REPORT

Small coral reef fishes with large ecological footprints

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Abstract Seascape connectivity can facilitate key ecosystem functions in complex ecosystems like coral reefs. Many reef fishes move across the seascape, bridging different ecosystems. However, their role in shaping important functions, such as biomass production and nutrient cycling, is still poorly understood. This study, therefore, assesses the extent of natural movements of cardinalfishes (Apogonidae), one of the major contributors to nocturnal fish biomass production with the potential for a major role in transferring energy and nutrients between sandy ecosystems and adjacent coral reefs. Consistent with previous work, showing their ability to move distances of 100 s to 1000 s of metres when displaced, we reveal that these small fishes undergo major voluntary nocturnal foraging forays extending up to at least 145 m from reef structures. Their estimated daily movement distances are at least 430 times greater than expected based solely on body size-home range expectations. Given their large travel distances and strong homing abilities, apogonids may provide a major conduit for material transfer between lagoonal soft sediment habitats and adjacent coral reefs. These results highlight the potential importance of apogonids in the cross-system or cross-habitat transport of energy and nutrients on coral reefs.

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Introduction

Because of the logistical challenges involved in studying coral reef systems at night, our knowledge of the ecosystem functions of nocturnal organisms has lagged behind our understanding of their diurnal counterparts. The nocturnal period on shallow coral reefs is known to be a time of increased biomass of low trophic level organisms, mainly plankton (Alldredge and King 1977, 2009; Ohlhorst 1982; Carleton and Hamner 2007). This increase in low tropic level organisms may provide a substantial source of energy/resources to coral reef ecosystems, facilitated by reef-associated nocturnal predatory organisms. However, we have a very poor understanding of if, how, and where reef organisms interact with these resources. It is well known that many reef fishes feed at night. Of these, the most energetically important on the Great Barrier Reef are the cardinalfishes, family Apogonidae (Collins et al. 2022). These highly abundant, nocturnal reef fishes have been recently shown to dominate biomass production by nocturnal coral reef fishes on the Great Barrier Reef (Collins et al. 2022).

In the present study, we focus on the potential role of tropical coral reef-associated apogonids in mediating energetic and nutrient connectivity, by moving and feeding away from coral reefs at night but resting on reefs during the day. Earlier research on apogonids significantly increased our understanding of apogonid ecology and breeding behaviour (Kuwamura 1985; Okuda 1999; Vagelli 1999). More recently, a great deal of research effort has focused on the movement of these fishes, highlighting their capacity to perform extreme 'homing' movements of up to 5 km,

and often larger than 1–2 km (Marnane 2000; Gardiner and Jones 2005, 2010, 2016; Rueger et al. 2016). 'Homing' studies involve the capture, tagging and releasing of individual fishes at varying distances from their place of capture. However, although valuable, these studies have only a limited ability to indicate space use by these fishes as even strongly site attached species are able to exhibit strong homing behaviour (Streit and Bellwood 2018). To date, the furthest recorded natural 'voluntary' daily movements of tropical coral reef apogonids was documented by Marnane and Bellwood (2002), who reported apogonid species moving up to 30 m off the reef at night. However, this distance was limited by the methods used, not the apogonids per se. To the best of our knowledge, there have been no reports of natural daily movement of coral reef apogonids beyond this distance.

Understanding how and where organisms interact with their environment is proving to be an extremely challenging question in ecology. The first step is to understand the ecological footprint of an organism or population, i.e. the spatial extent of their potential interactions. Only then can their functional footprint be established, i.e. the locations within this broader area where specific functions are actually delivered. It is an implicit assumption of many studies that if an organism is present at a location, then their function is delivered at that location (Bellwood et al. 2019). This would probably be a correct assumption for most sessile organisms. However, for mobile organisms, recent studies have shown that the delivery of functions is much more patchy and complex than expected (Streit et al. 2019). For highly mobile species of coral reef fishes, for example, their movement patterns can cover tens of kilometres (Zeller 1998; Kaunda-Arara and Rose 2004; Meyer et al. 2007; Welsh and Bellwood 2014). Furthermore, the functions of an individual are often not delivered to every location it passes through (i.e. Welsh and Bellwood 2012). There is also the potential for limited spatial overlap in the delivering of different, complementary functions (Tebbett et al. 2017, 2020; Streit et al. 2019). This issue raises three interesting points for nocturnal reef fishes, which often migrate to forage during the night (Nagelkerken et al. 2000; Nagelkerken and Velde 2004; Hitt et al. 2011b; Koeda et al. 2021). Firstly, it is more than likely that the functional feeding impact of nocturnal predators is delivered at locations that are away from diurnal resting sites (Holland et al. 1996; Holzman et al. 2007; Meyer et al. 2007). Secondly, that feeding areas vastly exceed an individual's space use while resting (Nagelkerken et al. 2000; Hitt et al. 2011a). And, finally, that their excretion is likely to be concentrated in small resting areas during the day (Randall 1967; Francis and Côté 2018), compared to their wider ranging feeding areas at night. This spatial decoupling of functions could mean that nocturnal reef fishes play important functional roles in both off-reef locations, as predators, and

