


# Habitat utilization by an invasive herbivorous fish (*Siganus rivulatus*) in its native and invaded range

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**Abstract** Movement is essential for understanding the distribution and abundance of animals. While it has been suggested that invasion success can be facilitated by species' ability to adapt to novel environments, direct comparisons of movement patterns between native and invaded ranges of animals in their natural habitat are rare. The rivulated rabbitfish *Siganus rivulatus* was introduced from the Red Sea into the Mediterranean, where it is now found in extremely high abundances, and has overgrazed the

coastal marine ecosystem in many locations. Through a continuous acoustic tracking system, we found that the movement of *S. rivulatus* individuals at a Mediterranean site differed substantially from those at a Red Sea site, with individuals in the Mediterranean having larger overall home ranges and lower site fidelity. However, no variation between sites was found in daily home range sizes. Results show that at the Mediterranean site *S. rivulatus* individuals have a larger spatial footprint, which may contribute to their impact and ability to expand their distribution. This study demonstrates a potential shift in individual movement of a marine invasive species between its

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native and invaded range, and highlights the role of movement in understanding biological invasions.

**Keywords** Invasive species · Habitat utilization · Movement · Reef fish · Mediterranean Sea · Red Sea

## Introduction

The establishment and spread of marine invasive species worldwide has led to devastating effects, including loss of biodiversity and ecosystem services (Bax et al. 2003; Ruiz et al. 1999), alteration of community structure (Shiganova 1998), and habitat degradation (Sala et al. 2011). Behavioral adaptation has long been identified as an imperative element in the invasion processes, and understanding this adaptation may greatly improve the predictive understanding of invasions (Holway and Suarez 1999; Sih et al. 2012).

Individuals encountering unfamiliar landscapes, such as in the invasive range, often display changes in behavior (Rothermel and Semlitsch 2002), which can impact key behaviors such as foraging strategies (Turcotte and Desrochers 2003), competition for resources (Forsman et al. 2002), and predator avoidance (Fernández-Juricic et al. 2001). For example, a study on house sparrows, *Passer domesticus*, showed through captive experiments that individuals from the invaded range were more likely to exploit unfamiliar resources than were individuals from a native population (Martin and Fitzgerald 2005). In its native range, the Argentine ant, *Linepithema humile*, exhibits high intraspecific aggression, whereas in the invaded range, intraspecific aggression is rarely exhibited (Suarez et al. 1999). This behavioral shift by *L. humile*, caused by the loss of ability for colony discrimination (Holway et al. 1998), has enabled the range expansion and wide-spread impact of this species. Changes in behavior, as may be reflected by changes in movement patterns across the landscape, are likely linked to the specific environments in the native and invasive ranges (Knowlton and Graham 2010).

Relatively few studies have looked at shifts in behavior of individuals within an invasive population under natural conditions. While most studies focus on populations that have undergone a genetic bottleneck or selection in the invaded region (McLain et al. 1999;

Tsutsui et al. 2000), few studies have considered genetically homogenous populations. However, these homogenous populations can elucidate the degree of behavioral plasticity expressed by invasive species (Liu et al. 2016; Vogt 2017). This lack of understanding is especially relevant to marine systems where tracking movement requires specialized and often expensive technology that was not available until recently (Cunjak et al. 2005; Espinoza et al. 2011b).

Upon introduction to a novel ecosystem (i.e., the invaded range), non-indigenous marine species often encounter novel environmental characteristics, which differ significantly from those found in their native range. These conditions may be abiotic, such as salinity and temperature (e.g., Belmaker et al. 2013; Braby and Somero 2006), or biotic such as community composition (Vaz-Pinto et al. 2013), predation pressure (DeRivera et al. 2005), and the degree of competition (Stachowicz and Byrnes 2006). Comparing the movement patterns of a successful invasive species in its native and invaded range may provide insights into behavioral shifts, and help understand on how environmental differences shape individual behavior across populations and ranges. However, to our knowledge no study has described individual-based movement and habitat utilization patterns in both the native and invaded ranges (but see Smith et al. 2018).

