Coral Reefs
https://doi.org/10.1007/s00338-022-02258-3

REPORT

Highly repetitive space-use dynamics in parrotfishes

Renanel Pickholtz[1,2] · Moshe Kiflawi[2,3] · Glenn T. Crossin[4] · Eliezer Pickholtz[5] · Revital Zamsky[1] · Inbal Kahan[2] · Tal Gavriel[1] · Jonathan Belmaker[1,6]

Received: 11 July 2021 / Accepted: 8 April 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract Understanding space-use patterns in parrotfish (Scarini) is especially important for coral reefs, where herbivores play a key role in maintaining reef health. However, we lack the long-term high-resolution data needed to understand parrotfish space-use patterns over time. We examine long-term space-use dynamics in parrotfish (median duration: 359 days) by tracking 23 terminal-males of three species along a coral reef in the Northern Red Sea Gulf of Aqaba. We used acoustic telemetry to track horizontal movement along the reef, depth, and activity (through tri-axial accelerometers), and quantify the effect of environmental factors such as water temperature and algal abundance on long-term patterns. We found that in the species examined, nearly all individuals maintained a highly consistent spatial pattern throughout the study duration, in which they repeatedly moved along a distinct route between nighttime sleeping areas and spatially constrained daytime areas. Individual patterns were surprisingly conserved over time, despite seasonal changes and variation in resource abundance. Individuals differed considerably in their daily travel distance, with some traveling up to 2000 m along the reef, while others moved only between deep and shallow areas. Activity levels consistently peaked around mid-day, regardless of the location of their daytime areas, which behavioral surveys confirm are associated with feeding activities. We also detected peaks in activity during early mornings when surveys detect that parrotfish interacted in large aggregates (typically 30–60 individuals). Our findings indicate that space-use patterns vary among individuals but are extremely conservative within individuals over long time periods. This in turn may have important consequences to the health of reefs, as individual parrotfish may be less likely to alter foraging patterns as conditions change. Furthermore, the high fidelity to limited sleeping and daytime areas may be a source of concern, as local small-scale disturbances may strongly disrupt individual space-use patterns.

Keywords Space-use · Herbivory · Individual behavioral variation · Parrotfish · Site fidelity · Telemetry

Topic Editor Andrew Hoey

✉ Renanel Pickholtz
renanel.pickholtz@gmail.com

1 School of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, 69978 Tel Aviv, Israel

2 The Interuniversity Institute for Marine Sciences of Eilat, 88103 Eilat, Israel

3 Department of Life-Sciences, Ben-Gurion University of the Negev, POB 653, 84105 Beer-Sheva, Israel

4 Evolutionary Physiology and Animal Ecology Laboratory, Department of Biology, Dalhousie University, Halifax, NS B3H 1J8, Canada

5 Independent Researcher, Piscataway, NJ, USA

6 Steinhart Museum of Natural History, Tel Aviv University, 69978 Tel Aviv, Israel

Introduction

Grazing can have a dramatic influence on the structure of plant and algal communities in both terrestrial and marine systems (Sommer 2000; Adler et al. 2001) and can affect ecosystem dynamics (Palmer et al. 2004). Ecologists and conservationists are increasingly interested in understanding the degree to which individual grazers differ from one another, as well as the persistence of these differences across time with respect to environmental conditions and resource availability (Riotte-Lambert and Matthiopoulos 2020; Shaw 2020; Webber et al. 2020). Marked inter-individual variation

Published online: 27 April 2022

can have consequences for population dynamics, dispersal, management, and conservation (Dall et al. 2012; Bierbach et al. 2016; Spiegel et al. 2017; Hertel et al. 2019; Moiron et al. 2020).

Heterogeneity in grazing intensity is particularly important for coral reefs whose resilience relies heavily on the ability to resist shifts toward a macro-algae-dominated state (Bellwood et al. 2004; Hughes et al. 2010). Resistance to such phase-shifts is largely attributed to herbivorous fish that feed on the algae that would otherwise outcompete the corals (Mumby et al. 2006; Hughes et al. 2007). Delivery of such critical ecosystem functions by herbivorous reef fishes has been shown to be highly heterogeneous and spatially restricted, which may have significant ramifications when assessing overall reef resilience (Streit et al. 2019). Among herbivorous reef fish, parrotfish (Labridae: Scarini) are widely considered key to maintaining healthy coral reefs (Bonaldo et al. 2014; Cramer et al. 2017). As such, the behavior and patterns of parrotfish habitat utilization are increasingly a focus of ecological and conservation studies.

Several studies have tracked parrotfish, mostly through acoustic telemetry, which allows the study of aquatic animals in their natural habitat (Hussey et al. 2015). Some general characteristics of parrotfish movement emerge despite the range of focal species and regions studied. Parrotfish utilize deeper habitats at night and migrate daily to shallower waters where they feed (Afonso et al. 2008; Welsh and Bellwood 2011; Gomi et al. 2021). Davis et al. (2017a) tracked *Chlorurus microrhinos* in Palmyra Atoll for up to 543 days and found that fish commonly traveled through the same areas during early mornings and evenings on their way from and to offshore sleeping sites. Parrotfish also consistently return to the same, often spatially constrained, feeding areas or sites (Welsh and Bellwood 2012; Davis et al. 2017a). Carlson et al. (2017) found that parrotfish defended and re-grazed the same areas, and that the most intensely grazed areas were highly restricted (250–800 m^2). Suggested factors that shape parrotfish space-use patterns include habitat complexity (Welsh and Bellwood 2011), dietary preference and resource availability (Carlson et al. 2017), social status (Afonso et al. 2008), and competition with other herbivores (Davis et al. 2017b). However, as most studies to date have either been limited to less than two months or conducted at relatively coarse spatial resolution (km^2), variation in fine-scale fish space use patterns over time remain unclear.

Behavioral ecologists have commonly examined individual variation in space-use in response to external factors such as social dynamics and environmental conditions (Hertel et al. 2020). However, a growing body of research indicates the importance of behavioral variation among individuals (e.g., Sih et al. 2004; Réale et al. 2007). Individual variation has been shown in relation to foraging site fidelity—where individuals can either repeatedly forage at the same site or utilize different areas over time (Baylis et al. 2012). Individual variation in space-use, particularly movement and site fidelity, can be indicative of individual variation in utilizing heterogeneous environments (Bell et al. 2009; Thorbjørnsen et al. 2021) and may have consequences for individual foraging efficiency under varying climate conditions (Hertel et al. 2020 and references therein). Behavioral variation in site fidelity within and among individuals can provide insight into processes that shape space-use dynamics, and have consequences for population resilience and conservation (Wakefield et al. 2015; Hertel et al. 2020). Tracking studies have reported behavioral variation among individual parrotfish (e.g., Lindholm et al. 2006; Afonso et al. 2008; La Mesa et al. 2012). However, the prevalence of individual variation in parrotfish behavior and its contribution to overall space-use patterns has not been assessed directly. This is key to understanding the underpinnings of grazing and space use patterns at both the individual and population level.

In this study, we used acoustic telemetry to examine patterns of habitat utilization by three species of parrotfish common to the Red Sea Gulf of Aqaba: daisy parrotfish (*Chlorurus sordidus*), rusty parrotfish (*Scarus ferrugineus*), and purple-brown parrotfish (*S. fuscopurpureus*). We continuously tracked individuals at high sampling rates (median < 5 min) for up to 18 months. We used these data to evaluate the degree of variation in space-use exhibited by individuals, and how space-use changes over time and in response to environmental factors.

Material and methods

Study species

As with most scarine labrids, *C. sordidus*, *S. ferrugineus,* and *S. fuscopurpureus* are all sequential protogynous hermaphrodites (Chaot and Randall 1986), who feed primarily on algae (Khalaf 2004; Hoey et al. 2016). We focused on terminal-phase males in order to avoid the potentially confounding effect of ontogenetic shifts in habitat-utilization (Welsh et al. 2013; Pereira et al. 2016; Smith et al. 2018).