on-reef resting sites, as prey or nutrient providers (Randall 1967; Beukers-Stewart and Jones 2004; Francis and Côté 2018). They may therefore be acting as important agents delivering cross-system subsidies (i.e. transferring energy or material from one area to another 'subsidising processes' in the latter with resources from other habitats, cf. Morais and Bellwood 2019). The first step in developing a functional understanding of these processes is to quantify space use by nocturnal fishes.

The goal of this study, therefore, was to characterise the natural movements of apogonids between reefs and the surrounding sandy habitats, to get an indication of the spatial extent of their ecological and functional footprints. To do this, a new, spatially comprehensive, method for assessing movement in nocturnal fishes was developed, aiming to detect the space use of apogonids within a coral reef lagoon. These space use data will further our understanding of how these fish move onto, and interact with, adjacent ecosystems. They offer a window into the potential role of apogonids in connecting coral reef ecosystem dynamics to the surrounding seascape.

Materials and methods

Nocturnal video units (NVU's)

To observe nocturnal fishes in situ and to quantify nocturnal feeding forays of the most common and abundant nocturnal reef fish, apogonids, we designed and constructed an autonomous nocturnal video unit for fish identification, which combines remote video and red illumination. These units are hereafter termed "Nocturnal Video Units" or NVUs (Fig. 1). Below, we briefly describe the camera and illumination components of the NVUs. For a more detailed description of each component, the setup, and the principles behind their use please see Supplemental Material S1.

The camera system for the NVUs was designed around a GoPro™ Hero8 and a 5200 milliampere external power bank which allowed the cameras to record uninterrupted for approximately five hours. This setup was housed in a 1.5 l glass clip top preserve jar (Fig. 1a). We used the GoPro™ Hero8 QR control feature (accessible in https://gopro.github.io/labs/control/) to replicate the settings for all GoPro™ cameras in every deployment, including a time overlay on the video footage (see Table S1). The light system for the NVUs consists of two LED systems connected to separate 10,000 mA power banks via a 12 V step-up cable. These two LED systems were also placed inside a 1.5 l clip top glass preserve jar. For this study, red light was used to balance the need to reduce disturbance to fish behaviour (compared to white light) and enhanced underwater penetration (compared to infrared

Fig. 1 **a** A Nocturnal Video Unit (NVU). The camera, light and support systems are highlighted. **b** Lizard Island map showing site locations (blue dots). **c** Individual NVU deployment locations (blue dots), within sites (larger numbers in circles) each based on three arrays over three nights. **d** A still from an NVU video of a school of Apogonidae visible on the left-hand side at 21:30
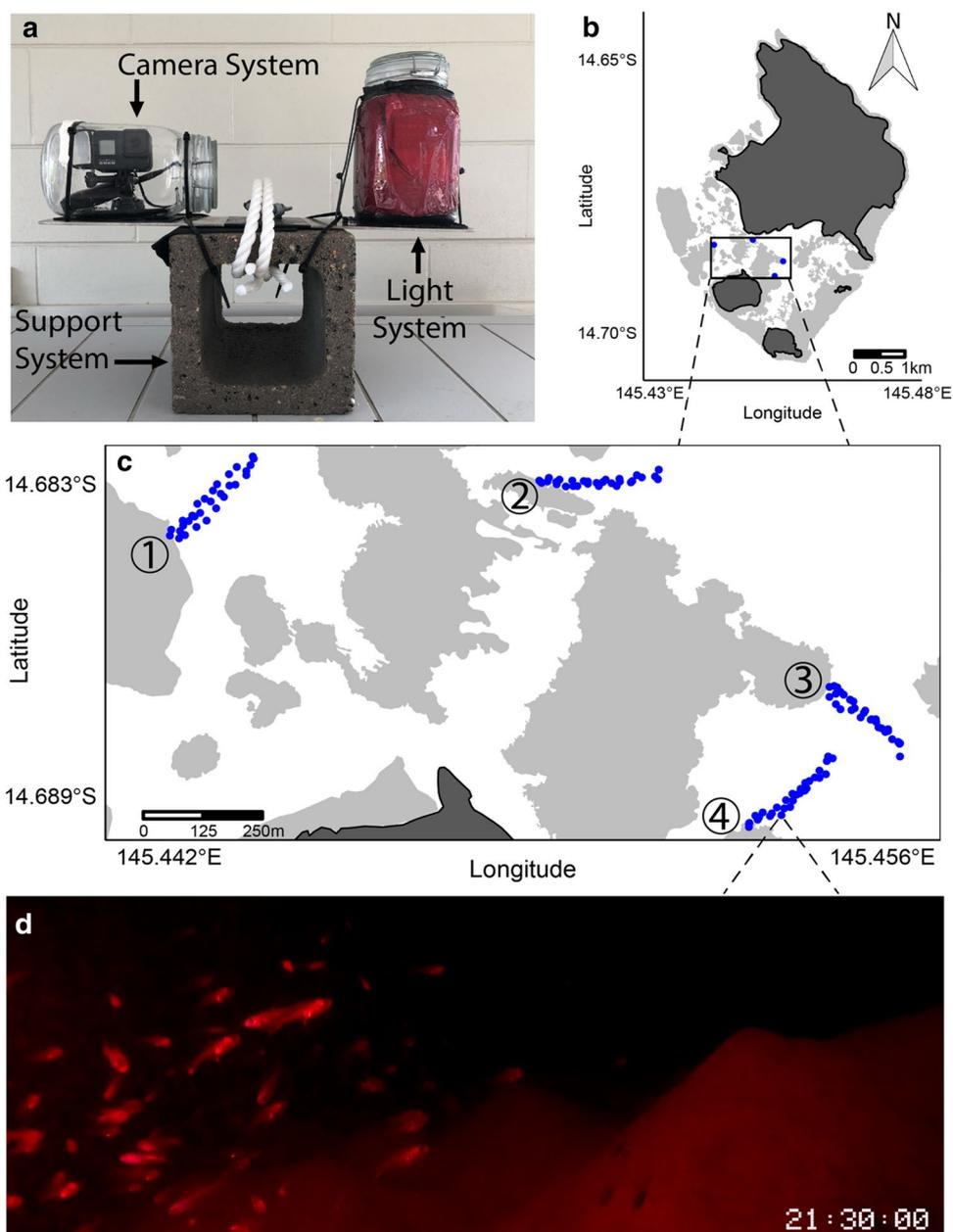

