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Environmental drivers of diurnal visits by transient predatory fishes to Caribbean patch reefs

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ABSTRACT

Video cameras recorded the diurnal visitation rates of transient (large home range) piscivorous fishes to coral patch reefs in The Bahamas, and identified 11 species. Visits by bar jack *Caranx ruber*, mutton snapper *Lutjanus analis*, yellowtail snapper *Ocyurus chrysurus*, barracuda *Sphyraena barracuda*, and cero *Scomberomorus regalis* were sufficiently frequent to correlate with a range of biophysical factors. Patch reef visitation rates and fish abundances varied with distance from shore, and all species except *S. regalis* were seen more frequently inshore. This pattern is likely to be caused by factors including close proximity to additional foraging areas in mangroves and on forereefs and higher abundances close to inshore nursery habitats. Visitation rates and abundances of *C. ruber*, *L. analis*, *O. chrysurus*, and *S. regalis* also varied seasonally (spring versus winter), possibly as fishes responded to temperature changes or undertook spawning migrations. The abundance of each transient predator species on the patch reefs generally exhibited limited diurnal variability, but *L. analis* was seen more frequently towards dusk. This study demonstrates that the distribution of transient predators is correlated spatially and temporally with a range of factors, even within a single lagoon, and these drivers are species specific. Transient predators are considered an important source of mortality shaping reef-fish assemblages and their abundance, in combination with the biomass of resident predators, was negatively correlated with the density of prey fishes. Transient predators are often targeted by fishers, and understanding how they utilise seascapes is critical for protecting them within reserves.

Key words: The Bahamas; barracuda; mangroves; marine reserves; video analysis; snapper.

INTRODUCTION

Predation is a key influence on the structure of reef-fish assemblages (Hixon, 1991), and has led to an extensive literature on the importance of predator refuges for prey (e.g. Hixon and Beets, 1993), the impacts of predator removal on trophic cascades (e.g. Stallings, 2008), and population regulation through density-dependent mortality (White *et al.*, 2010). While the impacts of predation have been examined through a series of correlative and manipulative studies, there are less data on the behaviour of predatory fishes. The advent of acoustic tracking technology has led to a growing literature on shark movements (Schlaff *et al.*, 2014), but the behaviour of large, teleost piscivores and smaller meso-predators is less well known (Lédée *et al.*, 2015). However, the few studies that have been conducted on fishes such as trevally, large snappers, groupers, and barracuda have highlighted how their movement varies seasonally, diurnally, across tidal cycles, and among habitats (Meyer *et al.*, 2007*a*; Meyer *et al.*, 2007*b*; O'Toole *et al.*, 2011; Matley *et al.*, 2015). Further elucidating the movement of predatory fishes is critical to better understand their functional role in reef ecosystems. In addition, predators are typically the most heavily targeted fishes in tropical fisheries and are important to maintain income from recreational fishers and divers (Stallings, 2009; Hammerschlag *et al.*, 2010), and are a key target of conservation initiatives such as marine reserves (Russ, 2002). Consequently, information on how and why predators move around seascapes is necessary to allow researchers to ensure that spatially explicit management efforts are as effective as possible (Meyer *et al.*, 2007*a*; Pittman *et al.*, 2014; Lédée *et al.*, 2015).

The need to study the movement of piscivores is particularly true for ‘transient’ predators (alternatively ‘pelagic’ predators, Ford and Swearer, 2013*a*), namely those species that chase prey and forage widely across multiple habitat patches and at spatial scales much larger than their prey home ranges (Carr and Hixon, 1995; Overholtzer-McLeod, 2004). Although there is increasing evidence that even large, mobile species such as carangids may not move as extensively among individual reefs as was presumed (Meyer *et al.*, 2007a; Lédée *et al.*, 2015), their daily movements are typically more expansive and varied than 'resident' predators that remain within predictable and relatively limited home ranges (e.g. groupers, Carr and Hixon, 1995). Consequently, resident and transient species are often quantified separately because of their different home ranges, especially in manipulative studies where resident fishes can be removed from treatment reefs but transients represent either an uncontrolled predatory threat (Overholtzer-McLeod, 2004) or are excluded through the use of cages (Hixon and Carr, 1997; Ford and Swearer, 2013*a*). This work has demonstrated that transient predators are an important cause of mortality to fishes on Caribbean (Carr and Hixon, 1995), Pacific (Hoey and McCormick, 2004), sub-tropical (Holmes *et al.*, 2012), and temperate reefs (Ford and Swearer, 2013*a*). Furthermore, a combination of both transient and resident predators may be necessary for density-dependent mortality of prey fishes, and potentially population regulation (Hixon and Carr, 1997).

Like all species, the movement of transient predators will be influenced by interactions with other species, such as prey availability and avoidance of their own predators. Furthermore, the location of a habitat within the seascape can have important influences on the abundance of predatory species, caused by factors such as nursery habitat availability (Mumby *et al.*, 2004). The present study focuses on abiotic factors that receive less attention than biological and benthic structural variables, but may be the most important influences on piscivorous fish abundance patterns (Karnauskas *et al.*, 2012). For example, as ectothermic organisms, fish activity is intrinsically linked to water temperatures, which will affect spatial resource use, daily activity patterns, and seasonal changes in fish behaviours (Lédée *et al.*, 2015). Furthermore, time of day influences the feeding rates of small predators, with greater activity of moon wrasse *Thalassoma lunare* L. 1758 during the mid-afternoon (Holmes *et al.*, 2012), and small groupers being more active during crepuscular periods (Randall, 1967). Water movement also has important influences on the species seen across gradients from sheltered to exposed habitats, because only some species with particular fin morphologies are able to cope with high wave energy environments (Fulton *et al.*, 2005).

This study considers the effects of abiotic and some biotic variables on one aspect of the movement of transient predators within a Caribbean lagoonal complex, namely their visits to patch reefs. Although transient predators visit both natural and artificial patch reefs (Carr and Hixon, 1995; Hixon and Carr, 1997; Overholtzer-McLeod, 2004; Karnauskas *et al.*, 2012), the factors determining species-specific visitation rates are rarely studied. Predation rates on patch reefs are important because this habitat functions as a site of direct settlement for juvenile fishes (Carr and Hixon, 1995), and as an intermediate habitat during ontogenetic shifts by nursery-using species from seagrass and mangrove areas to adult habitats (Mumby *et al.*, 2004). Therefore, predator-driven fish mortality rates on patch reefs may have important demographic consequences, especially as lagoons may be the preferred habitat of some transient species (O'Toole *et al.*, 2011). Furthermore, the spatial separation of prey-rich patch reefs within an environment dominated by fish-depauperate, soft-sediment habitats provides an opportunity to investigate variability in the abundance of transient predators within a complex foraging seascape.

Cameras were used to record diurnal visitation rates and abundances of transient predators to patch reefs across a gradient of increasing distance from shore, which encompassed a range of seascape-scale variables. In addition, by deploying the cameras at different times of day and tidal states, visitation rates could be linked to current speed and direction, and hours after sunrise. Finally, by filming the patch reefs in both winter and spring, the study aimed to detect differences in transient predator abundances over seasonal time scales. Linking the diurnal visitation rates and abundances of transient predators to actual mortality rates of prey fishes is problematic because of the difficulty of detecting rare predation events. Therefore, this study focuses on detecting which variables are most important for influencing visitation rates by transient predators, which is assumed to be a proxy of their diurnal predation pressure. It was hypothesised that this estimate of predation pressure would be consistent across the patch reefs within a section of a single lagoon because of the extensive home ranges of transient predators.

MATERIALS AND METHODS

STUDY SITE

Data were collected in November-December 2011 (subsequently 'winter') and April-May 2012 (subsequently 'spring') from patch reefs close to Cape Eleuthera, The Bahamas (Fig. 1). The lagoonal area east of Cape Eleuthera is ~2-3 m deep and predominantly comprised of soft-sediment habitats, but also contains hundreds of patch reefs of various sizes. This study focused on six small (≤ 30 m^2) reefs (pictured in Fig. SI, Supporting Information). Small reefs were chosen as they are common in the area (Fig. SII, Supporting Information), and allowed a camera to film the whole reef and immediate surrounding area from a distance that was close enough to allow for species-level identification. The reefs were positioned along a gradient of increasing distance from the shoreline (subsequently 'offshore gradient'). The reefs were an average of 1.07 km (minimum 0.31, maximum 1.56 km) apart, and ranged from 1.45 to 6.78 km from the shoreline. By focusing on patch reefs of varying distance from shore, this study examined whether transient predator visitation rates were affected by a range of biophysical variables. Eleuthera has a semi-diurnal tidal regime with a maximum range of only ~80 cm (Murchie *et al.*, 2010), but the geomorphology of Cape Eleuthera leads to strong ebbing and flooding currents close to the shoreline (Fig. 1). Maximum current speed then decreases with increasing distance from shore. The variation in maximum current speeds is a significant influence on the distribution of lagoonal habitats, meaning that the habitats surrounding each patch reef vary with increasing distance from shore (Fig. 1). Furthermore, the shoreline of Cape Eleuthera supports a series of mangrove creeks that provide important nursery areas and foraging grounds for juvenile and adult transient predators respectively (Mumby *et al.*, 2004; Harborne *et al.*, 2016). As these variables co-vary across the offshore gradient any patterns cannot be definitively attributed to a single factor. However, if visitation rates varied significantly across this gradient, the study provides a list of potential drivers and hypotheses of transient predator distributions that will inform further research in seascapes where their effects may be evaluated independently.