Study site

This study was conducted from July 2016 to February 2019, along a fringing coral reef in the North-eastern Gulf of Aqaba (N29.50156, E34.91792; Fig. 1). This shallow reef is mostly continuous but is highly heterogeneous in structural complexity. Hard substrate predominates the shoreline for several kilometers and is largely devoid of fleshy macroalgae (typical of healthy coral reefs; Hughes 1994; McManus and Polsenberg 2004). The site is situated within a no-take

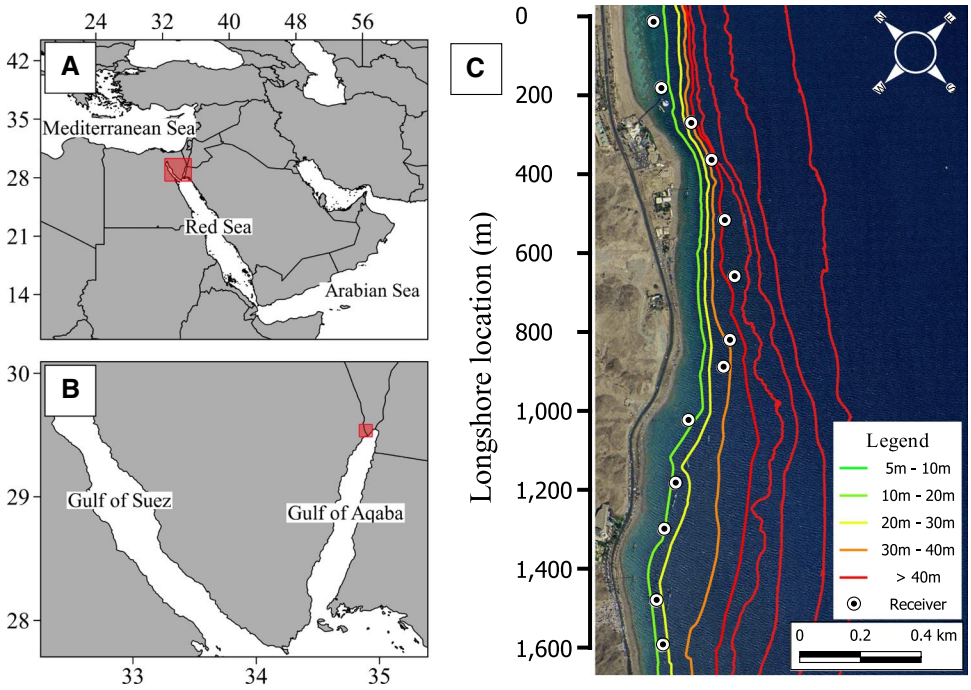

Fig. 1 The study site, located within the Red Sea (**A**), at the northernmost end of the Gulf of Aqaba (**B**). The array was deployed along the shallow reef, parallel to the coastline (**C**). Reef bathymetry is represented by depth contours (Monismith et al. 2006; Sade et al. 2008), and demarcates the depth beyond which parrotfish rarely occur (> 40 m; Fig. SI 1). Y-axis (**C**, left) shows the linear distance along the shoreline relative to the northernmost receiver (referred to throughout the paper as longshore position). Circles represent acoustic receivers (VR2W, Innovasea)

marine protected area, in which vessel traffic is extremely limited.

The reef at the study site is on a steep slope, where bottom depth drops rapidly to approximately 40 m over a distance of 100 m from shore (Hall 1978). The distribution of herbivorous reef fishes, including parrotfish, is limited to depths shallower than 30 m (Brokovich et al. 2010); similar to other reef systems (Nemeth and Appeldoorn 2009; Vergés et al. 2011; Lindfield et al. 2015). The study site therefore provides a uniquely narrow and elongated area where herbivorous fish move along two primary axes—along the coastline and within a finite depth gradient (which correlates to offshore distance). Importantly, parrotfish are highly associated with the substrate and typically follow reef topography (e.g., Bruggemann et al. 1994; Friedlander and Parrish 1998; Nemeth and Appeldoorn 2009); a fact that helped us estimate their position along the reef (see Fig. 1).

Acoustic telemetry tracking

We deployed an acoustic array of 13 underwater receivers (VR2W-69 kHz; Innovasea, Bedford, Nova Scotia) parallel to the coastline (see Fig. 1). The effective detection range of receivers (> 90% of transmissions recorded) was based on several range tests (see Pickholtz et al. 2018 for detailed procedures). Based on range test results, receivers were positioned at a conservative distance (90% detection rates) of 120 m apart from one another (Espinoza et al. 2011), and at depths ranging from 7 to 12 m. All receivers were moored to permanent pre-existing buoys, mostly along the deeper reef edge (> 40 m depth), which provided a largely unobstructed side-view of the shallow reef where parrotfish are commonly found.

Fish were tracked using surgically implanted acoustic transmitters (or *tags*) with unique IDs and equipped with a pressure (i.e., depth) sensor, a tri-axial accelerometer, or both (see table SI 1 for details). In order to obtain both high sampling (i.e., transmission) frequency and maximal tracking duration, tags were programmed to transmit at a nominal rate of 60 s for the first 70 days, then transmit every 300 s (5 min) for the remainder of their battery life. In order to avoid physiological or behavioral effects of the implanted transmitter, we strictly adhered to the accepted transmitter to fish mass ratio of 0.02 (Winter 1996). See supplemental information for fish collection and tagging procedures.

Space-use metrics

Depth

Depth was measured by pressure sensors (resolution = 0.075 m, measurement range 0–52 m). Given the tendency of parrotfish to swim close to the substrate and the fact that depth contours are essentially parallel to the shoreline (Fig. 1), depth measurement served both as an independent measure of space use (Matley et al. 2016) and as a proxy for horizontal distance from shore.

Longshore position

The linear layout of our receiver array did not support three-dimensional positioning (localization) of tagged fish, so detections were used as indicators of presence within the range of a given receiver. Given that parrotfish generally move within a narrow strip along the shoreline (due to depth restrictions), we used presence records to delineate longshore movements of fish. In order to not restrict estimated positions to those of receivers, we calculated the weighted mean position according to the relative frequency of each receiver's detections within 5 min windows (see Simpfendorfer et al. 2002 for details).

Longshore movement

Longshore movement is a standardization of *longshore position* references to each individual's northernmost record and scaled at the individual level and is thus less affected by the extent of the total array. While *longshore position* is a spatially explicit metric to estimate where fish are detected along the reef, *longshore movement* represents movement patterns of individuals throughout the study regardless of where on the reef they were detected. For example, in a case where two fish exhibit identical horizontal movements throughout the study but are located at different areas of the reef—*longshore position* patterns would inform the spatial distinction between the two, while *longshore movement* would capture the similarity in their movement patterns.

Activity

Activity was estimated in terms of acceleration, averaged across three axes (x = lateral, y = forward, and z = vertical) over each sampling period (5 s, at 5 Hz) (Brownscombe et al. 2017). This averaging is necessary with acoustic telemetry since tags can only transmit a single value. Though less detailed than most acceleration data used in animal tracking, valuable information on activity patterns could still be captured; such as the timing of onset, offset, and peak level of detected activity (e.g., de Almeida et al. 2013; Stehfest et al. 2015; Alos et al. 2017). We used accelerometers with the broadest available sampling range (0–5 $m \times s^{-2}$; Fig. SI 1.)

Environmental data

Environmental data used as predictors of fish movement patterns (see Fig. SI 2–3) were obtained from the Israeli National Monitoring program (https://iui-eilat.huji.ac.il/Research/NMPAbout.aspx), which maintains a meteorological station near the center of our acoustic array. These data include solar radiation (*S_rad*, W/m^2), water temperature (*Temp*, °C), and water level (*W_level*, cm), and are recorded every 10 min.

Seasonal variation in benthic algal availability was estimated through the use of settlement plates. Six sets of 10 × 10 cm PVC plates were placed arbitrarily at depths of 7–10 m in the middle of the acoustic array. Each set consisted of a plate protected by plastic mesh with 1 cm^2 holes. The plates provide a substrate for benthic algae settlement, while protecting it from herbivores such as fishes and sea urchins. Once a month, three sets were retrieved and replaced by a clean set, giving each set a two-month period of soaking underwater. Once extracted from the water, algal material was scraped off and filtered through a glass fiber GF/F filter. The filter was then placed in an acetone-methanol solution to extract photosynthetic pigments used to approximate the algal mass. Light absorption in the photosynthetic pigment wavelength (E647, E630, E664) was measured on a spectrophotometer for calculation of the amount of Chlorophyll-*a* (*Chl-a*, mg/cm^2). Due to local variability in algae settlement rates, each monthly estimate is the averaged abundance of the three sets retrieved that month. Settlement plates were maintained and measured by the Israeli National Monitoring program that tracks algal growth rates on the reef. A similar setup was used by Brokovich et al. (2010) to estimate growth rates of benthic algae, which also found that abundance of benthic algae on settlement plates coincided with the abundance of algal turf measured in situ. Many herbivorous reef fishes including parrotfishes have been shown to feed on turf algae (e.g., Tebbett et al. 2017, 2022), and target endolithic and epiphytic phototrophs (e.g., Clements et al. 2016; Clements and Choat 2018; Nicholson and Clements 2020). While *Chl-a* measurements from settlement plates do not discriminate between different algae nor their associated fauna, variation in *Chl-a* is used as an indirect approximation for long-term variation in resource availability.