light normally used for nocturnal filming in terrestrial systems). To ensure that only light at wavelengths greater than ~600 nm (i.e. red–orange to red) were emitted, we performed a series of tests using a Satlantic HyperOCR™ radiometer in a dark room. Tests showed that four layers of red-light filter plastic allowed for the removal of light at wavelengths less than 585 nm and kept 95% of light above 600 nm (see Fig. S1). The red wavelength has previously been found to provide adequate illumination for fish detection (e.g. Fitzpatrick et al. 2013; Madin et al. 2019) while producing minimal disturbance; it is outside the main area of detection for reef fishes (Job and Shand 2001).

Spatial deployment system of the NVUs across a coral reef lagoon

Four sites were established for the deployment of NVU arrays in the coral reef lagoon at Lizard Island, on the northern Great Barrier Reef (Fig. 1). At each site, the NVU array started on the edge of the reef, at the interface with the sand. From this starting location, ten NVUs were placed as evenly as possible along a 200 m virtual line perpendicular to the reef site out onto the sand (Fig. 1). GPS coordinates of each individual NVU in the array were recorded during each deployment. One array was deployed each night before

Fig. 2 The probability of detection of apogonids in NVUs against distance from the reef in a coral reef lagoon during both day and night. Dots represent the raw data points. The blue colour indicates data from the daytime (18:30–18:35) counts and black represents the night-time (21:30–21:35) counts. The solid black line shows the mean probability of detection and shaded intervals represent the 95 per cent confidence intervals
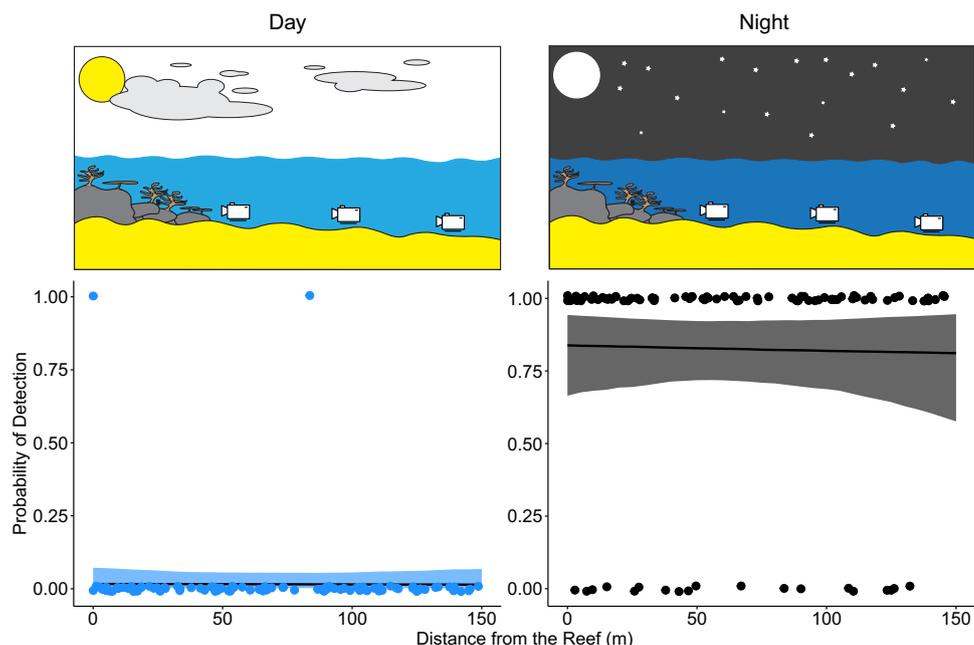
sunset, between 17:45 and 18:15, and retrieved between 07:00 and 07:15 the following morning. Over the study period, three array deployments were carried out at each site.