Following the opening of the Suez Canal in 1869, hundreds of marine species, including over 100 fish species, have entered the Mediterranean Sea from the Red Sea (Belmaker et al. 2013; Galil 2008; Galil et al. 2015; Golani et al. 2013; Por 1978; Quignard 2011; Verlaque et al. 2015). Many of these introduced species have an adverse impact on the local economy (e.g., fisheries and tourism; Boudouresque 1999; Streftaris and Zenetos 2006) and the recipient ecosystem (e.g., biodiversity and community structure; Belmaker et al. 2013; Edelist et al. 2013). The rivulated rabbitfish, *Siganus rivulatus*, was first reported in the Mediterranean Sea in 1927 (Ben-Tuvia 1964; Tortonese 1970). It is ranked among Europe's 100 worst invasive species (Delivering Alien Invasive Species Inventories for Europe, [www.europe-alien.org](http://www.europe-alien.org)) comprising, along with *S. luridus*, over 30% of total fish biomass over rocky habitats in the eastern Mediterranean and ~ 90% of herbivorous-fish biomass (Bianchi et al. 2014; Goren and Galil 2001; Lundberg et al. 2004). Furthermore, due to their

intensive grazing on rocky substrates, rabbitfishes deplete immense quantities of algae, degrade the biogenic habitat complexity, and displace indigenous species. (Bariche et al. 2004; Sala et al. 2011; Şeker-cioğlu et al. 2011). Rabbitfishes have likely colonialized the Eastern Mediterranean on multiple events and in large numbers, which resulted in the lack of genetic variation between the native population in the Red Sea and the invasive population of the Mediterranean (Bonhomme et al. 2003; Hassan et al. 2003).

While the basic ecology of rabbitfishes is known (Hoey et al. 2013; Woodland 1983), their habitat utilization patterns have been rarely studied with only two studies conducted on different species (*S. doliatus* and *S. lineatus*) in the Indo-Pacific (Brandl and Bellwood 2013; Fox and Bellwood 2011, respectively). No study examined rabbitfish spatial ecology in the invaded ranges. The paucity of data on the spatial ecology of rabbitfishes in general, and the lack of such data on *S. rivulatus* in particular, hinder the ability to predict spatial use patterns, and highlights the importance of providing high resolution movement data for this species. In this study, we described the spatial patterns of habitat utilization of *S. rivulatus* in two sites—one within a coral-reef (tropical) habitat in the Red Sea within the native range, and one within a rocky (sub-tropical) habitat in the invaded Mediterranean Sea. This study is among the very few to directly compare the spatial behavior of an invasive species between regions, and the first to do so for a marine species (but see Smith et al. 2018). Movement was recorded using an advanced underwater tracking system that provides high-resolution spatiotemporal movement data of fish as they move within their coastal habitat. Comparative studies such as this can provide important information on the role of movement in invasion, serve as a useful framework for studying the effects of environmental factors on individual decision-making, and improve the understanding of the spread and impact of rabbitfish in the Mediterranean.

## Methods

### Study sites

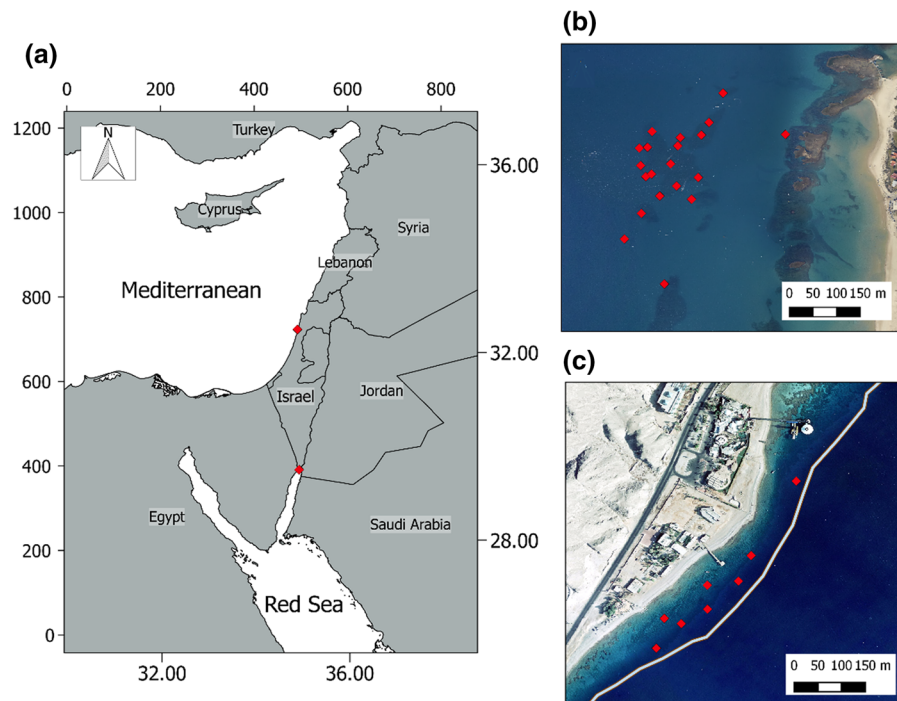
Movement patterns of *S. rivulatus* were recorded at the Red Sea and the Mediterranean Sea, representing the