The time of sunset and sunrise changed throughout the study. Thus, to model the effect of different periods of day (*Time*) on each of the dependent variables, we used solar position to divide the day into ordinal sections: 0 = midnight (nadir); 1 = sunrise; 2 = twilight end; 3 = mid-day (solar noon); 4 = twilight start; 5 = sunset; 6 = night starts; 7 = midnight. Decimal values represent relative time between categories (see Fig. SI 3). Sunlight phases and solar positions were obtained through r packages *suncalc* (Thieurmel et al. 2019) and *oce* (Kelley et al. 2021).

Behavioral surveys

Behavioral surveys were conducted to characterize fish behavior independently from the acoustic data. Surveys were performed within the area of the acoustic array and focused on male *S. fuscopurpureus* (the majority of the parrotfish

tagged in this study) during 2019 and 2021. In each survey (n = 150, total cumulative survey duration = 58 h.), a snorkeler followed a single fish for up to an hour, recording start and end time of focal activities, such as swimming and feeding. Behaviors were classified by a minimal threshold of five seconds. For example, when a fish was observed feeding, swimming, and resuming feeding while the time between feeding events lasted less than five seconds, the entire time was recorded as feeding. For longer intervals, behaviors were recorded as feeding and then swimming. Surveys began at randomized locations along the reef and times of day, and focal fish were selected at random (i.e., first male *S. fuscopurpureus* to be located). In the event of losing visual contact with a fish, e.g., when a fish descended to depths where it was no longer visible to the surveyor, the survey of that individual was terminated, and the cause of termination was recorded. Survey data were summarized as the ratio of time allocated per activity in each period of day (*Time*), rounded to 0.25 intervals (see Fig. SI 3).

Analyses

We excluded data from the first 21 days post-release, following recommendations for parrotfishes in tropical reefs (Chateau and Wantiez 2021). This acclimation period was to avoid irregular or misrepresentative behaviors after implantation of tags, the extent of which can vary significantly among species and habitats (e.g., Le Pichon et al. 2015; Wilson et al. 2017). In order to facilitate examination of space-use patterns at high temporal resolution (i.e., high sampling rates), we also excluded fish that had an overall median detection frequency > 60 min.

Space-use patterns

Diel patterns were analyzed through a generalized additive mixed effects model (GAMM), for each of the metrics (longshore position, longshore movement, depth, activity) using *Time*, *Fish ID* and their interaction as predictors. This enabled us to examine space-use patterns according to the time of day, without explicitly incorporating any other factor. We chose GAMMs to describe nonlinear patterns while including fish identity to account for variability among individuals (e.g., Papastamatiou et al. 2015). A cyclical smooth term was applied to *Time*. In order to avoid overrepresentation of days with more detections (or during specific periods), we used *Date* (which represents a specific calendar date) as a random effect. For each metric, we used model coefficients and associated errors for each individual to simulate the predicted responses throughout the day. GAMMs were performed in R (Team 2013) using the *mgcv* package (Wood 2006).

To estimate drivers of individual variation in long term patterns of longshore position, longshore movement, depth, and activity we used additional GAMMs in which *Fish ID* was used as a random-effect, and *S_rad*, *Temp*, *W_level*, *Chl-a*, *Species*, *Size* (nested within *Species*), and *Time* were fixed effect terms. A cyclical smooth term was applied to *Time*. By incorporating *Fish ID* as a random-effect term, our models control for unbalanced sample sizes (i.e., number of detections) among individuals (Gillies et al. 2006; Schielzeth et al. 2020) thus avoiding biases due to pseudo-replication or oversampling of individuals (Hegel et al. 2010). Statistical significance of incorporating the random effect term (*Fish ID*) was tested using likelihood ratio test (LRT), comparing the fit of a model including the random effect term to a model with fixed effects alone (null). Due to the boundary of possible parameter space (i.e., zero variance at the individual level), difference in log-likelihoods is assumed to follow a mixture distribution of a $\chi 2$-distribution with one degree-of-freedom (Nakagawa and Schielzeth 2010).

Utilization distribution kernels (KUDs)

To estimate and visualize space-use throughout the study, we used longshore positions and depth to estimate fish locations (i.e., coordinates). Based on positions of each fish across the entire tracking duration, we calculated individual kernel utilization distributions (KUDs, Worton 1989) based on all daylight positions, and for the following diel categories: night (sleeping) ranges including all records between nightfall and sunrise, and daylight ranges including all records between sunrise and sunset. An overall home range was estimated from daylight positions at a 95% probability level (KUD 95%) in order to estimate the overall area occupied by individuals during hours of activity. For periods of day and night, KUDs were estimated at 50% probability levels (also referred to as core areas). Day and night areas were described through KUD 50% as they are less likely to capture spatial variation occurring over short time frames (such as during crepuscular periods). KUD estimates accounted for the truncation produced by a physical barrier (i.e., the shoreline, Benhamou and Cornelis 2010; Calenge 2011). Two fish that were not equipped with depth sensors did not have the necessary data for calculating KUDs.

Repeatability estimates

The variation in individual space-use can be quantified using an index of 'repeatability,' *R*—the fraction of the phenotypic variation attributable to differences among individuals (Dingemanse et al. 2002). In mixed effects models, with individuals as the random effect, the adjusted repeatability is calculated as

$$R = \frac{BIC}{BIC + WIC} \quad (1)$$

where *BIC* is the between-individual component and represents the mean variation between individuals, and *WIC* is the within-individual component representing the mean variation associated with the residual variance of the model (Eqn. 1; Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013; Stoffel et al. 2017). We used an adjusted repeatability score which expresses the degree of individual variation after controlling for all other (fixed) effects (Dingemanse and Dochtermann 2013). Thus, *R* captures the variation across individual patterns (BIC) and the variance within individual patterns (predictability, WIC) while controlling for the effect of all exogenous factors (biological and environmental covariates). A theoretical maximal value of $R = 1$, indicating high repeatability would be obtained if each fish strictly adhered to a specific pattern (low WIC due to individuals exhibiting repetitive and predictable patterns) while displaying different patterns from one another (high BIC). Alternatively, a theoretical minimal value of $R = 0$ would be a result of each fish exhibiting high variation in space-use patterns (high WIC), and all individuals exhibiting a similar pattern (low BIC). Validity of estimated repeatability was tested using permutations by fitting a model without the random effect term, then adding permutated residuals to the fitted values of the model, and confidence intervals were calculated through parametric bootstrapping (Stoffel et al. 2017). All records during nighttime hours (from nightfall to sunrise) were excluded from repeatability analyses, to avoid artificially reducing or inflating variations in behavior. (e.g., activity patterns would appear to be highly similar when including periods when parrotfish sleep). Repeatability estimates from GAMMs were performed with the *rptGam* function in r (https://github.com/elipickh/rptGam). The function was adjusted from the rptR package which estimates repeatability from generalized mixed-effect models (Stoffel et al. 2017).

Repeatability (*R*) is inherently a relative measure, and thus can rarely be interpreted in absolute terms (e.g., high vs. low individual variation). Moreover, the degree of expected individual variation depends on the trait, species, and scale of interest (Bell et al. 2009; Hertel et al. 2020). A meta-analysis of studies reporting repeatability in behavioral traits specifies a mean repeatability of 0.37 across all taxa, and 0.32 in fish. An increasing number of studies have reported repeatedly estimates for marine fish in the wild, specifically for movement, home-range, and site fidelity (e.g., Harrison et al. 2014 [$R = 0.2$–0.4]; Villegas-Rios et al. 2017 [$R = 0.41$]) and diel activity patterns (e.g., Nakayama et al. 2016 [$R = 0.24$]; Alos et al. 2017 [$R = 0.3$–0.5]; Gavriel et al. 2021 [$R = 0.23$]).

Results

We tagged a total of 29 parrotfish of which 23 provided adequate data to be used in the analyses, (tracking duration > 21 days, median detection frequency < 60 min; see Tables 1, SI 1).