Each reef was surveyed in detail prior to filming to quantify any systematic differences in the characteristics of the patch reefs across the offshore gradient. These surveys quantified the biomass of other meso-predators, including serranids (mainly sub-adult Nassau grouper *Epinephelus striatus* (Bloch, 1792) and graysby *Cephalopholis cruentata* (Lacepède, 1802)) and the invasive lionfish *Pterois volitans* L. 1758 and *Pterois miles* (Bennett, 1828) that are abundant on the patch reefs of Eleuthera. Predator biomasses were calculated from *in situ* visual estimates of length using allometric relationships (Froese and Pauly, 2010). Visual surveys also determined the densities of potential prey items (damselfishes, small wrasses, and juvenile parrotfishes and grunts). Coral and algal cover was measured using replicate (10-15) 0.25 m^2 video quadrats placed randomly on each reef. Furthermore, the length, width, and maximum height of each reef were measured, along with replicate (8-21) 1 m chain transects to measure habitat complexity (Luckhurst and Luckhurst, 1978). Variables of patch reef characteristics were logit (for proportional data, Warton and Hui, 2011) or log transformed where necessary to fulfil linear modelling assumptions prior to linear regression against the distance from shore.

Tidal flow rates and temperatures at each patch reef could not be monitored continuously during the video deployments, and therefore models of current flow were generated using data collected in March 2015. A TCM-1 Tilt Current Meter (Lowell Instruments, LLC) was deployed at each reef for a mean of 9.4 tidal cycles, (with the exception of reef 2, which was modelled using an average of the data from reefs 1 and 3 because of their proximity). A regression model was fitted to current speed data from each reef using the explanatory variables of time since previous slack, a quadratic term of time since previous slack, and height of the previous slack tide as predicted by tide tables. These models were then used to predict the current speed at each reef every 15 minutes during the camera deployment period. The current meter also recorded the temperature at each reef at midday. Although temperature was not monitored continuously during the study, a temperature logger (HOBO Pendant Temperature/Light) recorded seasonal changes in temperature every 30 minutes from March 2014 to March 2015 at patch reef 6. Data were summarised as the mean temperature each day, along with the maximum daily variation.

VIDEO DATA COLLECTION

Video cameras were used in this study because they have numerous advantages over underwater visual censuses for transient (and often rare) predators, including the ability to monitor multiple locations for relatively long periods simultaneously, creating a permanent record of each fish seen, and reducing *in situ* disturbance. A GoPro camera was placed 3 m from each reef (total of six cameras per day of filming) and typically ran for approximately 4 hours (mean=239.8 mins, S.D.=56.3 mins). Filming was undertaken using a crossed experimental design to record transient fishes at both different times of day (from soon after sunrise to sunset) and different tidal states. All transient predators passing over or close to a patch reef (field of view ~5.6 m at 3 m from the camera representing a filmed area of 8.4 m^2) were identified and counted.

The majority of fishes were only seen briefly (<30 s) while swimming past the patch reefs, but some remained in the field of view for longer periods. While care was taken to try and not record the same fish multiple times, tracking highly mobile individuals was problematic across the entire duration of filming, particularly for transient species that form large shoals (e.g. bar jack *Caranx* *ruber* (Bloch, 1793)). Therefore, counts of each species of transient predator were conducted for consecutive five minute time periods. Because each replicate count represented the abundance of transient predators on each patch reef per unit of time (5 mins) individual fish only needed to be tracked for a short time period. Consequently, a transient predator remaining around a patch reef for an extended (>5 mins) time period was only recorded once within the five minute count when it first arrived at the reef, but could also be recorded in subsequent time periods. Recording a fish in multiple five minute time periods was consistent with the aims of the study, which were to identify variability in the potential predation pressure caused by transient predators. Thus a fish spending an extended period of time at a reef was a greater threat to prey species than an individual moving quickly past the reef, and this residence time was reflected in the data set in a way that would not have occurred if only arrival time had been recorded, and was not logistically possible by recording total residence time. While tractable for analysing the video footage, the temporal resolution of this technique is limited to 5 minutes (i.e. fish present for <1 minute are not distinguished from fish present for 4-5 minutes), but it was assumed that visits <5 mins were functionally equivalent in terms of predation risk. Although the focus of this study was on assessing visitation rates of transient predators to the reefs and the videos were not sufficiently detailed to record predation events, any apparent hunting or feeding behaviour by the predators was documented.

For each daily camera deployment, five minute fish counts (ranging in number from 1 to 12 individual counts) were averaged to calculate the mean number of fish per species per 5 mins present at each patch reef during each hour surveyed after sunrise (subsequently ‘time segment’; first time segment = from sunrise to 1 hr after sunrise, second time segment = from 1 to 2 hr after sunrise and so on). Each hour-long segment was associated with a time after sunrise by calculating the time from sunrise to the mid-point of each time segment (i.e. 30 mins after sunrise for the first time segment). The current speed and direction (ebb or flood) for each hour-long segment was then estimated from the model prediction at the mid-point of the segment. A schematic overview of the derivation of the data from the videos is provided (Fig. SIII, Supporting Information).

DATA ANALYSIS

For even the most common transient species, fish were recorded during less than 70% of the one hour time segments, leading to zero-inflated and left-skewed data distributions. Therefore, the data for each species were modelled using two-part ('hurdle') models to account for zero inflation (Fletcher *et al.*, 2005; Zuur *et al.*, 2009). Firstly, the data were transformed from number of fish seen 5 mins^{-1} to presence/absence per one hour time segment, and analysed using generalized linear models with binomial error structures and the logit link function. Explanatory variables were season (spring or winter), distance from shore (including a quadratic term to examine curvilinear relationships), hours after sunrise, current speed, and current direction (ebbing or flooding), plus the interaction between the two water flow variables. Because the number of five minute intervals recorded in each one hour segment varied and could affect the probability of recording a visit by each species, the number of intervals (ranging from 1-12) was also included as a covariate in the model. Since data from individual 1 hour 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. Therefore, generalized linear mixed-effects models were performed using the lme4 package (Bates *et al.*, 2014) in R (R Core Team, 2014).

The second part of the hurdle model analysed the mean number of fish recorded per 5 mins within each one hour time segment, but only when that species did visit a patch reef (i.e. modelling non-zero values only). The explanatory and random variables were as for the binomial model, with the exception of the variable representing the number of five minute intervals surveyed that was omitted because the response variable of number of fish per 5 mins was independent of survey effort. These models were fitted using linear-mixed effects models, with Gaussian error structures and the identity link function. Fish abundances were only modelled if the species occurred in >10% of one hour time segments. Response variables were log or reciprocal root transformed when necessary to improve normality of residuals. Where required, the product of the predicted probability of a visit by each species (from the binomial models) and the predicted number of fish during a visit (from the Gaussian models) were used to predict the number of fish at each patch reef at any time.

Finally, to investigate any predator-prey relationships, the density of prey species was regressed against both the modelled abundance of transient predators and the surveyed biomass of resident predators at each patch reef, and an interaction term between predator abundances.

Both binomial and Gaussian models were fitted using the procedure outlined by Crawley (2007). Briefly, a maximal model was fitted including all factors and the interaction. Least significant terms were then removed in turn, starting with the interaction. After each term was removed, models were compared to ensure that term removal did not lead to an increase of >2 of the Akaike information criterion (AIC) (Burnham and Anderson, 2004) or a significant increase in deviance. Terms were removed until the model contained only significant terms or removal of any non-significant terms caused a significant increase in deviance or an increase of >2 of AIC (minimal adequate model). Minimal adequate models were checked for violations of assumptions.

RESULTS

ABIOTIC AND BIOTIC CHARACTERISTICS OF THE PATCH REEFS

The physical characteristics of the six patch reefs were relatively homogeneous, with each having a similar size, height above the bottom, and complexity (Table I). Furthermore, these characteristics did not vary systematically with increasing distance from shore. The biological characteristics of the reefs were more heterogeneous, with some reefs having much higher biomasses of lionfish and native groupers, and densities of prey species, but the abundance of resident predators and prey fishes were not significantly correlated with distance from shore (Table I). Coral cover was lower than macroalgal cover (13.9 and 32.7% respectively), and the coral assemblage was dominated by *Porites astreoides* (Lamarck, 1816), *Porites porites* (Pallas 1766), and *Siderastrea siderea* (Ellis & Solander, 1786). Coral cover was the only variable that varied systematically with location, and was significantly positively correlated with distance from shore (Table I, adjusted $R^2 = 0.847$).

Multiple regression of current speeds against time since the most recent low or high tide, and tidal height, provided good model fits ($R^2>0.60$). Current speeds generally decreased with distance offshore, and at peak times varied from ~30-40 cm s^{-1} at patch reefs 1-3 compared to ~12 cm s^{-1} at patch reef 6. The models allowed predictions of current speeds at each reef throughout the period of the study (Fig. SIV, Supporting Information). The temperature logger at patch reef 6 recorded a variation in daily mean temperatures of 12.6°C over the one year time span, with a mean daily variation of 1.4 °C (Fig. SIV, Supporting Information). Temperatures were generally higher and increasing during May (spring), compared to the lower and decreasing temperatures in November (winter), which is likely to have also occurred during filming in 2011-12. Mean midday temperature was not correlated with distance offshore ($P=0.342$).