Video analysis and subsampling procedure

Over the course of this study, a total of 120 individual NVUs were deployed across the four deployment sites (i.e. ten NVUs per night × three nights per site × four sites), of these 120 deployments 36 could not be analysed due to technical issues (described in Supplemental Material S1). However, the remaining 84 videos yielded over 500 h of footage. To address the specific questions of this study, we subsampled this video footage pool. We first established two benchmark time periods, a pre-sunset period (between 18:30 and 18:35), hereafter 'day sampling'; and a nocturnal period (between 21:30 and 21:35, hereafter 'night sampling'). For each video (i.e. from an individual NVU) at each time period, an individual frame (i.e. a 'still') at the beginning of each minute was assessed for the presence and abundance of apogonids (i.e. six pseudo-replicated stills per video per time period). Whenever apogonids were present, they were counted and identified to family, genus, or species where possible. To obtain an abundance value from each camera in both time periods the highest abundance of the six stills was recorded as a MaxN value. Given the much greater visibility in the day sampling compared to the night, we endeavoured to standardise the survey area between time periods by limiting detection to a maximum of 1.5 m, our post-hoc estimate of average nocturnal visibility using the NVU system.

To get an understanding of the apogonid communities on the reef at each site and to obtain an estimate of the average size of apogonids, two 50 m underwater visual surveys were conducted at each site during the day (Fig. S3). These counts were carried out by a single observer (W. Collins) and focused exclusively on identifying apogonid species at each location. For further detail on the survey methods, see Supplemental Material S1, data from these counts is also provided in Supplemental Table S2.

The focus of this study is on the relationships between (A) presence (detection) and (B) abundance of apogonids recorded by the NVUs at night vs. their distance from the reef. Distance from the reef was measured as the distance from each NVU to the nearest reef. We created a georeferenced set of reef polygons in the Lizard Island reef complex using Google Earth Pro (2010/2011 images) and manually traced the outline of the reefs at an eye altitude between 150–400 m. These polygons were imported into R (R Core Team 2021) and the distance from each NVU deployment to its nearest reef location was calculated (for details see Supplemental Material S1). This calculation was used as a proxy for space use in apogonids assuming that apogonids return to the reef during the day to rest and leave to feed over sandy substrata at night. This is a reasonable assumption given the frequency with which apogonids are observed on the reef during the day at Lizard Island and given data on their distribution over sand from other locations (Marnane and Bellwood 2002). However, to ensure that was the case, we contrasted the detections and abundance of apogonids over sand during both day and night using the sampling scheme described above (i.e. day and night).

(A) Presence in each NVU deployment was assessed as the detection of at least one individual apogonid in
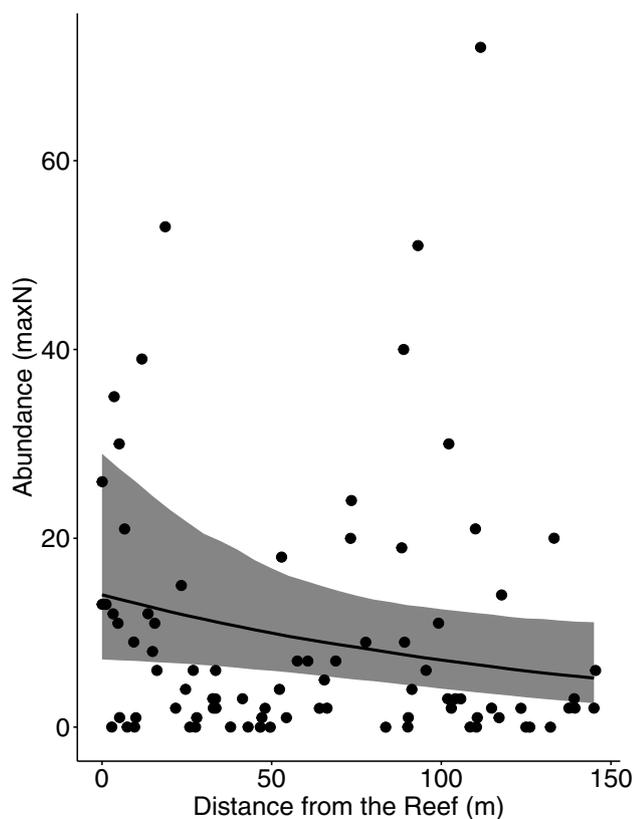
Fig. 3 Apogonid abundance (MaxN) from NVUs relative to their distance of detection from the reef. The dots represent the raw data, the solid black line shows the mean abundance, and the shaded intervals represent the 95% confidence intervals