Utilization distribution kernels (KUDs)

KUDs were estimated for 21 fish (individuals with sufficient data and those equipped with a depth sensor, necessary for approximating positions). Area of overall home range

Table 1 Summary of tagged fish, by species, with tracking durations (shortest, longest, and median), detection frequencies and size (TL) range

Species	Fish tagged	Tracking duration (days)			Detection interval (median; minutes)	Size range (cm)
		Median	Min	Max		
C. sordidus, daisy parrotfish	5	96	76	365	2.5	28–31
S. ferrugineus, rusty parrotfish	4	371	48	440	3.6	34–52
S. fuscopurpureus, purple–brown parrotfish	14	362	64	516	3	34–41

Table 2 Area (m^2) of estimated KUDs for parrotfish throughout their entire tracking duration

Period	KUD (%)	Fish	Mean	Median	SE	Min	Max
Overall	95	21	51,990	43,730	7174	21,994	134,097
Day	50	21	7155	6447	800	3397	19,913
Night	50	21	7752	7800	189	5635	15,165

KUDs were calculated separately as overall home range ($KUD_{95\%}$) using all positions, and core areas ($KUD_{50\%}$) for night (nightfall to sunrise) and day (end of twilight to beginning of twilight). KUDs were calculated for 21 of 23 fish, as two lacked a depth sensor required to approximate geo-referenced positions

varied greatly among individuals, ranging from 21,994 to 134,097 m^2 (mean ± SE = 51,990 ± 7174 m^2, Table 2; Fig. SI 6), mirroring the high variation in daily travel distances along the reef. Core areas utilized at night were much smaller with a mean (± SE) area of 7155 (± 800) m^2. The difference in size between overall home range and core areas at night was expected, and 'movement' is primarily driven by displacement between nights. Surprisingly, individual core areas (KUD 50%) during the day were found to be as confined as night with a mean (± SE) of 7752 (± 189) m^2. Thus, core areas utilized by parrotfish during the day constitute a small fraction of the individuals' overall home ranges (mean ± SE = 18 ± 0.4%, Table SI 2), on par with the size of sleeping areas.

Vertical movement (depth)

Parrotfish exhibited a consistent diel vertical (depth) pattern; in which they utilized deeper sleeping sites at night, and shallow parts of the reef where they remained during most of the day (Wilcoxon signed rank test for paired samples; *p* value = 0.0016; see Table SI 3). Depth ranges varied among parrotfish—ranging from 6.2 to 24.6 m (median = 10) at nighttime, and from 0.01 to 8.5 m (median = 3.4) during daytime. Individual patterns, however, remained highly consistent throughout the study. Individual vertical movements were consistent not only in terms of nighttime vs. daytime depth, but also in the path and timing of commutes between the areas. Vertical movement to daytime areas commonly began between the end of twilight and ended at noon, and travel back to sleeping areas began at the start of twilight and ended before sunset (see Fig. 2). Environmental and biological variables had little effect on depth use, with variation in individual patterns (random effect term, *Fish ID*) accounting for 28% of variance explained for depth versus 15% explained by fixed effects. Accordingly, the full model with *Fish ID* outperformed the model which excluded it ($\Delta AIC = 18{,}896$).

Horizontal movement (longshore position and movement)

Most parrotfish tracked in this study exhibited a consistent longshore pattern, in which they were found at a specific area when inactive at nighttime (i.e., sleeping) and another (often different) area during the day. The two spatial endpoints (nighttime and daytime areas) and the consistent commute between them are discernable in many individuals tracked. Individuals repeatedly and consistently utilized their respective sleeping and daytime areas throughout the study and commuted to and from daytime areas at times that correspond to vertical movement (i.e., at the end of twilight and start of twilight; Fig. 2). The

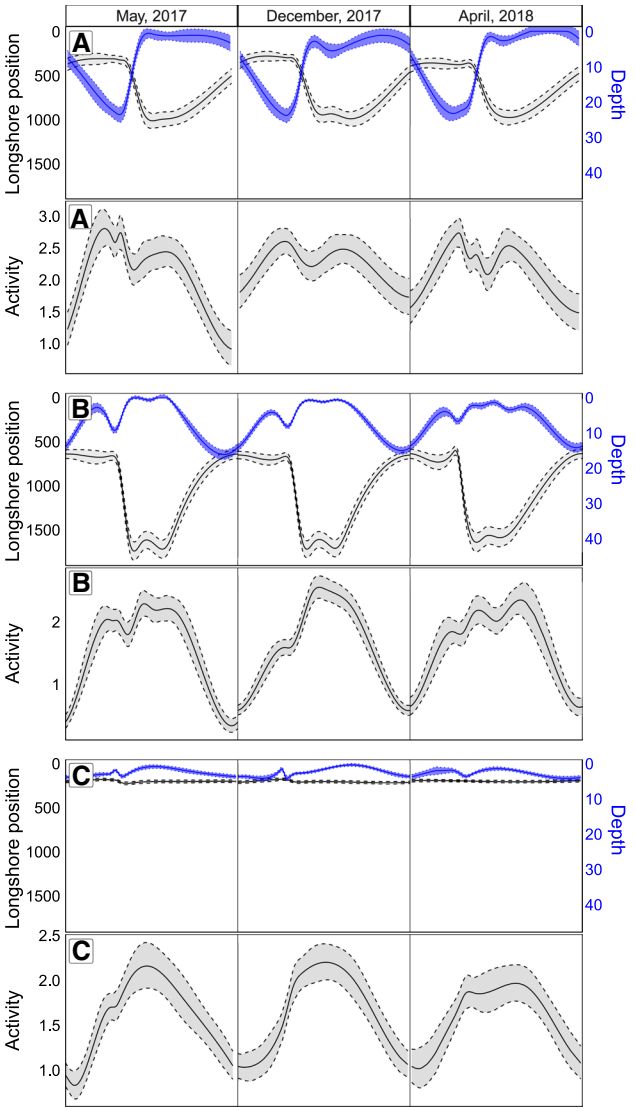

Fig. 2 Examples of three *S. fuscopurpureus* fish individuals (**A**–**C**), showing diel space-use and activity patterns from GAMMs with the interaction between the response variable and *Time* for each month separately. Longshore position (m) and depth (m) are shown as mean (solid line) and CI (shaded areas) in black and blue, respectively. These data illustrate the highly consistent and repetitive diel patterns of fish; spatial patterns (longshore movement, depth) are highly similar within-individuals across months yet vary substantially among-individuals. Contrarily, activity ($m \times s^{-2}$) patterns show higher within-individual variation, and higher similarity among individuals. See Fig. SI 4 and Fig. SI 5 for diel spatial patterns and activity patterns for all fish across the entire study

distance separating the sleeping and daytime areas (commute distance) varied considerably among individuals, ranging from zero to 1.3 km (400 ± 137 m; mean ± SE; see Fig. SI 4; Fig. SI 6 for individual space-use patterns). No significant differences in daily commuting distance were found among species (Kruskal–Wallis chi-squared = 1.82, d*f* = 2, *p* value = 0.4).

Table 3 Summary of GAMMs for each space-use metric used in this study, specifying variance explained by all environmental and biological variables (fixed effects), *Fish ID* (random effect), and model residuals

Metric	Variance explained			LRT		
	Fixed effects	Random effect	Residuals	χ^2	*F*	*p* value
Longshore position (m)	0.089	0.618	0.293	1,541,151.6	70,052	< 0.01
Longshore movement (m)	0.366	0.382	0.252	425,022.8	19,319	< 0.01
Depth (m)	0.148	0.284	0.568	39,729.3	2091	< 0.01
Activity ($m \times s^{-2}$)	0.12	0.103	0.777	17,736.2	806	< 0.01

Statistical significance is tested by likelihood ratio test (LRT) comparing the model fit of a model including the random effect-term to a model with fixed effects alone (null)

Table 4 Summary of GAMMs for each space-use metric used in this study, specifying variance explained by all environmental and biological variables (fixed effects) and *Fish ID* (random effect, also the unadjusted repeatability); variation between individuals (BIC), within individuals (WIC), and adjusted repeatability estimates *R* [±CI]

Metric	Repeatability			Permutations
	BIC	WIC	*R*	*p* value
Longshore position (m)	0.618	0.161	0.79 [±0.1]	< 0.001
Longshore movement (m)	0.382	0.262	0.59 [±0.14]	< 0.001
Depth (m)	0.284	0.567	0.33 [±0.14]	< 0.001
Activity ($m \times s^{-2}$)	0.103	0.637	0.14 [±0.1]	< 0.001

Biological and environmental (fixed effects) variables consistently accounted for less variation in the horizontal patterns of tracked parrotfish, compared to the contribution of variation among individuals (Table 3). In longshore positions, variation in individual patterns (random effect term, *Fish ID*) accounted for 62% of variance versus 9% explained by fixed effects, and in longshore movement fixed effects explained 37% of variance compared to 38% explained by the random effect. The adjusted repeatability of long-shore movement, based on the full model (including all predictor variables), was $R = 0.79 \pm 0.1$ (mean ± CI, $p < 0.001$; Table 4), resulting from high BIC and low WIC scores. Accordingly, removing *Fish ID* from the full model resulted in a model with lower empirical support ($\Delta AIC = 128{,}667$). For longshore movement, repeatability estimates were lower (mean ± CI) 0.59 ± 0.14, and here too the model without the random effect term was inferior to the full model ($\Delta AIC = 102{,}917$). Lower repeatability in longshore movement is expected as this metric does not account for where fish are situated on the reef compared to one another, which reduced between-individual variation (lower BIC). Moreover, longshore movement is more sensitive to variation within individual patterns (higher WIC), especially for parrotfish that occupy a highly limited region of the reef (such as fish C, Fig. 2). Overall, we find that individual parrotfish maintained highly consistent longshore patterns over time, while varying substantially from one another (high BIC and low WIC). Compared to horizontal (longshore) patterns, vertical movements showed higher similarity among individuals (higher BIC) as all individuals generally traveled between deep sleeping sites and shallow daytime areas, while also varying more at the individual level across time (higher WIC, Table 4).