VISITS BY TRANSIENT PREDATORS

A total of 15 camera deployments (six cameras deployed on each of 15 days) were conducted, resulting in 347.7 hr of video footage (details of deployments in Table SI, Supporting Information).

These deployments were distributed across 420 one hour time segments after sunrise (not every segment included a full hour of footage) and fish counts from 3,752 five minute intervals. Video footage from these deployments recorded the presence of 11 species that were categorised as transient predators based on previous categorisations (Beets, 1997), home range sizes (Farmer and Ault, 2011), and the inclusion of fishes in their diets (Randall, 1967; Froese and Pauly, 2010), although they are not all obligate piscivores. There were a total of 10,763 fishes within the five minute counts. The transient predators were yellow jack *Carangoides bartholomaei* (Cuvier, 1833), *C. ruber*, blue runner *Caranx crysos* (Mitchell, 1815), reef shark *Carcharhinus perezii* (Poey, 1876), nurse shark *Ginglymostoma cirratum* (Bonnaterre, 1788), mutton snapper *Lutjanus analis* (G. Cuvier, 1828), lemon shark *Negaprion brevirostris* (Poey, 1868), yellowtail snapper *Ocyurus chrysurus* (Bloch, 1791), cero *Scomberomorus regalis* (Bloch, 1793), barracuda *Sphyraena barracuda* (Edwards in Catesby, 1771), and houndfish *Tylosurus crocodilus* (Péron & Lesueur, 1821). Six of these species were too rare for detailed analyses (≤16 individuals, <0.005 fish 5 mins^{-1}, seen in <0.05 of 1 hr segments): *C. bartholomaei*, *C. crysos*, *C. perezii*, *G. cirratum*, *N. brevirostris*, and *T. crocodilus*. Therefore, the focus of this study was on patch reef visitation rates by the remaining species: *C. ruber* (5991 fish, 1.55 fish 5 mins^{-1}, seen in 0.43 of 1 hr segments), *L. analis* (2827, 0.81, 0.67), *O. chrysurus* (1793, 0.51, 0.32), *S. barracuda* (59, 0.02, 0.08), and *S. regalis* (58, 0.01, 0.05). Only *C. ruber*, *L. analis*, and *O. chrysurus* were sufficiently abundant to allow hurdle models of both the probability of each species visiting the patch reefs and the number of fish seen when they were recorded on the reefs. Obvious feeding or hunting behaviour was only detected in <0.01% of visits by these transient predators.

Generalized linear mixed-effects models demonstrated that the probability of each transient species, or any of the five focal species, visiting a reef was significantly correlated with one or more of the physical drivers and survey effort (Table II, Figs 2, 3 and 4). The strongest trend was that the probability of recording each species varied along the offshore gradient, with visitation rates generally decreasing with distance from shore except for *S. regalis* that was more frequently seen at the furthest reefs [Fig. 4(b)]. For example, not a single *O. chrysurus* was seen on patch reefs 4-6 [Fig. 3(a)]. Visitation rates also varied seasonally, with *C. ruber* and *S. regalis* seen more frequently during the winter and *O. chrysurus* more frequent in the spring. Time of day only significantly affected sightings of *L. analis*, which was recorded more often later in the day [Fig. 2(d)]. The metrics of tidal flow were generally not correlated with visits by transient species, but *S. regalis* was seen more often on ebbing tides. These species-level patterns combined to lead to a decrease in the probability of a visit by any of the five focal species with increasing distance offshore, and an increase in the probability of a visit with increasing time since sunrise [Fig. 3(d)].

For the three species that were sufficiently common to also investigate the number of fish seen during patch reef visits, linear mixed-effect models suggested that not only were patch reefs visits by *C. ruber* more frequent during the winter and closer to shore, but these variables were significantly positively correlated with the number of fish recorded [Table III, Fig. 2(b)]. In addition, the number of *C. ruber* was positively correlated with current speed. Unlike the probability of a visit, the number of *L. analis* recorded increased during the winter and were higher midway along the offshore gradient [Table III, Fig. 2(e)]. The model for the number of *O. chrysurus* was qualitatively the same as the model for the probability of a visit, with fewer fish seen further offshore and during the winter [Table III, Fig. 3(b)]. These species-level patterns combined to lead to a decreased probability of a visit by any of the five focal species with increasing distance offshore [Fig. 3(e)]. Furthermore, predictions of the number of transient predators visiting the patch reefs decreases with distance offshore [Fig. 3(f)] with a minimal influence of season, reflecting the species-level patterns of generally fewer visits further offshore, and a mixture of responses to the change of season [Figs 2(c), 2(f), and 3(c)].

There was a negative relationship between the abundance of transient and resident predators and surveyed prey density on the six patch reefs (intercept coefficient 4.958, *P*-value 0.004; resident coefficient -0.119, *P*-value 0.008; transient coefficient -0.106, *P*-value 0.032; interaction *P*-value >0.05; adjusted R^2=0.89). The abundance of transient predators was the predicted abundances of the five focal transient species at each patch reef [Fig. 3(f)]. Resident predators were included in the regression using their biomass recorded at each reef during visual surveys. Models including only one of the predator types had no significant correlation with prey density (*P*-value >0.05).

DISCUSSION

Increasingly accessible technologies, such as acoustic tagging, are demonstrating that wide-ranging carnivorous fish species do not represent a uniform predatory threat across seascapes, but are responding to a range of biophysical drivers (Meyer *et al.*, 2007*a*; Meyer *et al.*, 2007*b*; Lédée *et al.*, 2015). The present study contributes to this growing literature by highlighting that the abundances of transient predators visiting patch reefs varies significantly even within a single lagoon, despite the species considered having previously documented home ranges of >4.2 km^2, migrating among sites >42 km apart, and covering distances >12 km in a single day (Farmer and Ault, 2011; O'Toole *et al.*, 2011; Pittman *et al.*, 2014). This study also demonstrates that in addition to significant intra-habitat variability in the abundance of transient predators, there were inter-specific differences in the drivers influencing visits to patch reefs. For example, although most species were more abundant close to shore, *S. regalis* was seen more frequently further offshore. Finally, although it should be interpreted with care given the limited number of patch reefs and difficulties of inferring prey mortality rates and influxes without any temporal replication, the negative correlation between the abundance of transient predators and prey densities suggests that the spatial variability of transient species has impacts on the demographics of small patch-reef fishes. Furthermore, the impact on prey species of varying abundances of transient species appeared only to be significant when combined with the abundance of resident predators, supporting the hypothesis that there is synergistic predation between these two functional groups (Hixon and Carr, 1997).

The change in visitation rates and abundances on patch reefs along the offshore gradient was apparent in all common transient predators, but this pattern cannot easily be attributed to a single factor because multiple variables co-vary with increasing distance from shore. Similarly, the relative importance of this gradient is likely to vary among lagoons with different biophysical characteristics. However, it seems likely that proximity to mangrove creeks is an important cause of this pattern. There are three major mangrove creeks close to the studied patch reefs, and at least three of the common transient predators (*C. ruber*, *O. chrysurus*, and *S. barracuda*) use these creeks for foraging and refuge (Harborne *et al.*, 2016). Therefore, the complex of creeks and inshore patch reefs may represent a centre of activity for many transient predators. Use of the creeks by these species also varies across tidal cycles (Harborne *et al.*, 2016), and fishes may forage or refuge on the closest patch reefs when the creeks are inaccessible at low tide. Furthermore, four of the species (*C. ruber*, *L. analis*, *O. chrysurus*, and *S. barracuda*) use mangroves and seagrass beds as nursery habitats (Nagelkerken *et al.*, 2000), and their abundances are typically higher on patch reefs close to their settlement habitats (Mumby *et al.*, 2004). Finally, patch reefs closer to shore may receive higher influxes of small prey fishes that also used mangroves nurseries. The increase in visitation rates by *S. regalis* to patch reefs further from the shore is consistent with the proximity to mangroves being an important driver of the distribution of other transient predators, as this species is not recorded as using mangrove creeks to forage (Harborne *et al.*, 2016) and does not appear to be found in surveys of mangroves (e.g. Serafy *et al.*, 2003), as might be expected for a species using this habitat as a nursery.

In addition to being close to the mangrove creeks, and other inshore habitats that may be important nurseries, the patch reefs closer to shore are closer to the deeper forereefs just west of Eleuthera.

Transient species that move widely across seascapes are likely to use both patch reefs and forereefs for foraging, and may also use the lagoon as a refuge from their own predators. When foraging or refuging on lagoonal patch reefs, these fishes may prefer to visit patch reefs closer to the deeper reefs in order to conserve energy. For example, pelagic predators in a temperate bay were four times more abundant on reefs close to an oceanic entrance than on reefs further inside the bay (Ford and Swearer, 2013*b*). Similarly, the distance to a channel connecting a lagoon and adjacent forereefs explained nearly half of the variation in fish assemblages on Belizean patch reefs, with species such as *S. barracuda* being more abundant close to channels (Karnauskas *et al.*, 2012). Furthermore, fish moving between the deeper reefs and patch reefs closer to shore can utilise the higher speed tidal currents to swim efficiently between these habitats, as observed in other large transient predators (Meyer *et al.*, 2007b) and many shark species (reviewed by Schlaff *et al.*, 2014).