species' native and invaded range; respectively (Fig. 1). Within each region, we chose a study site that is typical of the habitat occupied by *S. rivulatus*. The study sites in both regions consisted of hard substrate habitats and located in coastal shallow water, chosen due to the strong affinity of siganids to reefs and other hard substrates (Woodland 1983). The Red Sea study site was a fringing coral reef on the north-eastern coast in the northern Gulf of Aqaba (N29.50156, E34.91792). The shallow fringing coral reef is mostly continuous, and hard substrate is available along the shoreline. The reef borders a steep slope, where bottom depth rapidly increases to approximately 40 m over a distance of 100 m from shore (Hall and Ben-Avraham 1978).

The Mediterranean site was located 400 m off the coast within a large rocky reef of submerged sandstone (N32.49052, E34.88180). The bathymetry at the Mediterranean site is moderately flat, with depths ranging from 5 m to approximately 15 m. Here, the seascape is less structurally complex compared to Red Sea coral reef habitat, and is separated from nearby habitat patches by large sandy areas. Thus, the Mediterranean site posed no physical barrier for *S. rivulatus* in terms of depth, while potentially limiting movement between reef patches due to the physical configuration of the seascape.

Seascape characteristics at both study sites represent common features found within the native and invaded ranges of rabbitfishes. Specifically, the Red Sea in general, and the Gulf of Aqaba in particular, are characterized by shallow fringing coral reefs parallel to the coastline, with a sharp drop in bottom depth within short distances from shore (e.g., Reches et al. 1987; Sade et al. 2008; Tibor et al. 2010). The coastal seascape in the eastern Mediterranean is characterized by a mosaic of rocky substrate surrounded by sand, and by a moderate incline of the seabed across the continental shelf (e.g., Beydoun 1976; García-Charton and Pérez-Ruzafa 2001; Gvirtzman et al. 2015; Herut and Galil 2000).

Since patterns of habitat utilization are likely to be affected by factors such as rabbitfish density (Sala et al. 2011) and predation risk (Catano et al. 2014; 2016; Rizzari et al. 2014; Turgeon et al. 2010), we used existing data to compare the two site with respect to both parameters (using predator densities as a proxy for ambient predation risk). To measure rabbitfish abundance and estimate predation risk, we used



**Fig. 1** **a** Location of the study sites. Right and bottom axes represent latitude and longitude respectively, left and upper axes show the scale in kilometers. **b** The Mediterranean array deployed at a rocky coastal reef. **c** the Red Sea array in the Gulf

of Aqaba deployed along the shallow coral reef. Diamond shapes (red) represent the locations of acoustic receivers. Light blue line in the Red Sea delimits the proximate depth limit for *S. rivulatus* (30 m)

existing data from underwater visual surveys of fishes along the fringing reef in the Red Sea site ( $n = 247$ , Brokovich 2001) and along the Israeli Mediterranean coastline ( $n = 618$ , Frid and Yahel 2015; Supplemental material Table 1). Survey data included species abundance and size estimates (total length, TL). Data used for the purpose of this manuscript were restricted to transect depths between 0 and 30 m, where rabbitfish are commonly found (Bariche et al. 2004 and references therein).

#### Acoustic telemetry array

The Red Sea array consisted of eight receivers (VR2W-69 kHz, by VEMCO) that were distributed in an overlapping fashion across the fringing reef. The array was deployed parallel to the coastline, since the maximum depth where *S. rivulatus* is found (Bariche et al. 2004 and references therein) is reached within less than 150 m from shore. The Mediterranean array consisted of 20 receivers that were distributed in an overlapping fashion across a large rock reef. Unlike

the Red Sea site, the bathymetry at the Mediterranean site is moderately flat, so bottom depth was not considered an obstacle for the movement of *S. rivulatus*. While the array was deployed at the Mediterranean site, 12 acoustic receivers were lost along with their stored data, due to entanglement in fishing gear and extreme weather conditions.