Activity

All individuals tracked in this study exhibited a similar diel activity pattern, measured through body acceleration. Activity gradually increased from the end of twilight to noon, was maintained at high levels until the start of twilight, and gradually decreased toward sunset. Increases in activity levels correspond to the time of day when fish commute to their respective daytime areas and decrease while fish return to their sleeping sites. Similarity in diel activity patterns among individuals is surprising considering that some fish commute long distances between night and daytime areas, while others travel very short distances (see Fig. 2, Fish B and C, respectively). Diel activity patterns indicate that high activity levels are predictably and consistently exhibited in all individuals during a specific (and similar) time of day.

Parrotfish exhibited highly similar patterns of activity throughout the day, with little variation among species and individuals, regardless of their respective longshore and depth positions (low BIC, Table 4). Concomitantly, parrotfish showed little repeatability in diel activity patterns (mean ± CI; 0.14 ± 0.1), due to the high similarity between individuals (low BIC), relative to the variation within individuals (high WIC). Exclusion of the random effect term (Fish ID) also resulted in a model with reduced empirical support ($\Delta AIC = 3280$) though the fixed effects explained 12% of variance compared to 10% by the random effect term. The high variation in activity levels is likely a result of the tri-axial accelerometers which provide a single value for overall body movement within the limited sampling windows (5 s).

Behavioral surveys

Visual surveys were initially intended to focus on feeding and swimming behaviors. However, another regularly

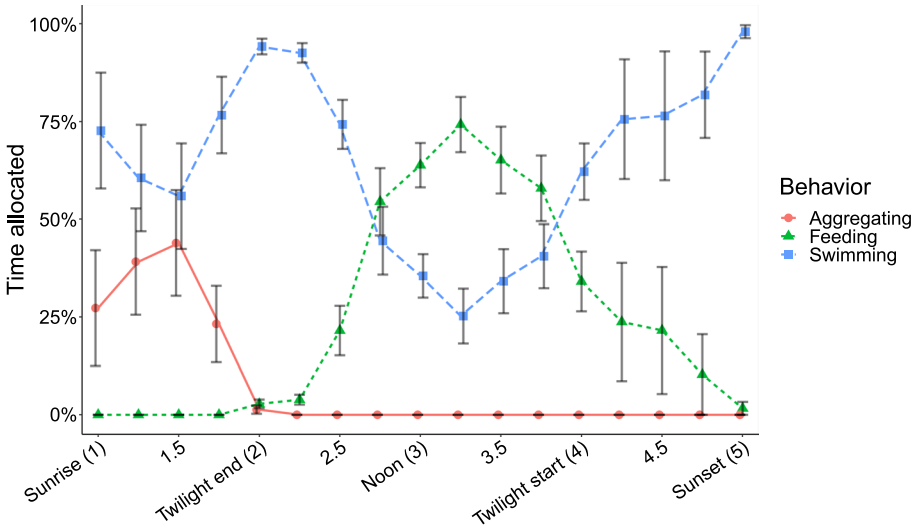

Fig. 3 Direct observational data from behavioral surveys on the time spent swimming, feeding, and aggregating (mean ± SE), across all surveys ($n = 150$ fish, total survey duration = 58 h.). Survey data were summarized as the ratio of time allocated per activity in each period of day (*Time*), rounded to 0.25 intervals

observed behavior was that of males and females aggregating in large groups (typically 30–60 fish) during early morning (sunrise to twilight end). These social interactions (classified in surveys as 'aggregating') commonly entailed directed movement of individuals toward sites of aggregation (see Video SI 1), limited horizontal movement upon arrival, and high levels of body movement as fish interact within the group. All aggregations observed in our surveys varied in depth, ranging from 1 to 20 m.

Visual surveys show a surprisingly consistent behavioral pattern throughout the day (Fig. 3). At sunrise individuals swam toward aggregation sites in a highly directed movement, often accompanied by other parrotfish. Toward the end of twilight, aggregation ended and individuals commenced swimming along the reef. Nearly, all records between sunrise to late morning were either aggregating or swimming behaviors. Feeding gradually increased toward the middle of the day and peaked in the afternoon (Time = 2.75–3.75) with nearly 75% of time allocated to feeding. While 25% of time was classified as swimming, these movements were commonly within very small areas where parrotfish grazed. Toward evening parrotfish stopped feeding, often abruptly, and swam away, usually in highly directional and fast movements.

Discussion

We found that most parrotfish tracked in this study all exhibited a similar spatial use pattern in which fish were highly centered around two areas—a deep area utilized for sleeping at night, and a shallow (daytime) area where fish spent most of the time while highly active. Individuals repeatedly and consistently utilized their same respective nighttime and daytime areas throughout the study's duration and commuted between the two on a daily basis. All individuals displayed surprisingly high fidelity to their respective sleeping and activity areas over an extended period (up to 18 months) despite seasonal changes in ambient conditions, including resource availability. We also detected peaks in activity during early mornings when parrotfish often interacted in large aggregates (typically 30–60 individuals) which, to our knowledge, has not been reported previously. Such long-term site fidelity is likely to have large implications for parrotfish grazing patterns across space and time, and their ability to maintain healthy coral reefs.

Parrotfish concentrated their daytime activity in a confined longshore reef stretch of 170 ± 17 m (mean ± SE), area = 7155 ± 800 m^2, regardless of their commuting distance (Fig. 4). This high activity area compares to a total home range of 51,990 ± 7174 m^2 (mean ± SE). Further support for highly constrained and temporal conserved space-use patterns of individuals can be found in several herbivorous reef fishes including parrotfish (e.g., Welsh and Bellwood 2012; Carlson et al. 2017; Semmler et al. 2021), surgeonfish (Claisse et al. 2011; Marshell et al. 2011), and rabbitfish (Fox and Bellwood 2011; Pickholtz et al. 2018). Previous studies on parrotfish report home range sizes of 800–2,400,000 m^2 (e.g., Lindholm et al. 2006; Afonso et al. 2008; La Mesa et al. 2012; Welsh and Bellwood 2012), which is consistent with this study, but may wrongly imply that individuals forage across a larger fraction of their overall home range. Although we cannot equate high activity levels to foraging, we can say that tracked parrotfish remained within an area far smaller than their overall home range during most of their waking hours. The gap between overall area traversed by individual parrotfish and limited space utilized during the day may suggest that the spatial extent of grazing may be substantially overestimated based on home range estimates alone.