Changes in current speed across tidal cycles weren't a significant variable in the models of fish visitation rates, although groups of *C. ruber* were larger when visiting reefs at higher current speeds. High abundances of *C. crysos* were also strongly associated with areas of high water flow in Brazil (Floeter *et al.*, 2007). However, other transient fishes may preferentially associate with patch reefs that have higher maximum current speeds, which could contribute to the negative relationship between fish visitation rates and distance offshore since maximum current speed decreases with increasing distance from shore. In addition to facilitating movement to deeper reefs, the higher current speeds may provide fusiform predators with an advantage over prey that are less well adapted to swimming in rapidly moving water, and are thus less able to escape. Such asymmetries in predator-prey interactions are rarely studied, but there is some evidence that smaller fishes with less swimming ability are more susceptible to predators where water currents are strongest (Holmes and McCormick, 2006). In contrast, a preference for more moderate maximum current speeds may lead to the higher abundance of *L. analis* towards the middle of the offshore gradient.

In addition to close proximity to mangroves and deep water and higher maximum current speeds, the mosaic of habitats surrounding each patch reef varied, and the habitats surrounding reefs close to shore may offer better foraging than those further offshore. While prey fish are concentrated on the patch reefs, some juveniles settle and remain in soft-bottom habitats, particularly seagrass (Mumby *et al.*, 2004), and may offer important food resources to transient predators. The distribution of hard-bottom habitats surrounding patch reefs has also been demonstrated to affect the abundance of lutjanids (Karnauskas *et al.*, 2012). Finally, reefs closer to the shore in Eleuthera may be visited more frequently because of factors such as their size distribution and proximity to neighbouring patches. For example, *O. chrysurus* does visit aggregated artificial reefs (5 m apart) more frequently than isolated reefs 50 m apart (Overholtzer-McLeod, 2006), and the abundance of *O. chrysurus* and *C. ruber* was significantly influenced by the proximity to other patch reefs in a Belizean lagoon (Karnauskas *et al.*, 2012).

Most other characteristics of the patch reefs did not change systematically with increasing distance from shore, and seem unlikely to be significant influences on transient predator visitation rates. The only variable that did change systematically along the offshore gradient was coral cover. However, coral cover increased with increasing distance offshore, while transient predator visitation rates decreased. Fishes typically become less abundant on reefs with lower coral cover (Pratchett *et al.*, 2008), but transient predators may hunt more frequently on low coral cover reefs where prey have fewer refuges. However, because the reefs in this study are typically characterised by encrusting corals, increasing coral cover did not cause systematic differences in rugosity, which is typically a more important control of the abundance of small prey fishes (Gratwicke and Speight, 2005).

In addition to changing their visitation rates to patch reefs along the offshore gradient, the probability of a visit by *C. ruber*, *O. chrysurus*, and *S. regalis*, and the group size of *L. analis*, varied significantly among seasons. All species except *O. chrysurus* were more abundant around the patch reefs during the winter, and this may be in response to fishes seeking optimal temperatures. Temperatures on deeper reefs are typically more stable, in contrast to shallower water where there is a greater variability and more extreme highs and lows (Potts and Swart, 1984). As this study considers diurnal activity, fishes may be seeking energetically beneficial warmer water in the shallow lagoon during the winter days. Seasonal variations in transient predator visitation rates may also be caused by fishes migrating to deeper reefs to spawn, or preparing to undertake spawning migrations. Despite the significant decrease in spring visits to patch reefs by transient species, further work is necessary to determine how predator abundance and prey mortality rates are coupled. Although predators may be more abundant during the winter, species such as *S. barracuda* may feed less intensely at this time of year because of lower water temperatures (Hammerschlag *et al.*, 2010).

Lutjanus analis was the only species that displayed a significant diurnal pattern, and visited the patch reefs more frequently later during the day. Sharks feed optimally at dusk because they have a sensory advantage in low light conditions and their body temperatures are higher than that of their prey (Papastamatiou *et al.*, 2015), and *L. analis* may have a similar metabolic benefit. *Lutjanus analis* may also be returning to the patch reefs later in the day in order to seek nocturnal shelter. Relatively limited video observations of visits to patch reefs elsewhere in The Bahamas have previously suggested that *C. ruber* and *S. barracuda* may be seen more frequently towards the middle of the day compared to at dawn and dusk (Carr and Hixon, 1995), and acoustic data from Eleuthera indicated that *S. barracuda* moves from lagoonal habitats to deeper forereefs from mid-morning to mid-afternoon before returning in the late afternoon (O'Toole *et al.*, 2010). These patterns were not apparent in the present study, and may suggest significant variability within species, across seasons, and among locations. In addition to changing their patch reef visitation rates, transient predators may also alter their feeding rates throughout the day. For example, *L. analis* appears to feed less frequently at midday compared to during mornings or evenings (Mueller *et al.*, 1994). Combining the spatial and temporal movements of transient predators with their foraging behaviour and feeding rates represents an important next step in elucidating the functional role of these species within Caribbean seascapes.

This study has provided new insights into the abundance of five transient predators, but the use of video cameras limited observations at night when their distributions may be different. For example, there is some evidence from artificial reef studies that *L. analis* may disperse away from habitat structures at night (Eggleston *et al.*, 1990). Indeed many transient predators may make diurnal migrations across the seascape, as documented for Pacific trevallys and snappers (Meyer *et al.*, 2007*a*; Meyer *et al.*, 2007*b*). There are potential solutions to the problem of filming at night (Holmes *et al.*, 2012), but acoustic tracking may be better for quantifying nocturnal movement. Data are also required from different life stages of each species, as some transient predators change their foraging behaviour ontogenetically (Mueller *et al.*, 1994), which may affect their behavioural patterns as it does in sharks (Schlaff *et al.*, 2014). Furthermore, the importance of the offshore gradient for influencing transient predator distributions suggests there is a need for additional research at locations where the individual importance of individual factors, such as mangrove proximity and distance to deeper reefs, can be examined independently to test the hypotheses suggested by this study. Finally, studies are required to elucidate where the transient predators swim to when not in lagoons in order to fully understand their movements, and elucidate their role in seascape-scale connectivity among habitats (McCauley *et al.*, 2012).

The focus of this study was on providing new insights into the variability of visits by transient predators to patch reefs, but these data also provide indications of the potential impacts of environmental change. Firstly, temperature is likely to be at least partly causing the seasonal variation seen in some of the species, and warmer sea surface temperatures under global climate change scenarios may affect the movement of transient predators (Currey *et al.*, 2015). The consequences on fish abundances of clearing mangrove nursery and foraging habitats have frequently been stated (Valiela *et al.*, 2001), and the present study also suggests that changes to the distribution of transient predators may occur if inshore habitat connectivity is affected by coastal development. The functional role of transient predators will also be impacted by fishing (e.g. *O. chrysurus* is increasingly being targeted in Belize, Mumby *et al.*, 2012). In addition, the removal of apex predators might increase the abundance of smaller transient predators, and also affect their behaviour if the threat of predation decreases (Preisser *et al.*, 2005). Predicting how all these changes may cascade spatially and temporally through tropical food webs is challenging, but it is clear that a better understanding of the behaviour of transient predators is important to conserve and manage the ecosystem services provided by coral reefs.

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TABLE I. Abiotic and biotic characteristics of the six patch reefs filmed for transient predator visitation rates, and the results of regression analysis of each factor against distance from shore. Regression results are coefficient and significance of coefficient in parentheses, with significant correlations highlighted in bold. Prey category comprised of damselfishes, small wrasses, and juvenile parrotfishes and grunts.

Reef	**Distance offshore (km)**	**Height (m)**	**Area (m^2)**	**Rugosity**	**Coral cover (%)**	**Algal cover (%)**	**Lionfish biomass (g m^{-2})**	**Grouper biomass (g m^{-2})**	**Prey density (m^{-2})**
1	1.45	0.85	16.1	1.32	4.7	35.4	0.0	0.0	2.2
2	1.76	1.20	22.7	1.37	9.1	59.4	0.0	14.2	0.8
3	2.19	0.64	18.9	1.25	9.0	8.7	9.8	12.6	1.3
4	3.50	0.75	18.0	1.44	11.6	45.5	1.6	25.3	0.3
5	5.22	0.77	30.4	1.28	14.6	24.5	0.0	0.0	4.6
6	6.78	0.83	22.5	1.34	34.6	22.6	7.0	29.3	0.7
Mean (S.D.)	**3.48 (2.13)**	**0.84 (0.19)**	**21.4 (5.1)**	**1.33 (0.07)**	**13.9 (10.6)**	**32.7 (18.1)**	**3.1 (4.3)**	**13.6 (12.3)**	**1.7 (1.6)**
Regression v. distance	**-**	-0.024 (0.606)	0.062 (0.218)	<0.001 (0.996)	**0.347 (0.006)**	-0.106 (0.650)	0.168 (0.528)	58.460 (0.335)	-0.003 (0.988)

TABLE II. Minimal adequate generalized linear mixed-effects models (fixed effects only) for the presence / absence hr^{-1} of each transient predator species on patch reefs along an offshore gradient. Values are model coefficients with *P*-values in parentheses. Coefficients for categorical variables are for winter in comparison to spring (season) and for flooding in comparison to ebbing tide (current direction). Curr. = current. ×: interaction term. ns: non-significant term (*P*>0.050) not contained in minimal adequate model.