any of the six analysed frames of each video in each time period. We modelled the probability of detection of apogonids (response) as a function of time period (day or night) and distance from the reef (explanatory variables) using a Bayesian generalised linear mixed effect model with a binomial error distribution and a log link function. We also included sampling date as a random effect to account for the distribution of individual images per site in consecutive nights. Finally, we also included site and an interaction between site and distance from the reef as facultative predictors to evaluate whether this would enhance model fitting.

(B) A similar procedure was carried out for modelling the abundance data. Abundance was determined as the maximum number of individuals (i.e. MaxN) counted on any single frame analysed in each video of each time period. This time, however, the response variable was the abundance of apogonids as approximated by their video-specific MaxN. The exact same explanatory variables and random effects were used in this model procedure, also resulting in three different models.

Models used the No-U-Turn Markov Chain Monte Carlo (MCMC) sampler in Stan via 'rstan' (Stan Development Team 2020) and 'rstanarm' (Goodrich et al. 2020) in R (R Core Team 2021). All further model details (i.e. distributions, priors and diagnostics) are described in Supplemental Material S1.

Transforming and modelling occupancy area data

To compare the likely movement distances of apogonids, as obtained from our NVU spatial design, with the literature, we compiled 'home range' estimates (hereafter termed 'occupancy areas') as a function of fish body mass from multiple published studies following (Nash et al. 2015; Streit et al. 2021). As the shape of these estimates of occupancy area was not readily accessible, we conservatively assumed that estimates stemmed from circular occupancy areas. To relate the published occupancy areas back to our recorded movement distances of apogonids, we calculated the diameter of the circular occupancy areas, which we considered as the estimated maximum (fish movement) distance (EMD).

Using these derived diameter estimates, we then modelled the relationship between body mass and estimated maximum fish movement distance (see Supplementary Material for modelling details). Finally, we used this model to estimate the expected maximum movement distance of fishes from our reef-based counts based on fish body sizes.

Results

Day vs. night samples

The majority of the NVUs (69 of 84) detected apogonids, regardless of the deployment site and distance from the reef. One camera detected apogonids only during the day, and one camera detected apogonids during both the day and the night. All other cameras detected apogonids only at night (i.e. they were surveyed and found to be absent during the day). The mean probability of detecting apogonids over the sandy substrata away from the reef during the day period (i.e. 18:30–18:35) was, thus, only 2% (95% CI 0–6%; Fig. 2). This contrasted sharply with the 84% (95% CI 72–92%) mean probability of detecting apogonids during the night period (i.e. 21:30–21:35; Fig. 2). This probability of detecting apogonids on sandy substrata during either day or night was not affected by distance from the reef, as this predictor had a negligible effect on the probability of detection that overlapped with 0 (distance effect $= -0.001$, 95% CI -0.012 to 0.011).

As there were only two individual apogonid detections in the day period, we subsequently only evaluated the

patterns of abundance at night. Abundance (as proxied by the MaxN across six frames analysed) ranged from 0 to 72 individuals across all samples, with a mean of 9.15 individuals (95% CI = 5.52–15.19; Fig. 3). In contrast to detections, the median abundance of apogonids declined markedly as the distance from the reef increased. This followed an average decline of 0.06 individuals (95% CI = −0.19 to 0.01) per additional m away from the reef (e.g. $\bar{x}$ = 14.0 individuals, ± 95% CI = 7.2–29.0 at 0 m; to $\bar{x}$ = 5.2 individuals, ± 95% CI = 2.5–11.1 at 145 m; Fig. 3).

When assessing site-specific differences in apogonid movement we found that in all sites both the maximum and average detection distances were substantially greater than the previously documented maximum of 30 m (mean of 62 m across all sites; Fig. 4). At all sites, apogonids were consistently detected at the furthest distance that cameras were deployed from the reef.

The model relating body mass and potential movement distance of reef fishes using occupancy area data collected from the literature predicted that the estimated movement distance of an average-sized apogonid from our counts (2.3 cm) would be only ~ 33 cm (Fig. 5). This

estimate is roughly 430 times smaller than the maximum distance from the reef where we detected apogonids using the NVUs (145 m, Figs. 3,4, 5).