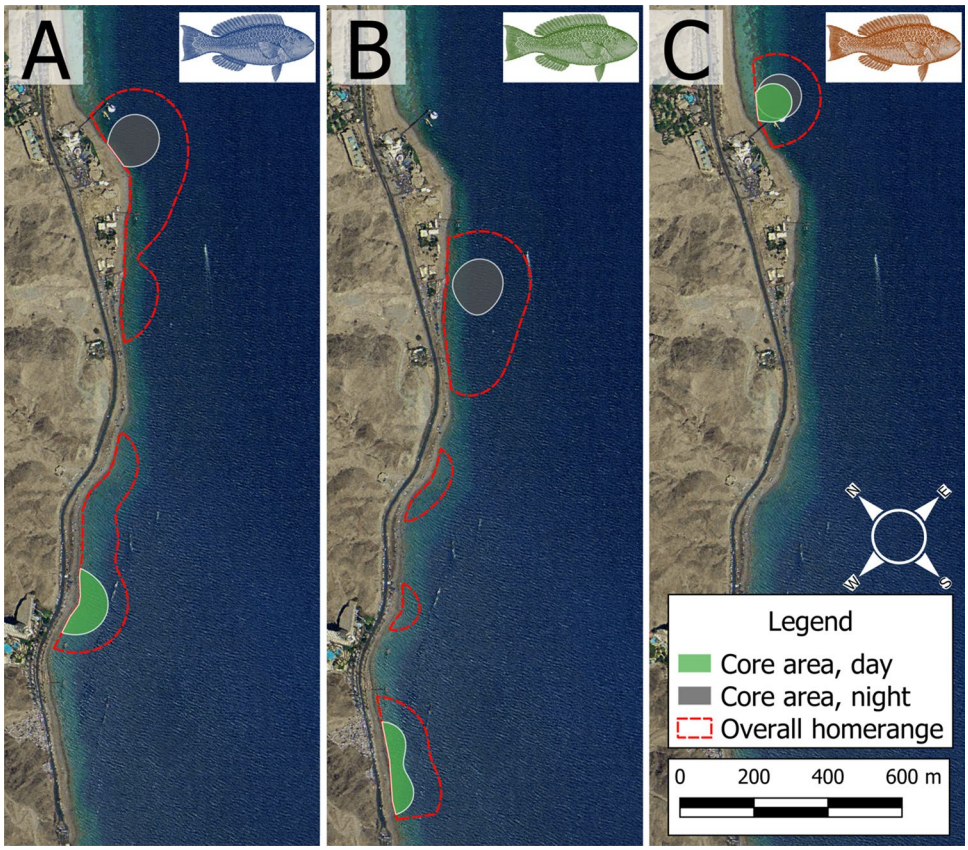

Fig. 4 Estimated utilization distributions for three fish (**A**–**C**) shown in Fig. 2, across their entire tracking duration, A = 516 days; B = 446 days; C = 438 days. Red dashed lines depict the overall home range (KUD 95%) and include all recorded positions during daylight (sunrise to sunset). Core areas (KUD 50%) were calculated separately by period of day for daytime positions (between sunrise and sunset, green) and night-time (from nightfall to sunrise, gray). Note that distance between day and night areas varies among fish by an order of magnitude (for example, fish B = 1284 m, C = 34 m). See Fig. SI 6 for maps of all fish

Individual behavioral variation is increasingly recognized in shaping space-use and diel activity patterns. As such, a growing number of studies have estimated the degree of individual repeatability in wildlife populations, including mammals (e.g., Hertel et al. 2019), birds (e.g., Potier et al. 2015; Wakefield et al. 2015), reptiles (Spiegel et al. 2015), and fishes (Harrison et al. 2014; Gavriel et al. 2021). The highly consistent individuals-level habitat utilization patterns found in this study are supported by previous studies on parrotfish conducted over shorter time scales of days or weeks (Afonso et al. 2008; Welsh and Bellwood 2011; Davis et al. 2017a). At those scales, space use patterns were attributed to habitat complexity (Welsh and Bellwood 2011), reef topography (Howard et al. 2013), feeding selectivity (Davis et al. 2017a), and habitat and resource availability (Afonso et al. 2008, for a temperate species). Over long durations, we expected to observe intra-individual variations in space use as environmental conditions, reproductive activity, and social interactions vary throughout the year (Romare and Hansson 2003; Dubois and Giraldeau 2014). Surprisingly, our data showed a markedly low degree of variation over a 2–18 month period, resulting in unexpectedly high homogeneity in space-use. These persistent individual-level patterns suggest that the importance of direct environmental effects on spatial and activity patterns is surprisingly low.

Our findings that parrotfish maintain highly consistent space-use patterns across seasons seemingly contrast with a previous study by Afeworki et al. (2013). They report a significant shift in habitat use between low and high water-temperature seasons (January–March and July–September, respectively) for herbivorous reef fish (including *C. sordidus* and *S. ferrugineus*) in the Southern Red Sea. This shift was attributed to extreme temperatures at the study site during summer (up to 36 °C), conditions uncommon to most coral reefs, including our study site, which typically do not exceed 28 °C. Thus, temporally consistent individuals-level space use patterns may be restricted to non-extreme environmental conditions.

Macroalgae blooms regularly occur in the Gulf of Aqaba mid-winter, with macroalgae more than doubling in mass (Israel National Monitoring Program; Genin and Silverman 2004; Haas et al. 2009). These blooms are patchy, occurring more in shallow parts of the reef than in deeper and sand-dominated areas (Haas et al. 2009). Tracked parrotfish maintained their respective space-use patterns throughout the year, despite this variation in resource abundance and distribution, indicating that they may not actively track algae abundances at a reef-scale; although they may at finer scales within foraging sites (Nash et al. 2012; Carlson et al. 2017). Notably, Tootell and Steele (2016) visually tracked daisy parrotfish (*C. sordidus*) over short periods of time (3–5 m.),

and found that parrotfish increase their foraging area as algal abundance decrease, presumably swimming longer distances where resources are more scarce. However, as their behavioral surveys did not differentiate between surveyed parrotfish, differences in foraging areas might have stemmed from variation among individuals rather than a response to exogenous factors such as resource abundance. Our findings suggest that even though parrotfish may differ substantially in range of diel movements, behavior remains constant within individuals, even as resource abundance fluctuates.

Parrotfish exhibited higher similarities in vertical (i.e., depth) patterns compared to horizontal movement (lower BIC, Table 4), as most fish traveled away from deeper areas at sunrise and were restricted to very shallow areas (0–5 m) while highly active around mid-day (Figs. 2, SI 4). However, fish also exhibit higher within-individual variation (WIC) in depth patterns, mostly at crepuscular periods, which suggests that although parrotfish have a clear fidelity to specific areas of the reef for sleeping, the precise site (e.g., a reef hole or crevice) at any given night might change. Nocturnal ecology, and specifically the influence of ecological factors of selection of sleeping sites is severely understudied (e.g., Lima et al. 2005; Singhal et al. 2007; Mohanty et al. 2021). Further investigation should aim at understanding what drives habitat selection at night, and why individuals commute daily (up to a kilometer in each direction) between daytime activity areas and highly conserved nighttime sleeping grounds.

Body kinematics and acceleration in herbivorous reef fishes have been shown to be a major component in feeding by herbivorous reef fishes (Perevolotsky et al. 2020). Species from the genus *Chlorurus* are commonly classified as excavators, while *Scarus* are considered to be scrapers (Bellwood and Choat 1990). The two groups have been shown to exhibit marked differences in body acceleration and body angle when feeding (Rice and Westneat 2005). Interestingly, we find that while individuals tracked in this study show a similar diel activity pattern, the amplitude of overall body acceleration differs by functional groups, with excavators exhibiting consistently higher values compared to scrapers (*Chlorurus* and *Scarus*, respectively; Fig. SI 7). However, in order to directly evaluate spatial and temporal patterns of grazing over extended periods of time, it is necessary to distinguish feeding from other behaviors, using information such as accelerometers and tilt (Føre et al. 2011), which was beyond the scope of this study.

In this study, tracking a large number of individuals at high sampling rates and over a long duration, we found that parrotfish commute daily between highly conserved sleeping areas and surprisingly small areas where they remain throughout most of the day. Patterns did not change with environmental conditions, biological conditions, or across seasons. While previous work attributed small foraging areas to feeding selectivity (Davis et al. 2017a) and resource abundance (Carlson et al. 2017), this study demonstrates that individual space-use patterns persist over months and seasons despite varying resources. Highly conserved space-use patterns may indicate stability in local reef conditions. However, as space-use dynamics seem less responsive to exogenous factors such as algal abundance, consistency in space use may also mean individual parrotfish are unlikely to alter foraging patterns when conditions change. This may hinder parrotfish's ability to mitigate phase shifts (Green and Bellwood 2009; Roff et al. 2018). Furthermore, the high fidelity parrotfish exhibit to unexpectedly limited areas (sleeping and daytime areas) may be a source of concern, as local small-scale disturbances may strongly disrupt individual space-use patterns. To understand the implications of conserved individuals-level space-use patterns, further studies are needed in which parrotfish are explicitly tracked over reefs that are undergoing disturbances or shifts in their ecological state.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-022-02258-3.

Acknowledgements We thank the *Ocean Tracking Network* at Dalhousie University for technical support and data storage; Daphna Shapiro-Goldberg for proofreading and language editing; Tal Perevolotsky for help with fieldwork and meaningful feedback on the project; and Oded Gon for support with processing geospatial data. Finally, we thank the reviewers for their valuable and insightful review of the manuscript.

Author contributions Study was conceived by RP, MK, GC, and JB. Study design was performed by RP, MK, GC, TG, and JB. Collection of acoustic (tracking) data was performed by RP and supported by IK, RZ and TG. Collection of visual survey data was performed by IK and RZ. Analyses were performed by RP and supported by MK, EP, and JB. Analytical tools (rptGAM package) were developed by EP and supported by RP. The first draft of the manuscript was written by RP and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work was supported by the *Schulich Ocean Studies Center Initiative* at Dalhousie University (Canada), a Natural Sciences and Engineering Research Council of Canada Discovery Grant.