Variable	***Caranx ruber***	***Lutjanus analis***	***Ocyurus chrysurus***	***Sphyraena barracuda***	***Scomberomorus regalis***	**All five species**
Intercept	0.915 (0.163)	-1.997 (0.021)	15.575 (<0.001)	-3.974 (<0.001)	-10.953 (<0.001)	3.386 (<0.001)
Season	0.753 (0.003)	ns	-6.755 (<0.001)	ns	2.325 (0.002)	ns
Distance from shore	-1.416 (<0.001)	0.803 (0.034)	-6.315 (<0.001)	1.543 (0.057)[a]	2.736 (0.007)	-0.710 (<0.001)
Distance from $shore^2$	0.135 (0.001)	-0.153 (0.001)	ns	-0.276 (0.026)	-0.240 (0.023)	ns
Hours since sunrise	ns	0.186 (0.002)	ns	ns	ns	0.260 (<0.001)
Curr. speed (CSPD)	ns	ns	ns	ns	ns	ns
Curr. direction (CDIR)	ns	ns	ns	ns	-1.225 (0.037)	ns
Number of 5 min intervals	0.126 (0.001)	0.147 (<0.001)	0.182 (0.071)[a]	ns	ns	ns
CSPD×CDIR	ns	ns	ns	ns	ns	ns

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[a] Removal of non-significant terms led to a significant increase in model deviance and AIC.

TABLE III. Minimal adequate linear mixed-effects models (fixed effects only) for the number 5 mins^{-1} (when present) of the three most abundant transient predator species, and all five focal species combined, on patch reefs along an offshore gradient. Values are model coefficients with *P*-values in parentheses. Coefficients for categorical variables are for winter in comparison to spring (season) and for flooding in comparison to ebbing tide (current direction). ×: interaction term. ns: non-significant term (*P*>0.050) not contained in minimal adequate model.

Variable	***Caranx ruber***	***Lutjanus analis***	***Ocyurus chrysurus***	**All five species**
Intercept	-2.011 (<0.001)	-1.773 (<0.001)	1.164 (<0.001)	-0.155 (0.341)
Season	0.418 (0.015)	0.328 (0.046)	-0.171 (0.058)[a]	ns
Distance from shore	-0.132 (0.001)	0.702 (0.002)	-0.186 (0.001)	-0.380 (<0.001)
Distance from shore^2	ns	-0.087 (0.002)	ns	0.025 (0.047)
Hours since sunrise	ns	ns	ns	ns
Current speed (CSPD)	0.027 (0.005)	ns	ns	ns
Current direction (CDIR)	ns	ns	ns	ns
CSPD×CDIR	ns	ns	ns	ns

[a] Removal of non-significant terms led to a significant increase in model deviance and AIC.

[a] Removal of non-significant terms led to a significant increase in model deviance and AIC.

Figure captions

FIG. 1. Location of (a) Eleuthera within The Bahamas, (b) the study area, and (c) the six patch reefs used in the study (1-6) and the surrounding habitats. Grey arrow shows approximate directions of strong, inshore tidal currents. Deep water and forereef habitats are found just to the west of Eleuthera, bordering Exuma Sound.

FIG. 2. Scatter plots between the distance of patch reefs from shore and the patch reef visitation rates of (a)-(c) *Caranx ruber* and (d)-(f) *Lutjanus analis* separated by (a, d) probability of a visit, (b, e) number of fish seen during a visit, and (c, f) predicted number of fish seen (combining the probability of a visit and the number of fish seen during the visit). Lines show predicted values from statistical models (left-hand axis) and (a, d) vertical marks (horizontally and vertically jittered) and (b, e) circles (horizontally jittered) represent actual data points (right-hand axis). Predicted and actual data are segregated by season (spring = grey, winter = black), except for (d) where data are segregated by time after sunrise (morning = grey, afternoon = black). Predictions are (b, c) at slack tide (current speed = 0 cm s^{-1}) and (f) in the morning (time after sunrise = 3 hours).

FIG. 3. Scatter plots between the distance of patch reefs from shore and the patch reef visitation rates of (a)-(c) *Ocyurus chrysurus* and (d)-(f) any of the five focal transient predators separated by (a, d) probability of a visit, (b, e) number of fish seen during a visit, and (c, f) predicted number of fish seen (combining the probability of a visit and the number of fish seen during the visit). Lines show predicted values from statistical models (left-hand axis) and (a, d) vertical marks (horizontally and vertically jittered) and (b, e) circles (horizontally jittered) represent actual data points (right-hand axis). Predicted and actual data are segregated by (a)-(c) season (spring = grey, winter = black) or (d, f) time after sunrise (morning = grey, afternoon = black).

FIG. 4. Scatter plots between the distance of patch reefs from shore and the probability of a visit by (a) *Sphyraena barracuda*, and (b) *Scomberomorus regalis*. Lines show predicted values from statistical models (left-hand axis) and vertical marks represent actual data points (right-hand axis, horizontally and vertically jittered). Predicted and actual data in (b) are segregated by season (spring = grey, winter = black). Predictions for *Scomberomorus regalis* are on an ebbing tide.

