps and Broad Creeks, and *G. cirratum* was recorded only in Kemps Creek. Indeed, the abundance of *N. brevirostris* in Page Creek, but the lack of sightings of other shark species at this site, provides further evidence for the inter-specific spatial segregation of mangrove creeks that has been reported elsewhere (DeAngelis et al., 2008). Consequently, uninformed protection of representative creeks by conservation initiatives may not be sufficient to maintain the demographic processes of species using shallow inshore areas. Furthermore, the abundance of *N. brevirostris* in the relatively small Page Creek demonstrates that creek size is a poor proxy of functional importance, and provides another example of the challenges of identifying critical sites for conservation using remotely sensed imagery to generate habitat maps at large spatial scales (Fernandes et al., 2005).
Habitat loss is often the highest profile threat to shallow inshore areas, but modifications that reduce hydrologic connectivity are arguably more pervasive and frequently overlooked (Pringle, 2001). This study demonstrates the importance to transient predators of water depth and access to shallow wetlands during high tides. Fragmentation of mangrove creeks causes a range of impacts, including a reduction in tidal exchange leading to deleterious changes in physiochemical parameters, a lower influx of planktonic larvae and juveniles, and sediment accumulation that leads to mangrove encroachment into channel areas and a further slowing of water movement (Layman et al., 2004). Developments such as roadways also provide physical barriers stopping transient predators from moving into wetlands (Layman et al., 2004). Relatively simple restoration activities can have a wide range of positive effects in mangrove creeks by increasing hydrologic connectivity (Valentine-Rose and Layman, 2011). The data presented here suggest that such initiatives may be extremely beneficial to transient predators in degraded locations by re-establishing access to important feeding grounds and refuge areas. Their very nature makes the study of transient predators a challenging undertaking, but video and tracking technologies provide extremely useful tools for understanding their behaviour and ecology. Such insights will be critical for ensuring the effective conservation of these predators within tropical marine food webs, through both the establishment of protected areas and the restoration of damaged habitats.

ACKNOWLEDGEMENTS

This paper was made possible by funding to ARH from the Australian Research Council (fellowship DE120102459) and the Earthwatch Institute. We are grateful for funding by an anonymous donor and the Cape Eleuthera Foundation to EJB, and a Research Assistantship from the Cape Eleuthera Foundation to BT. C. Bessey and I. Rossiter aided planning and data collection. Two reviewers provided comments that improved an earlier version of the manuscript.

REFERENCES


**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web site.