Data availability Acoustic telemetry: Metadata are stored online at the Ocean Tracking Network data portal (https://members.oceantrack.org/projects). Detection data and explanatory variables are available at https://github.com/belmaker-lab/parrotfish_telemetry/raw/main/data_for_repository.rds. Meteorological data are available at (http://www.meteo-tech.co.il/eilat-yam/eilat_download_en.asp). Algae abundance

and growth rate data are available at (http://www.meteo-tech.co.il/EilatYam_data/ey_algae_plates_download_data.asp).

Code availability Package rptGam for repeatability estimates from GAMMs is available at (https://github.com/elipickh/rptGam).

Declarations

Conflict of interest We declare we have no conflict of interest nor competing interests.

Ethical approval Tagging and handling of parrotfish were conducted according to ethical guidelines, specified by the committee for ethical care and use of animals in experiments, Ben Gurion University of the Negev (permit #IL-17-04-2016). Fish collection and deployment of acoustic equipment on the reef were approved by the Israeli Nature and Parks Authority (INPA, permits #41872, #42197).

References

Adler P, Raff D, Lauenroth W (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Afeworki Y, Videler JJ, Bruggemann JH (2013) Seasonally changing habitat use patterns among roving herbivorous fishes in the southern Red Sea: the role of temperature and algal community structure. Coral Reefs 32:475–485

Afonso P, Fontes J, Holland KN, Santos RS (2008) Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. Mar Ecol Prog Ser 359:215–227

Alos J, Martorell-Barcelo M, Campos-Candela A (2017) Repeatability of circadian behavioural variation revealed in free-ranging marine fish. R Soc Open Sci 4:160791

Baylis AMM, Page B, McKenzie J, Goldsworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: continental shelf vs. oceanic habitats. Mar Mamm Sci 28:276–294

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. Anim Behav 77:771–783

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications alternative life-history styles of fishes. Springer, Berlin, pp 189–214

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Benhamou S, Cornelis D (2010) Incorporating movement behavior and barriers to improve kernel home range space use estimates. J Wildl Manage 74:1353–1360

Bierbach D, Laskowski KL, Brandt A-L, Chen W, Jourdan J, Streit B, Plath M (2016) Highly variable, unpredictable activity patterns in invasive, but not native amphipod species. Aquat Ecol 50:261–271

Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs. Oceanogr Mar Biol 52:81–132

Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M (2010) Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. Mar Ecol Prog Ser 399:69–80

Brownscombe JW, Cooke SJ, Danylchuk AJ (2017) Spatiotemporal drivers of energy expenditure in a coastal marine fish. Oecologia 183:689–699

Bruggemann JH, Van Oppen MJ, Breeman AM (1994) Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. Mar Ecol Prog Ser 106:41–41

Calenge C (2011) Home range estimation in R: the adehabitatHR package. Office national de la classe et de la faune sauvage, Saint Benoist

Carlson PM, Davis K, Warner RR, Caselle JE (2017) Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. Mar Ecol Prog Ser 577:165–176

Chaot J, Randall E (1986) A review of the parrotfishes (family Scaridae) of the great barrier reef of Australia with description of a new species. Rec Aust Mus 38:175–228

Chateau O, Wantiez L (2021) Post-release activity of three coral reef fish species in a marine reserve: analysis and recommendations for telemetry studies. Environ Biol Fishes 104:15–26

Claisse JT, Clark TB, Schumacher BD, McTee SA, Bushnell ME, Callan CK, Laidley CW, Parrish JD (2011) Conventional tagging and acoustic telemetry of a small surgeonfish, *Zebrasoma flavescens*, in a structurally complex coral reef environment. Environ Biol Fish 91:185–201

Clements KD, Choat JH (2018) Nutritional ecology of parrotfishes (Scarinae, Labridae) biology of parrotfishes. CRC Press, Boca Raton, pp 42–68

Clements KD, German DP, Piché J, Tribollet A, Choat JH (2016) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Lin Soc 120:729–751

Cramer KL, O'Dea A, Clark TR, Zhao JX, Norris RD (2017) Prehistorical and historical declines in Caribbean coral reef accretion rates driven by loss of parrotfish. Nat Commun 8:14160

Dall SR, Bell AM, Bolnick DI, Ratnieks FL (2012) An evolutionary ecology of individual differences. Ecol Lett 15:1189–1198

Davis K, Carlson PM, Lowe CG, Warner RR, Caselle JE (2017a) Parrotfish movement patterns vary with spatiotemporal scale. Mar Ecol Prog Ser 577:149–164

Davis K, Carlson PM, Bradley D, Warner RR, Caselle JE (2017b) Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish. Oecologia 184:139–149

de Almeida PR, Pereira TJ, Quintella BR, Gronningsaeter A, Costa MJ, Costa JL (2013) Testing a 3-axis accelerometer acoustic transmitter (AccelTag) on the Lusitanian toadfish. J Exp Mar Biol Ecol 449:230–238

Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol 82:39–54

Dingemanse NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim Behav 64:929–938

Dubois F, Giraldeau LA (2014) How the cascading effects of a single behavioral trait can generate personality. Ecol Evol 4:3038–3045

Espinoza M, Farrugia TJ, Lowe CG (2011) Habitat use, movements and site fidelity of the gray smooth-hound shark (Mustelus californicus Gill 1863) in a newly restored southern California estuary. J Exp Mar Biol Ecol 401:63–74

Føre M, Alfredsen JA, Gronningsater A (2011) Development of two telemetry-based systems for monitoring the feeding behaviour of Atlantic salmon (*Salmo salar* L.) in aquaculture sea-cages. Comput Electron Agric 76:240–251

Fox RJ, Bellwood DR (2011) Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. Funct Ecol 25:1096–1105

Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1–30

Gavriel T, Pickholtz R, Belmaker J (2021) Large individual-level variability in diel activity and depth use for the common Lionfish