Figure 1 revised

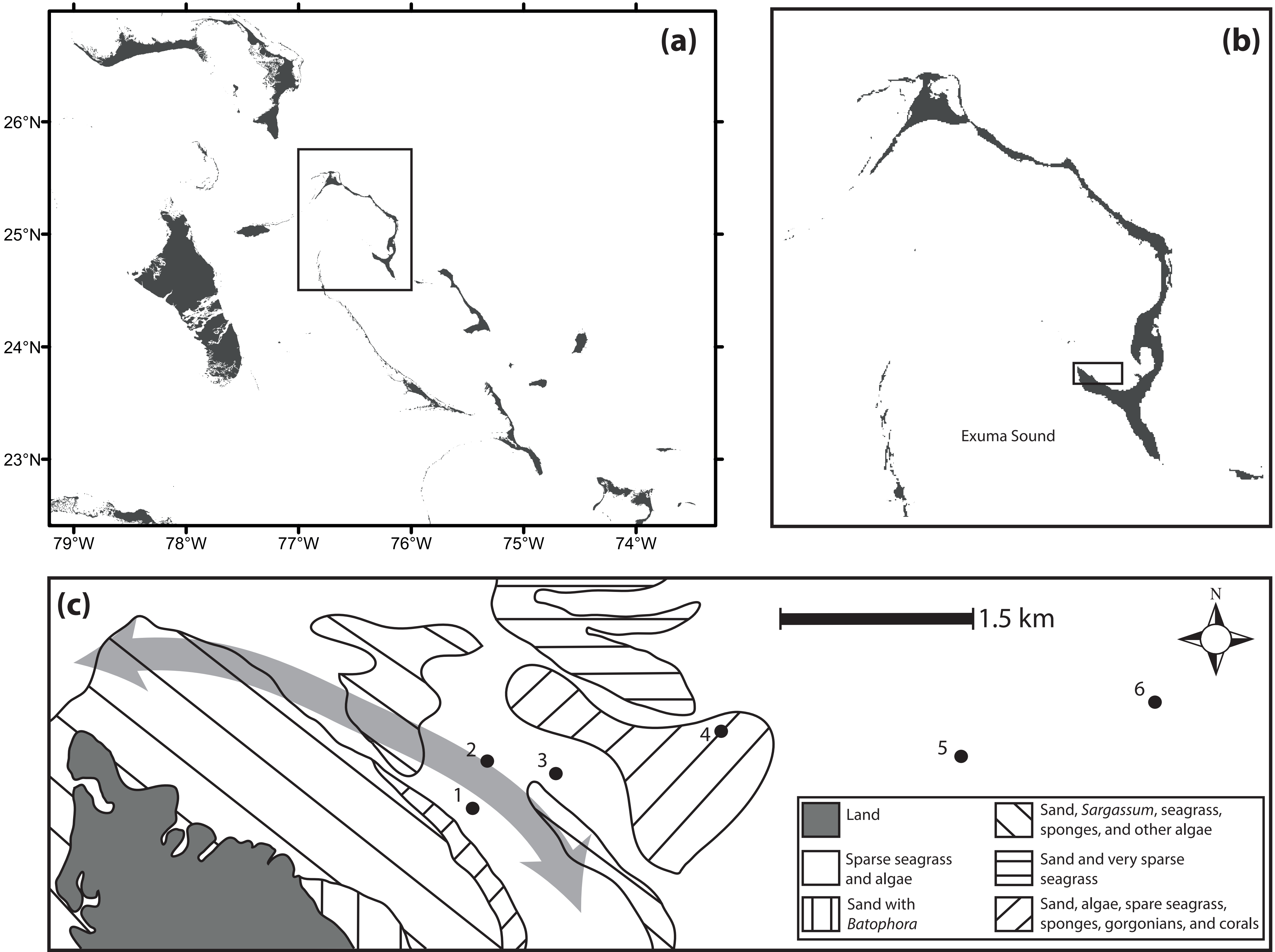


Figure 2 revision 2

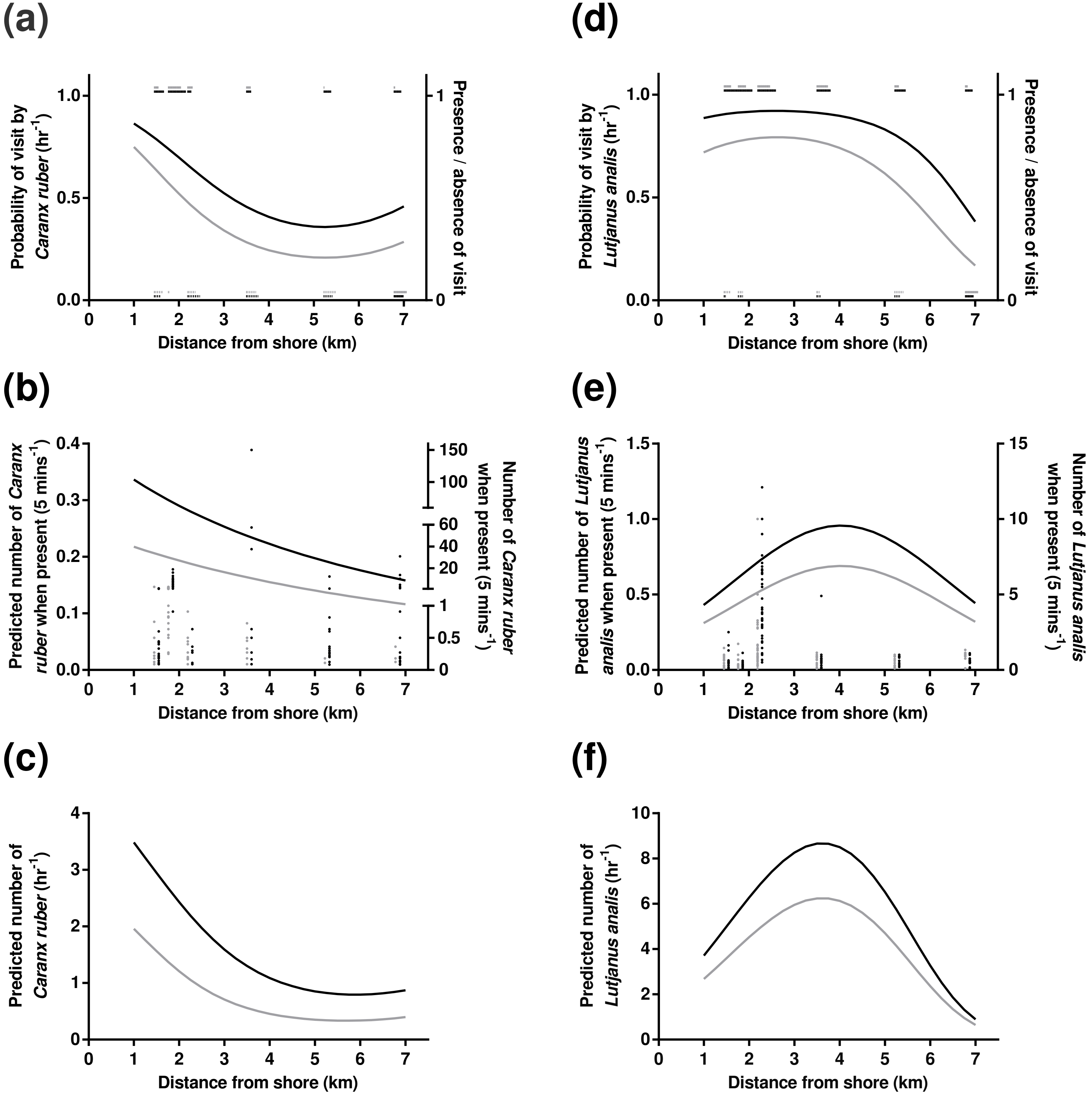


Figure 3 revision 2

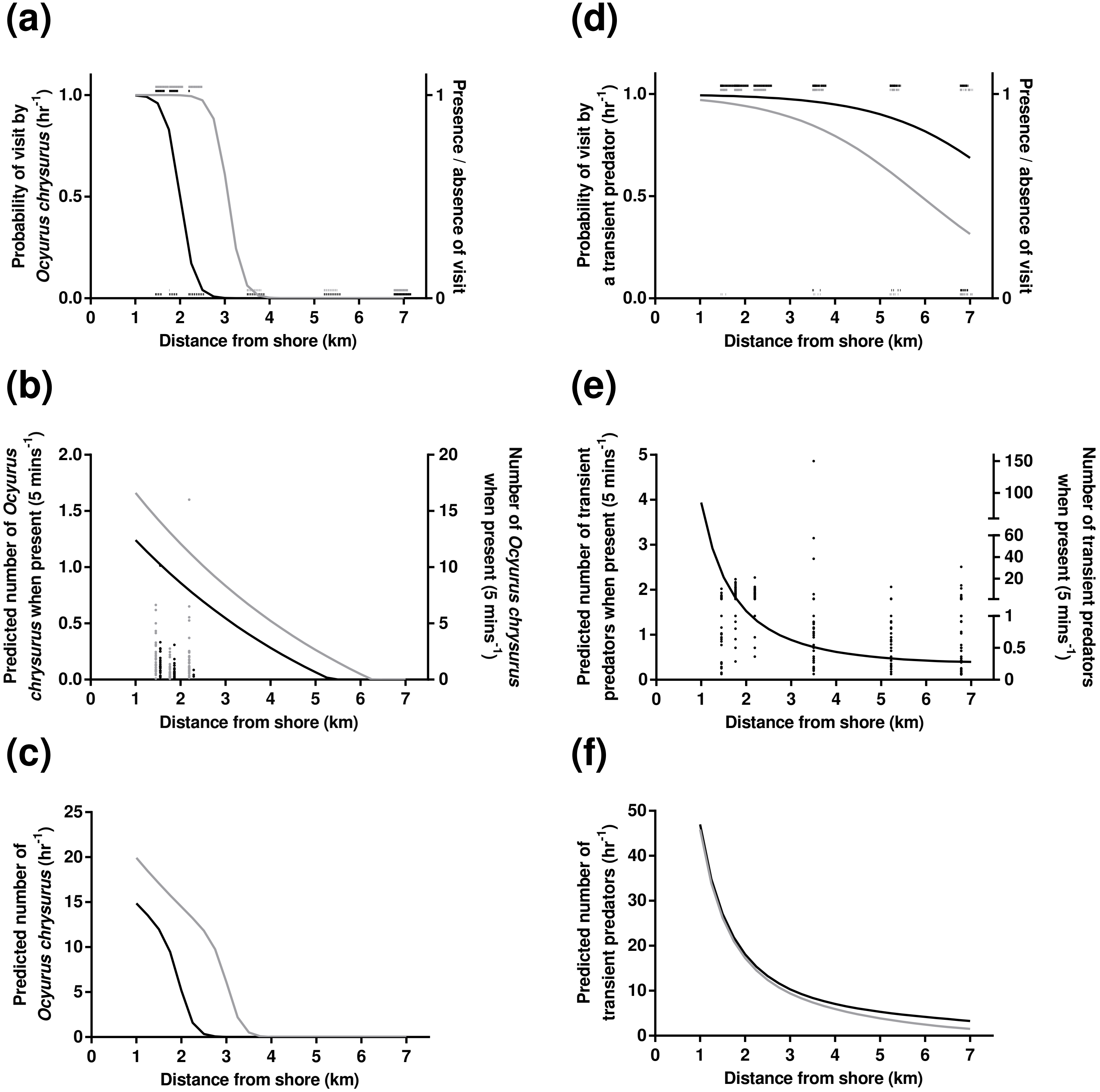
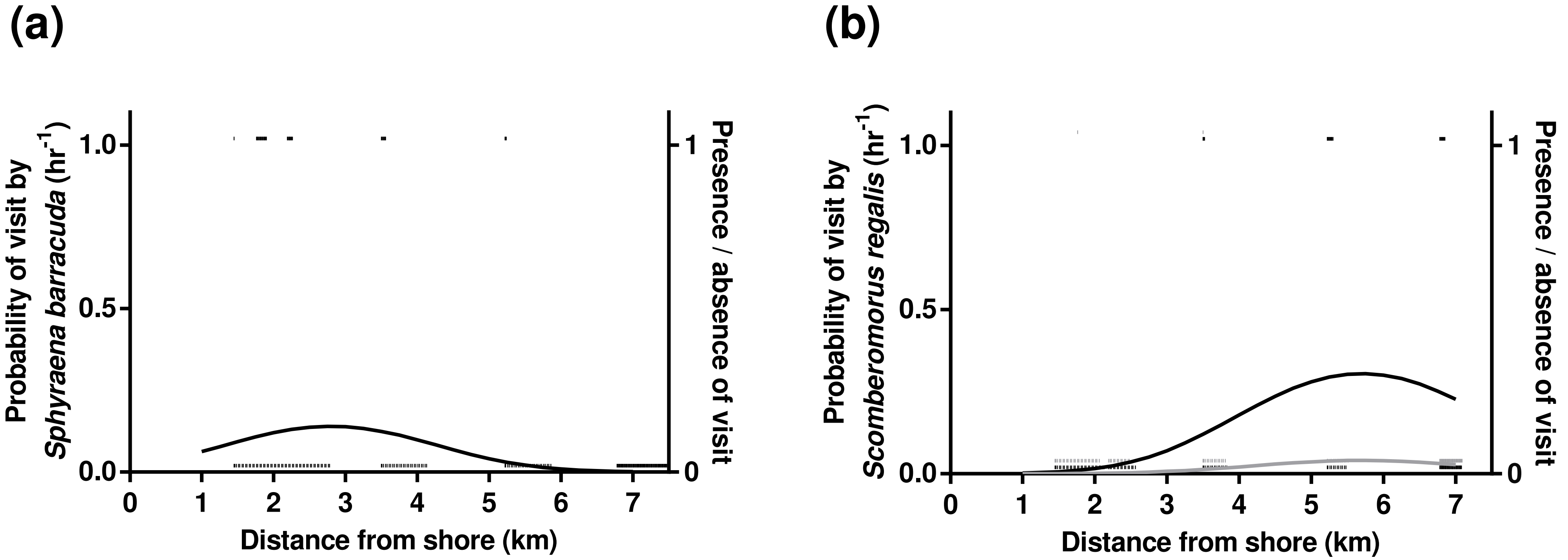