Fine scale movements were calculated using an underwater acoustic positioning system (Vemco Positioning System; VPS), which can track multiple individuals simultaneously. Positions are derived by calculating differences in arrival times of acoustic signals at three or more receivers, with georeferenced positions (i.e., coordinates) processed and analyzed by the manufacturer (VEMCO, Nova Scotia, Canada). Receivers in the Red Sea were positioned with overlapping detection ranges according to the site's steep bathymetry, resulting in a largely linear array of receivers along the shallow part of the reef. The appropriate length of coastline for the array was estimated from movement data from three fish, obtained through manual acoustic tracking (VR100,

by VEMCO). In the Mediterranean, the bathymetry is far more gradual and depth did not pose a limitation of rabbitfish movement. Hence, we required many more receivers cover the study area in an overlapping fashion.

Prior to the deployment of the receivers, range tests were conducted to assess effective mean detection ranges of the receivers. Range tests were performed during the day, dusk, and nighttime to account for varying ambient noises (Gjelland and Hedger 2013; Heupel et al. 2005; Kessel et al. 2014). Range test tags (Vemco V9-2x 69 kHz) were moved by SCUBA divers underwater and using a kayak near the surface, along a straight line from a receiver and up to 250 m away (five replications per receiver). Range tests were performed in several areas within the array, with different representative bathymetry and reef complexity. In the Red Sea, detection efficiency of  $> 90\%$  was maintained at a distance of 150 m, but a conservative range of 120 m was selected for the array's design (Espinoza et al. 2011a). In the Mediterranean, array detection efficiency of  $> 90\%$  was maintained at a distance of 200 m, but a conservative range of 150 m was selected. We used acoustic transmitters or “tags” that transmit at a nominal frequency of 30 s (within a range of 15–45 s), for a maximal duration of 50 days (Vemco, V9-2x, at a frequency of 69 kHz).

#### Fish collection and tagging

Fish were collected by handnet using SCUBA or snorkeling at night while fish were inactive/sleeping. Collection by hand enabled us to gather rabbitfish with minimal stress. Tags were surgically implanted into the peritoneal cavity of anesthetized fish (using clove oil, Ghanawi et al. 2013). Incisions were sutured with two separate stitches, using Ethicon absorbable coated monofilament 3–0. Fish were kept in a large tank of fresh seawater until they exhibited clear signs of normal swimming and feeding behavior (24–48 h). All fish were released at their respective capture site ( $\pm 40$  m). Tracking data from the first 24 h post-release period were omitted from all analyses to account for behavior stemming from potential disorientation and re-acclimation. All individuals included in the analyses were tracked during the cold season (December to March, Supplementary material Table 2). A total of 24 fish were collected and tagged (17 in the Mediterranean, 7 in the Red Sea,

Supplementary material Table 2). Sixteen fish in the Mediterranean site, with little to no data—were excluded from all analyses. Two fish were considered dead due to post-surgery related trauma, and 14 additional fish, though detected by the array, did not provide sufficient data for calculating positions due to weaker transmitter output, and the loss of 12 receivers, along with their stored data. Thus, the data presented in this paper pertain to a total of eight individuals; five from the Red Sea and three from the Mediterranean.

#### Auxiliary environmental data

Night was defined as 30 min after sunset and 30 min before sunrise (Kohda 1988), day as 30 min after sunrise and 30 min before sunset, and the period in between defined as crepuscular (dusk, dawn). Sunrise and sunset times were obtained through an online solar calculator by NOAA (Cornwall et al. 2007).

### Analyses

#### Habitat utilization

Home-range sizes were estimated using a bivariate Kernel Utilization Distribution (KUD), which represents the probability of finding an animal within a given area (Worton 1989). Fish positions in the VPS array can be acquired only when tag transmissions are detected by several overlapping receivers, which often results in uneven sampling due to geometry of transmitter and receivers locations (Biesinger et al. 2013). For example, transmissions from a fish in an open area may be recorded every 30 s, whereas the same individual foraging within the reef may be detected once an hour. In order to correct for this uneven signal-detection probabilities, home-range calculations were performed following an adapted bootstrap approach for time-series (Manly 2006; Rogers et al. 2007), where a single position was randomly sampled at a minimum of one-hour intervals.