Discussion

Homing and natural movements of apogonids

Early observational reports suggested that tropical coral reef-associated apogonids moved only a few metres away from the reef to feed (Allen 1993). Furthermore, the only systematic survey of tropical coral reef apogonids in off-reef nocturnal feeding locations had restricted sampling to 30 m away from the reef (Marnane and Bellwood 2002). In the present study, using a comprehensive survey of non-reef habitats at night, we found apogonids undergoing daily movements of up to 145 m from the reef. Furthermore, this maximum was limited by the local reef geomorphology, which constrained the distance we could survey away from the closest reef. Given that the probability of detection of apogonids did not decrease between 0 and 145 m from the reef, there is strong evidence to suggest that these are

Fig. 4 The estimated ranges of apogonids at four sites in Lizard Island lagoon using nocturnal video units (NVUs). The blue circumference represents the maximum detected distance, central radius represents the mean distance detected and the 30 m radius represents the maximum detected distance from the literature for coral reef apogonids (Marnane and Bell-wood 2002). Small black dots represent the expected potential movement distance, based on body size, of a few randomly selected individuals from our visual counts
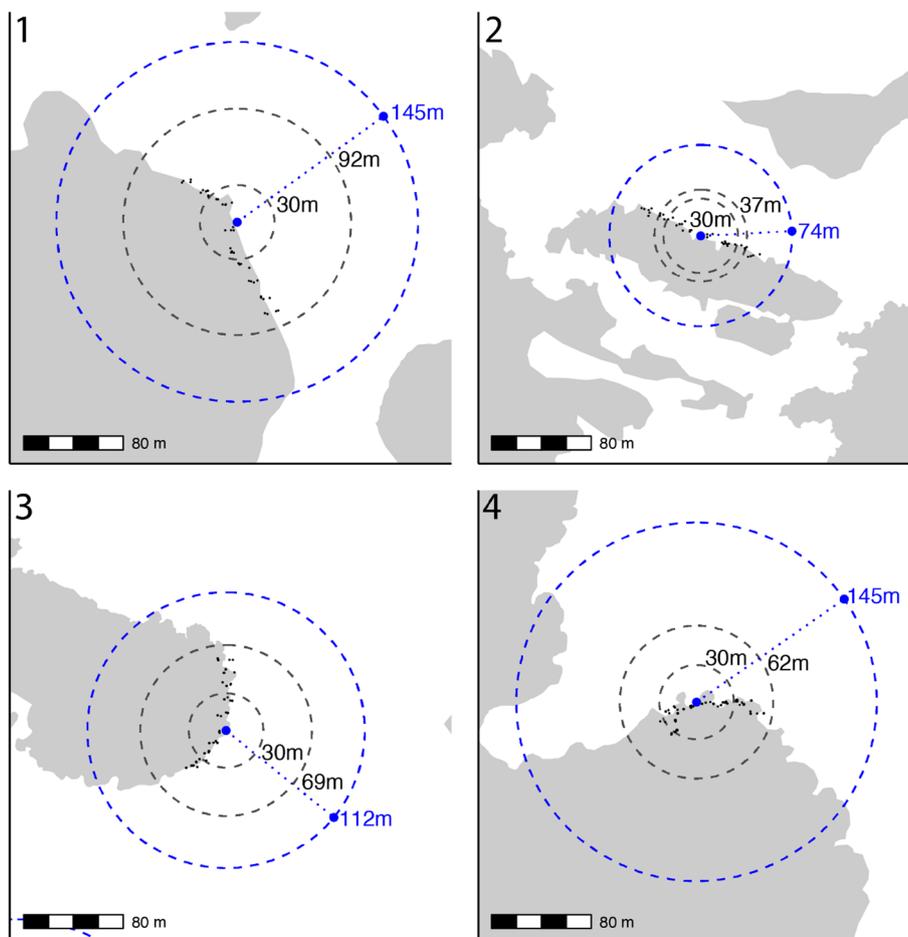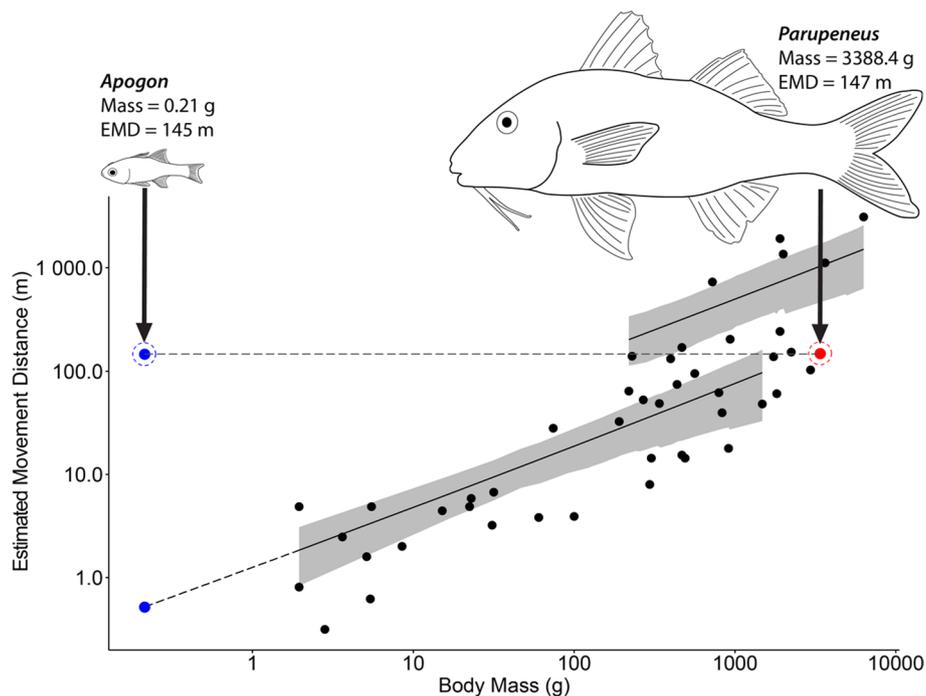
Fig. 5 Estimated *maximum* movement distances (EMD) (m) as a function of species maximum body size (g) for coral reef fishes. Note the log scale on both axes. Data collated from Nash et al. (2015) and Streit et al. (2021). Grey bars represent the upper and lower 95% highest posterior density intervals. Black lines represent the mean posterior predicted values. Lower blue dot indicates the average body mass and EMD of individuals from the counts. Upper blue dot represents the movement distance we found in this study. Red dot represents the species with the closest EMD to the apogonids we detected. Of the two separate trend lines on the figure, the top line represents the trend for studies using acoustic telemetry and the lower line represents studies which used visual surveys