Figure 4 revision 2



Supporting Information

Patch reef 1 **Patch reef 2**

Patch reef 3 **Patch reef 4**

Patch reef 5 **Patch reef 6**

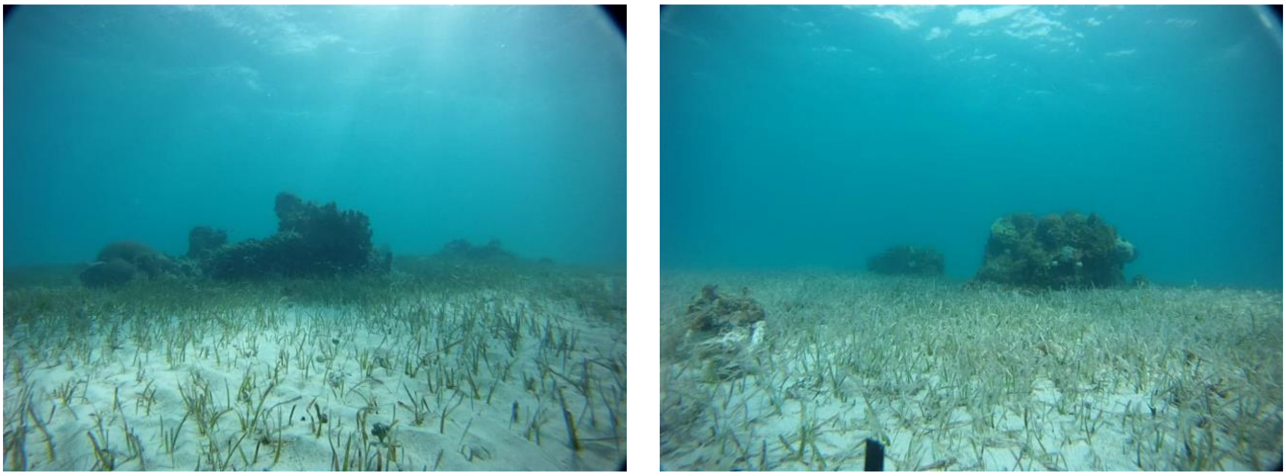


FIG. SI. Video stills of each of the patch reefs used in the study.

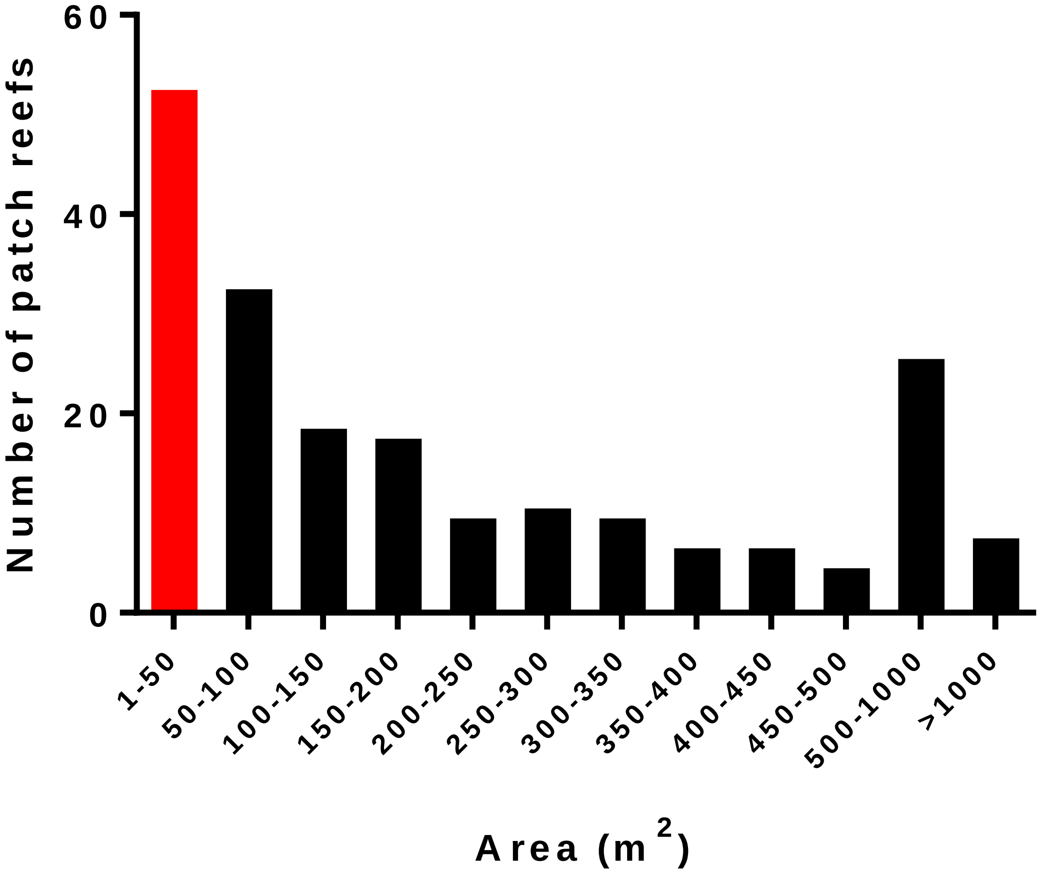
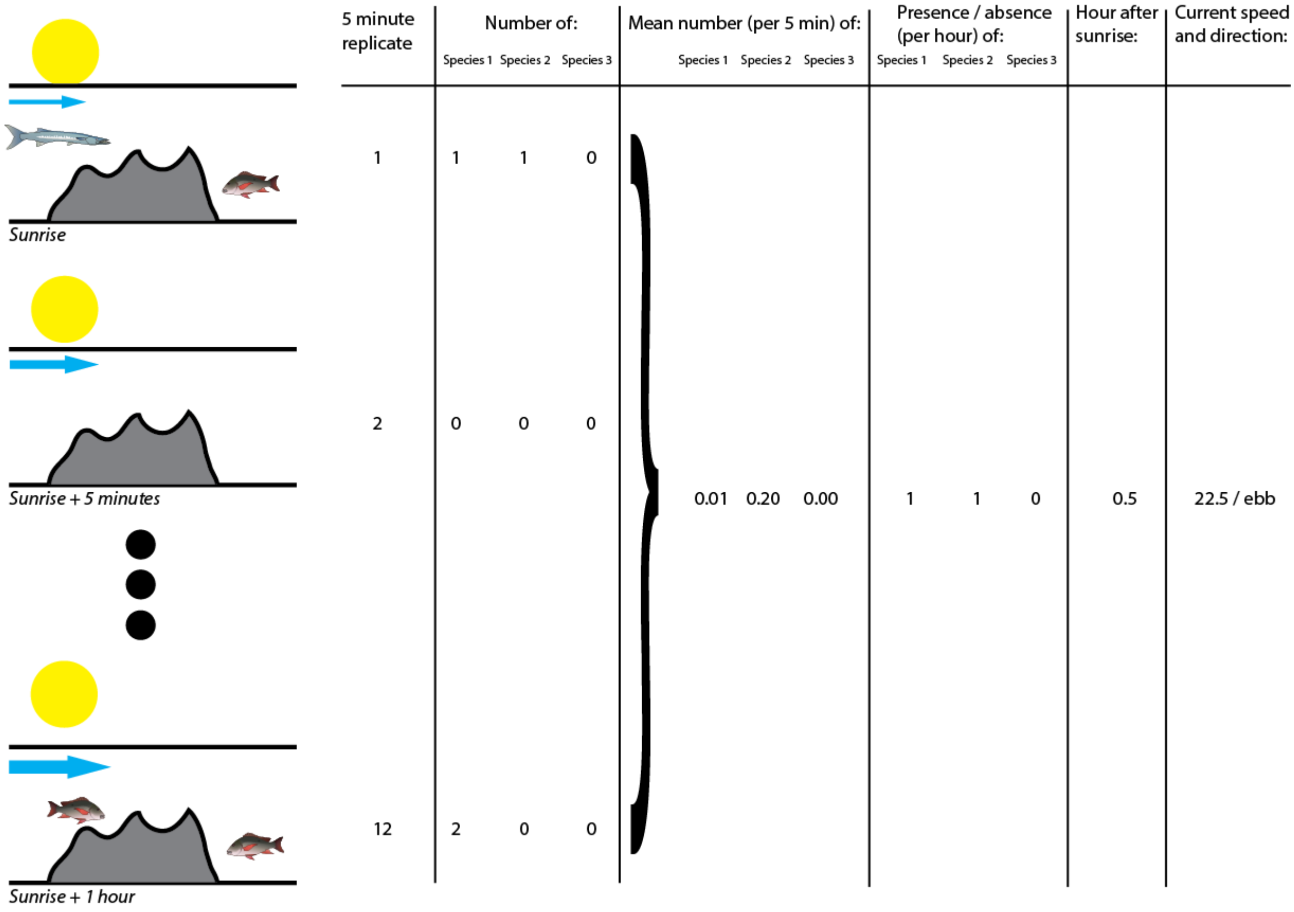


FIG. SII. Size distribution of 195 patch reefs measured within the study area. Size class of the patch reefs used in this study highlighted in red. Note last two size categories include a wider range of sizes than the other classes.