(Pterois miles). Front Mar Sci. https://doi.org/10.3389/fmars.2021.790930
Genin A, Silverman J (2004) The Israel National Monitoring Program in the Northern Gulf of Aqaba. Science report for year
Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL (2006) Application of random effects to the study of resource selection by animals. J Anim Ecol 75:887–898
Gomi K, Nakamura Y, Kanda M, Honda K, Nakaoka M, Honma C, Adachi M (2021) Diel vertical movements and feeding behaviour of blue humphead parrotfish *Scarus ovifrons* in a temperate reef of Japan. J Fish Biol 99:131–142
Green AL, Bellwood DR (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific region. IUCN, Gland
Haas A, El-Zibdah M, Wild C (2009) Seasonal monitoring of coral–algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. Coral Reefs 29:93–103
Hall J (1978) New bathymetric map of the Gulf of Eilat (Aqaba). Tenth Int Conf Sedimentol 1978(1):285
Harrison PM, Gutowsky LFG, Martins EG, Patterson DA, Cooke SJ, Power M (2014) Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). Behav Ecol 26:483–492
Hegel TM, Cushman SA, Evans J, Huettmann F (2010) Current state of the art for statistical modelling of species distributions spatial complexity, informatics, and wildlife conservation. Springer, Berlin, pp 273–311
Hertel AG, Leclerc M, Warren D, Pelletier F, Zedrosser A, Mueller T (2019) Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Anim Behav 147:91–104
Hertel AG, Niemela PT, Dingemanse NJ, Mueller T (2020) A guide for studying among-individual behavioral variation from movement data in the wild. Mov Ecol 8:30
Hoey AS, Feary DA, Burt JA, Vaughan G, Pratchett MS, Berumen ML (2016) Regional variation in the structure and function of parrotfishes on Arabian reefs. Mar Pollut Bull 105:524–531
Howard KG, Claisse JT, Clark TB, Boyle K, Parrish JD (2013) Home range and movement patterns of the Redlip Parrotfish (*Scarus rubroviolaceus*) in Hawaii. Mar Biol 160:1583–1595
Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551
Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360–365
Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633–642
Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, Whoriskey FG (2015) ECOLOGY. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642
Kelley D, Richards C, Layton C (2021) Package 'oce'
Khalaf M (2004) Fish fauna of the Jordanian Coast, Gulf of Aqaba, Red Sea. J King Abdul Aziz Univ Mar Sci 15:23–50
La Mesa G, Consalvo I, Annunziatellis A, Canese S (2012) Movement patterns of the parrotfish *Sparisoma cretense* in a Mediterranean marine protected area. Mar Environ Res 82:59–68
Le Pichon C, Coustillas J, Rochard E (2015) Using a multi-criteria approach to assess post-release recovery periods in behavioural studies: study of a fish telemetry project in the Seine Estuary. Anim Biotelemetry 3:1–15
Lima SL, Rattenborg NC, Lesku JA, Amlaner CJ (2005) Sleeping under the risk of predation. Anim Behav 70:723–736
Lindfield SJ, Harvey ES, Halford AR, McIlwain JL (2015) Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. Coral Reefs 35:125–137
Lindholm J, Knight A, Kaufman L, Miller S (2006) Site fidelity and movement of the parrotfishes *Scarus coeruleus* and *Scarus taeniopterus* at Conch Reef (northern Florida Keys). Caribb J Sci 42:138–144
Marshell A, Mills JS, Rhodes KL, McIlwain J (2011) Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. Coral Reefs 30:631–642
Matley JK, Tobin AJ, Ledee EJI, Heupel MR, Simpfendorfer A (2016) Contrasting patterns of vertical and horizontal space use of two exploited and sympatric coral reef fish. Mar Biol 163:1–12
McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Prog Oceanogr 60:263–279
Mohanty NP, Wagener C, Herrel A, Thaker M (2021) The ecology of sleep in non-avian reptiles. Biol Rev Camb Philos Soc 97:505
Moiron M, Laskowski KL, Niemela PT (2020) Individual differences in behaviour explain variation in survival: a meta-analysis. Ecol Lett 23:399–408
Monismith SG, Genin A, Reidenbach MA, Yahel G, Koseff JR (2006) Thermally driven exchanges between a coral reef and the adjoining ocean. Journal of Physical Oceanography 36:1332–1347
Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101
Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev Camb Philos Soc 85:935–956
Nakayama S, Laskowski KL, Klefoth T, Arlinghaus R (2016) Between- and within-individual variation in activity increases with water temperature in wild perch. Behav Ecol 27:1676–1683
Nash KL, Graham NAJ, Januchowski-Hartley FA, Bellwood DR (2012) Influence of habitat condition and competition on foraging behaviour of parrotfishes. Mar Ecol Prog Ser 457:113–124
Nemeth M, Appeldoorn R (2009) The distribution of herbivorous coral reef fishes within fore-reef habitats: the role of depth, light and rugosity. Caribb J Sci 45:247–253
Nicholson GM, Clements KD (2020) Resolving resource partitioning in parrotfishes (Scarini) using microhistology of feeding substrata. Coral Reefs 39:1313–1327
Palmer SCF, Gordon IJ, Hester AJ, Pakeman RJ (2004) Introducing spatial grazing impacts into the prediction of moorland vegetation dynamics. Landsc Ecol 19:817–827
Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLoS ONE 10:e0127807
Pereira PH, Santos M, Lippi DL, Silva P (2016) Ontogenetic foraging activity and feeding selectivity of the Brazilian endemic parrotfish *Scarus zelindae*. PeerJ 4:e2536
Perevolotsky T, Martin CH, Rivlin A, Holzman R (2020) Work that body: fin and body movements determine herbivore feeding performance within the natural reef environment. Proc Biol Sci 287:20201903

Pickholtz RSM, Kiflawi M, Friedlander AM, Belmaker J (2018) Habitat utilization by an invasive herbivorous fish (*Siganus rivulatus*) in its native and invaded range. Biol Invasions 20:3499–3512

Potier S, Carpentier A, Gremillet D, Leroy B, Lescroel A (2015) Individual repeatability of foraging behaviour in a marine predator, the great cormorant, *Phalacrocorax carbo*. Anim Behav 103:83–90

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318

Rice AN, Westneat MW (2005) Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae). J Exp Biol 208:3503–3518

Riotte-Lambert L, Matthiopoulos J (2020) Environmental predictability as a cause and consequence of animal movement. Trends Ecol Evol 35:163–174

Roff G, Bejarano S, Priest M, Marshell A, Chollett I, Steneck RS, Doropoulos C, Golbuu Y, Mumby PJ (2018) Seascapes as drivers of herbivore assemblages in coral reef ecosystems. Ecol Monogr 89:e01336

Romare P, Hansson LA (2003) A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. Limnol Oceanogr 48:1956–1964

Sade AR, Hall JK, Tibor G, Niemi TM, Ben-Avraham Z, Al-Zoubi AA, Hartman G, Akawwi E, Abueladas A-R, Amitc G (2008) The Israel national bathymetric survey: Northern Gulf of Aqaba/Eilat Poster. Israel Journal of Earth Sciences 57:139–144

Schielzeth H, Dingemanse NJ, Nakagawa S, Westneat DF, Allegue H, Teplitsky C, Reale D, Dochtermann NA, Garamszegi LZ, Araya-Ajoy YG (2020) Robustness of linear mixed-effects models to violations of distributional assumptions. Methods Ecol Evol 11:1141–1152

Semmler RF, Brandl SJ, Keith SA, Bellwood DR (2021) Fine-scale foraging behavior reveals differences in the functional roles of herbivorous reef fishes. Ecol Evol 11:4898–4908

Shaw AK (2020) Causes and consequences of individual variation in animal movement. Mov Ecol 8:12

Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–378

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can J Fish Aquat Sci 59:23–32

Singhal S, Johnson MA, Ladner JT (2007) The behavioral ecology of sleep: natural sleeping site choice in three *Anolis lizard* species. Behaviour 144:1033–1052

Smith KM, Quirk-Royal BE, Drake-Lavelle K, Childress MJ (2018) Influences of ontogenetic phase and resource availability on parrotfish foraging preferences in the Florida Keys, FL (USA). Mar Ecol Prog Ser 603:175–187

Sommer U (2000) Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. Oecologia 122:284–287

Spiegel O, Leu ST, Sih A, Godfrey SS, Bull CM (2015) When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. Proc Biol Sci 282:20151768

Spiegel O, Leu ST, Bull CM, Sih A (2017) What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol Lett 20:3–18

Stehfest KM, Lyle JM, Semmens JM (2015) The use of acoustic accelerometer tags to determine seasonal changes in activity and catchability of a recreationally caught marine teleost. Ices J Mar Sci 72:2512–2520

Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol 8:1639–1644

Streit RP, Cumming GS, Bellwood DR (2019) Patchy delivery of functions undermines functional redundancy in a high diversity system. Funct Ecol 33:1144–1155

Team RC (2013) R: a language and environment for statistical computing

Tebbett SB, Goatley CH, Bellwood DR (2017) Algal turf sediments and sediment production by parrotfishes across the continental shelf of the northern great barrier reef. PLoS ONE 12:e0170854

Tebbett SB, Siqueira AC, Bellwood DR (2022) The functional roles of surgeonfishes on coral reefs: past, present and future. Rev Fish Biol Fish 32:1–53

Thieurmel B, Elmarhraoui A, Thieurmel MB (2019) Package "suncalc"

Thorbjørnsen SH, Moland E, Villegas-Ríos D, Bleeker K, Knutsen H, Olsen EM (2021) Selection on fish personality differs between a no-take marine reserve and fished areas. Evol Appl 14:1807

Tootell JS, Steele MA (2016) Distribution, behavior, and condition of herbivorous fishes on coral reefs track algal resources. Oecologia 181:13–24

Vergés A, Vanderklift MA, Doropoulos C, Hyndes GA (2011) Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. PLoS ONE 6:e17115

Villegas-Rios D, Reale D, Freitas C, Moland E, Olsen EM (2017) Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. Anim Behav 124:83–94

Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fidelity—why some gannets don't change their spots. Ecology 96:3058–3074

Webber QMR, Laforge MP, Bonar M, Robitaille AL, Hart C, Zabihi-Seissan S, Vander Wal E (2020) The ecology of individual differences empirically applied to space-use and movement tactics. Am Nat 196:E1–E15

Welsh JQ, Bellwood DR (2011) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. Coral Reefs 31:55–65

Welsh J, Bellwood D (2012) How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. Coral Reefs 31:991–1003

Welsh JQ, Goatley CH, Bellwood DR (2013) The ontogeny of home ranges: evidence from coral reef fishes. Proc Biol Sci 280:20132066

Wilson AD, Hayden TA, Vandergoot CS, Kraus RT, Dettmers JM, Cooke SJ, Krueger CC (2017) Do intracoelomic telemetry transmitters alter the post-release behaviour of migratory fish? Ecol Freshw Fish 26:292–300

Winter J (1996) Advances in underwater biotelemetry. In: Murphy BR, Willis DW (eds) Fisheries techniques, 2nd edn. American Fisheries Society, Bethesda, pp 555–590

Wood S (2006) Generalized additive models: an introduction with R. Texts in statistical sciences. Chapman and Hall/CRC, London, pp 67–391

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.