highly conservative estimates of minimum voluntary movement distances, and these apogonids are likely moving much further than we observed. Furthermore, as the starting locations are assumed to be the nearest reef, actual movement of individuals may be much further than estimated even at this location. However, taking 145 m as a conservative estimate of the potential foraging distance implies a daily movement of ~ 290 m (out to feeding areas at night and returning before sunrise). This suggests that their minimum homing ability from Gardiner and Jones (2016), of ~ 400 m, is comparable to the inherent daily movement of some of these fishes.

The distances we found apogonids moving are far greater than what one would expect given their typical body size. Extrapolating from the data in Fig. 5, the potential movement distance (i.e. diameter of a circular occupancy area) of the average size apogonids from the counts, would be only on the order of 33 cm. However, we detected them at distances up to 145 m, roughly 430 times greater than the estimate based on body size. Furthermore, if this estimated movement distance (EMD) is taken as the radius of a circular occupancy area rather than a diameter, this would mean a EMD of up to 290 m, over 860 times greater than the estimate from body size alone, representing a distance over 12,600 body lengths. Even the most conservative estimate

(i.e. diameter) would still yield a potential daily movement distance for the average apogonid in this study that is comparable to a much larger species (e.g. *Parupeneus porphyreus*, with an average body mass of 3.34 kg, 16,135 times larger; Meyer et al. (2000) and Nash et al. (2015)).

The fact that these apogonids are moving such disproportionally large distances across habitats that lack any physical structure for protection against predation suggests that either (1) predation on these fishes is not sufficient to constrain their movements; or (2) that there are other ecological benefits in this movement that outweigh the predation risk. This, then, begets yet another question: how do such small fishes engage in such long-distance, presumably daily, movements, and what are the functional consequences of these movements? Functionally, this movement has the potential to facilitate spatial subsidies, i.e. these apogonids could be transporting energy and nutrients from sandy areas to coral reefs (e.g. Hobson and Chess 1978; Graham et al. 2017; Benkwitt et al. 2019, 2021; Morais et al. 2021; Skinner et al. 2021).