5 minute replicate	Number of:			Mean number (per 5 min) of:			Presence / absence (per hour) of:			Hour after sunrise:	Current speed and direction:
	Species 1	Species 2	Species 3	Species 1	Species 2	Species 3	Species 1	Species 2	Species 3		
1	1	1	0	0.01	0.20	0.00	1	1	0	0.5	22.5 / ebb
2	0	0	0								
12	2	0	0								

FIG. SIII. Schematic overview of the process of deriving mean abundance and presence / absence of each species for a single 1 hr time segment at a study patch reef. Total species counts are made for each species in each of up to 12 five minute intervals, and then averaged. These values are then associated with the number of hours after sunrise at the mid-point of the 1 hr segment (the example is for the first hour after sunrise, with the mid-point quantified as 0.5 hrs after sunrise), and the predicted current speed (cm s^{-1}) and direction at that time point. Blue arrow represents tidal flow, with the width of the arrow indicative of the speed.

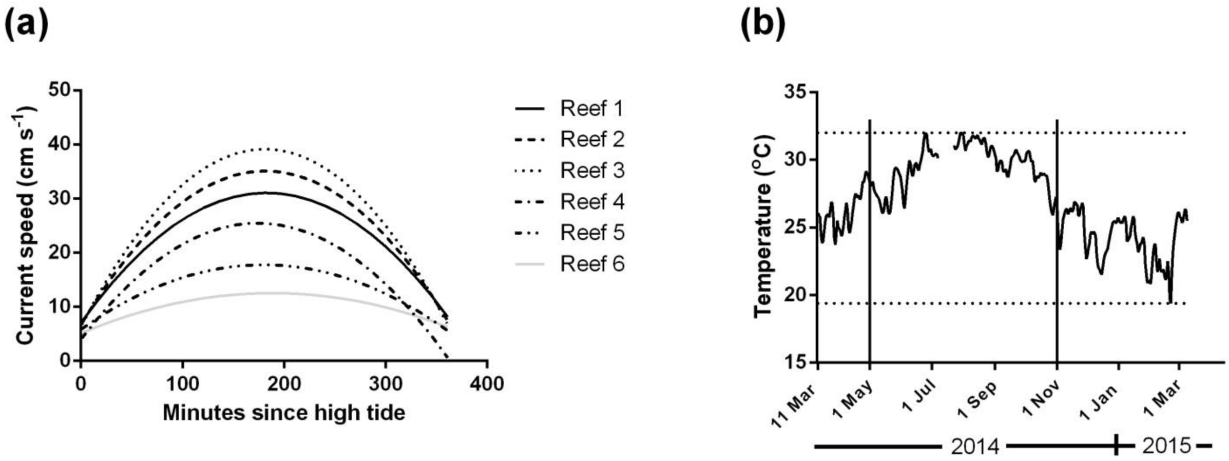


FIG. SIV. (a) Example of predicted current speeds at each patch reef (here following a 1.02 m high tide during the first day of filming, 31st October 2011). (b) Annual changes in mean daily temperature from March 2014 – March 2015. Dotted lines show minimum and maximum mean temperatures (19.4 and 32.0°C), and vertical lines represent the spring and winter filming times.

TABLE SI. Details of the camera deployments on each day of the study. 1 hr segments refer to division of the day into time periods after sunrise (e.g. deployment 1 = 07:12 – 08:12; 08:12-09:12 and so on). Each 1 hr segment was split into replicate 5 min fish counts.

Date	Season	Deployment	Sunrise	Reef	Start time	Duration	Number of 1 hr segments	Number of 5 min intervals
31/10/2011	Winter	1	07:12:00	1	-	-	-	-
				2	14:22	02:52:55	3	30
				3	15:10	01:59:27	2	20
				4	15:43	01:18:14	2	15
				5	-	-	-	-
				6	-	-	-	-
01/11/2011	Winter	2	07:12:00	1	11:56	02:26:15	4	26
				2	11:52	04:42:50	6	51
				3	11:46	04:30:08	5	48
				4	11:39	04:35:05	5	49
				5	11:31	04:31:43	5	50
				6	11:25	04:41:36	5	50
03/11/2011	Winter	3	07:14:00	1	15:28	03:11:17	4	33
				2	16:43	01:53:28	3	21
				3	15:19	03:18:45	4	35
				4	15:06	03:28:55	4	37
				5	14:48	03:49:10	5	40
				6	14:32	04:03:55	5	43
05/11/2011	Winter	4	07:15:00	1	07:26	04:27:02	5	48
				2	07:30	04:47:09	5	52
				3	07:37	02:21:02	3	25
				4	07:43	04:44:42	6	52
				5	07:50	04:47:01	6	52
				6	07:57	04:45:05	6	51
06/11/2011	Winter	5	06:16:00	1	10:36	04:16:25	5	45
				2	10:33	04:44:34	5	52
				3	10:28	04:13:27	5	45
				4	10:22	02:41:05	3	29
				5	10:15	04:42:00	5	51
				6	10:07	04:41:32	6	51
07/11/2011	Winter	6	06:16:00	1	13:49	03:49:10	5	41
				2	13:54	03:39:09	5	39
				3	13:58	03:39:08	5	39
				4	14:04	03:33:45	5	39
				5	14:12	03:18:55	4	36
				6	14:28	02:45:11	3	30
09/11/2011	Winter	7	06:17:00	1	10:41	04:27:37	5	48
				2	10:37	04:44:49	6	52
				3	10:32	04:18:33	5	46
				4	10:26	04:40:55	5	52
				5	10:19	02:46:57	3	30
				6	10:11	04:44:51	6	52
10/11/2011	Winter	8	06:18:00	1	06:28	04:28:32	5	49
				2	06:34	02:36:58	3	28
				3	06:40	04:18:48	5	47
				4	06:45	04:40:12	5	50
				5	06:53	04:36:53	5	49
				6	06:59	04:23:12	5	47
28/11/2011	Winter	9	06:31:00	1	14:03	03:24:04	4	37
				2	14:10	02:47:40	4	30
				3	14:15	02:24:11	4	25
				4	14:24	02:40:28	4	30
				5	14:31	02:38:28	3	28

Date	Season	Deployment	Sunrise	Reef	Start time	Duration	Number of 1 hr segments	Number of 5 min intervals
				6	14:38	02:40:35	3	29
04/04/2012	Spring	10	06:53:00	1	15:08	04:34:24	5	50
				2	15:12	04:29:24	5	49
				3	15:17	04:24:24	5	48
				4	15:24	04:14:10	5	46
				5	15:33	04:04:10	5	44
				6	15:40	03:59:10	5	43
11/04/2012	Spring	11	06:46:00	1	14:44	04:11:20	5	45
				2	14:41	04:42:03	5	51
				3	14:38	04:20:21	6	47
				4	14:34	04:01:15	5	43
				5	14:28	04:40:08	6	50
				6	14:23	01:43:46	3	19
19/04/2012	Spring	12	06:38:00	1	10:54	04:21:52	5	47
				2	10:49	04:33:43	5	48
				3	10:44	04:14:18	5	46
				4	10:38	04:39:57	5	50
				5	10:32	04:43:34	6	51
				6	10:25	04:44:10	6	52
22/04/2012	Spring	13	06:36:00	1	07:47	04:29:27	5	49
				2	07:51	04:53:19	6	53
				3	07:54	04:22:21	5	47
				4	07:58	04:47:30	6	52
				5	08:04	01:06:35	2	12
				6	08:07	04:53:53	6	53
02/05/2012	Spring	14	06:28:00	1	06:44	04:23:33	5	47
				2	06:47	04:57:00	6	54
				3	06:52	04:15:46	5	46
				4	06:58	04:41:37	6	52
				5	07:05	04:48:59	6	51
				6	07:16	04:42:15	6	51
11/05/2012	Spring	15	06:22:00	1	10:53	04:27:13	5	48
				2	10:57	04:47:35	6	52
				3	10:59	04:26:12	5	48
				4	11:03	04:38:32	6	50
				5	11:08	04:49:47	6	53
				6	11:13	04:45:11	6	51