The seascape functional role of apogonids

As various studies on the diet of apogonids have shown, these fishes feed mainly on relatively large (> 1 mm) 'planktonic' organisms (Hobson and Chess 1976; Gladfelter 1979; Marnane and Bellwood 2002; Holzman and Genin 2003). In this study, apogonids were seen in almost all of the NVU footage preying on small organisms just above the sand (see supplementary text 1.4. Behavioural Observations), highlighting the role of these fishes as off-reef nocturnal predators (whether they represent 'planktivores' requires further consideration). Given their high resting site fidelity (Rueger et al. 2014, 2018; Gardiner and Jones 2016), there is the potential for apogonids to play an important role in transferring energy and nutrients from off-reef locations to the reef (cf. Marnane 2000). This seascape function differs from that of diurnal planktivores as apogonids are moving off the reef to find prey while diurnal planktivores require currents to carry the prey to them (Morais et al. 2021). However, both types of fish contribute by falling prey to reef predators (Randall 1967; Shpigel and Fishelson 1989; Kingsford 1992; Beukers-Stewart and Jones 2004) and through excretion and (presumably) defecation at diurnal reef resting sites. Furthermore, the whole area over which individual apogonids forage remains to be determined; this may have important ecosystem implications. If these areas extend from their resting areas up to the feeding locations where they were detected herein, then it is possible that these fishes reflect similar patterns to small diurnal planktivores. As an assemblage, these diurnal planktivores exploit resources from areas several orders of magnitude larger than would be expected based on individual body size alone; they thus have an over-sized 'ecological footprint' (cf. Morais et al. 2021). This spatially extensive presence also suggests that these inherently reef-associated fishes may also have a large functional footprint (they were regularly seen feeding in the NVUs). They may thus be dependent upon the resource production of near-reef sandy habitats and may be susceptible to habitat changes occurring beyond the reef. However, if their off-reef feeding areas are substantially further than the distances we saw them travelling, then apogonids could still provide spatial subsidies to reefs but may be dependent on the productivity of another type of habitat (beyond the lagoon). Regardless of the areas harvested by apogonids, they are likely to have a much larger ecological and functional footprint than expected based on their body size alone.

A regular migration or something else?

Although apogonids were detected up to 145 m off the reef at night, they were as likely to be detected at 1 m, and indeed at every other distance in-between. What factors, then, may be driving some individuals to travel 145 m while others

only 1–2 m? Marnane and Bellwood (2002) noted a vertical spatial segregation of apogonid species at night. It would also be conceivable that the off-reef distribution patterns described herein are in part driven by a species-level segregation by distance. Although most individuals seen in NVUs were visually similar, the resolution of red-light images was limited, thus we could rarely identify the species involved. This species segregation hypothesis, thus, remains to be tested. Nevertheless, it must be noted that the abundance of apogonids was not evenly spread across the lagoon; it declined with distance from the reef. Why most individuals remained close to the reef remains to be determined.

The distribution of nocturnal predators such as apogonids could also be influenced by the availability/distribution of their prey. Emergent plankton slowly rise from the substratum at differing times (Ohlhorst 1982). This slow release of plankton from the substratum provides a steady supply of prey for predators that could be likened to the suggested 'wall of mouths' of planktivores (Hamner et al. 1988). The 'wall of mouths' describes the consumption of pelagic plankton as it hits the external edges of reefs (Hamner et al. 1988). In the nocturnal case, we suggest the term 'blanket of mouths', in which planktivorous nocturnal predators distribute themselves horizontally, instead of vertically, to feed on the newly available 'plankton' that emerges from the substratum to enter the water column.

One of the major consequences of the 'wall of mouths' is that predators can exploit areas where currents converge or are met with more topographically complex structure, increasing prey density or accessibility (Hamner et al. 1988; Brandl et al. 2019). Although studies have assessed the abundance and biomass of emergent plankton among different reef and non-reef substrata (Alldredge and King 1977; Ohlhorst 1982; Lewis and Boers 1991; Carleton and Hamner 2007; Carleton and McKinnon 2007; Kramer et al. 2013a), how this resource is distributed across a distance gradient from the reef is unclear. However, if we were to assume that predator abundance mirrors prey abundance, the higher abundance of apogonids we found near to the reef suggests that there could be an increase in abundance of larger emergent plankton closer to the reef. Alternatively, if emergent plankton exhibits similar population dynamics to crustaceans in algal turfs, then it is possible that their abundances are so large that fishes that feed on them have a negligible impact (Kramer et al. 2013b). In this case, the higher abundance of apogonids closer to the reef could simply be a consequence of individuals minimising travel distance, with distributions reflecting an expected null distribution as fishes slowly move away from the reef after sunset.

Conclusion

This study provides us with new insights into the natural nocturnal movement patterns of tropical coral reef-associated apogonids. These results expand our understanding of the potential functions that these fish perform on coral reefs and the locations where these functions may occur. We found that apogonids make voluntary diel migrations up to 12,600 times their body length, which is 430 times greater than expected based on their body size. These diel migrations allow these fishes to feed on organisms over broad expanses of near-reef lagoonal sandy substrata. These individual fishes then return to regular resting sites during the day, concentrating material gathered over a much larger areas during the night into a small resting location during the day. This finding provides yet another spatial link between the off-reef and on-reef food webs that, given the high rates of biomass production of apogonids, may represent a significant, if unseen, source of external subsidies for coral reef ecosystems.

Data availability Data and code required to reproduce all the analyses and results will be made available in "Zenodo", a public data repository.

Declarations

Conflict of interest The authors declare no competing interests.

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