Home ranges were calculated multiple times (1000 bootstrap iterations per individual) and the mean of these values calculated to provide a more reliable estimate of home range sizes. When calculating the KUD of individuals, one must select a method for smoothing parameter which controls the “width” of



kernel functions at each position (Calenge 2011). Following a visual evaluation of several accepted methods (Calenge 2015), and adhering to recommendations for visual assessment of a suitable smoothing parameter by Wand and Jones (1995), we used the ‘reference bandwidth’ calculated based on the standard deviations of  $x$  and  $y$  coordinates, which was found to be robust to variation in sampling intensity (Bauder et al. (2015). Home range sizes were robust to common alternative methods (smoothing parameter  $h$  which is calculated based on ‘least square cross validation’, Worton 1989).

Cumulative home ranges were calculated to describe the variation in home range size over the tracking period. Cumulative home range was calculated at daily increments by measuring the area covered by 95% of the nearest recorded positions from release up to each corresponding day. Density based methods such as KUDs are less suitable for depicting cumulative home ranges when sampling frequency is irregular. For example, if detection rate is proportionally high at a given area, the cumulative home range will effectively decrease to reflect the home range size for that specific period. Minimum convex polygons (MCP, Mohr 1947) were therefore selected to describe cumulative home ranges that better depict variation in size in terms of area rather than volume (i.e., probability density).

Home-range size comparison between regions (Red Sea and Mediterranean; Table 1) was performed separately at each utilization level (ranging between KUD<sub>50%</sub> to KUD<sub>95%</sub>) using independent student’s  $t$  test. Overall home ranges were estimated using the 95% utilization distribution (KUD<sub>95%</sub>), whereas the

core areas of activity was estimated using 50% utilization distribution (KUD<sub>50%</sub>) (White and Garrott 1990; Worton 1987). Since rabbitfish are diurnal species, we also differentiated home range sizes by period of day (*dawn*, *day*, *dusk*, *night*), with the expectation of finding the nocturnal distribution to be significantly smaller. Variation in home-range size per day-period were calculated for each fish across the study duration, and were compared using Kruskal–Wallis rank sum test.

We were also interested in understanding what factors contribute to the possible differences in home ranges between the Red Sea and the Mediterranean. For this, we used a mixed effect model with daily home range size as the response variable. Region (Red Sea and Mediterranean), and length of day (sunlight duration) were used as fixed effects. The latter factor was selected since rabbitfish are active during the day, and it is therefore plausible that longer daylight durations could enable more time for movement—possibly covering larger areas. Individual fish identities (IDs) were added as a random effect.

### Site fidelity

To test whether site fidelity differed between the Red Sea and Mediterranean sites we compared changes in the nocturnal positions of fish over time, and calculated the distance between Centers of Activity (COA, centroid of recorded position; Ofstad 2013 and references therein). This was done by calculating the COA in consecutive tracking nights and calculating the distance between them. Differences in site fidelity between regions were analyzed using a mixed effect

**Table 1** Summary of metrics used in this paper for home range size and site fidelity

Feature	Metric	Description
Home range	Core areas (KUD <sub>50%</sub> )	Utilization distribution kernel of the nearest 50% of an individual’s positions. Commonly referred to as core area, in which there is a 50% probability to locate an individual
	Overall home range (KUD <sub>95%</sub> )	Utilization distribution kernel of the nearest 95% of an individual’s positions. Commonly referred to simply as the home range, in which there is a 95% probability to locate an individual
	Cumulative home range (MCP <sub>95%</sub> )	Area of a Minimum Convex Polygon (MCP) of the nearest 95% of an individual’s positions. Calculated by all recorded positions from start of tracking to each respective day, for the entire tracking period
Site fidelity	Centers of activity (COA)	The centroid of an individual’s recorded positions date. Distances between COAs on consecutive days or nights are used to estimate an individual’s site fidelity (daily or nocturnal, respectively)

model with region and intervals between nights as fixed effects, and individual IDs as a random effect. Daily distances were also calculated for each individual, by summing the Euclidian distance traveled between all positions within each date excluding nocturnal positions (Table 1).

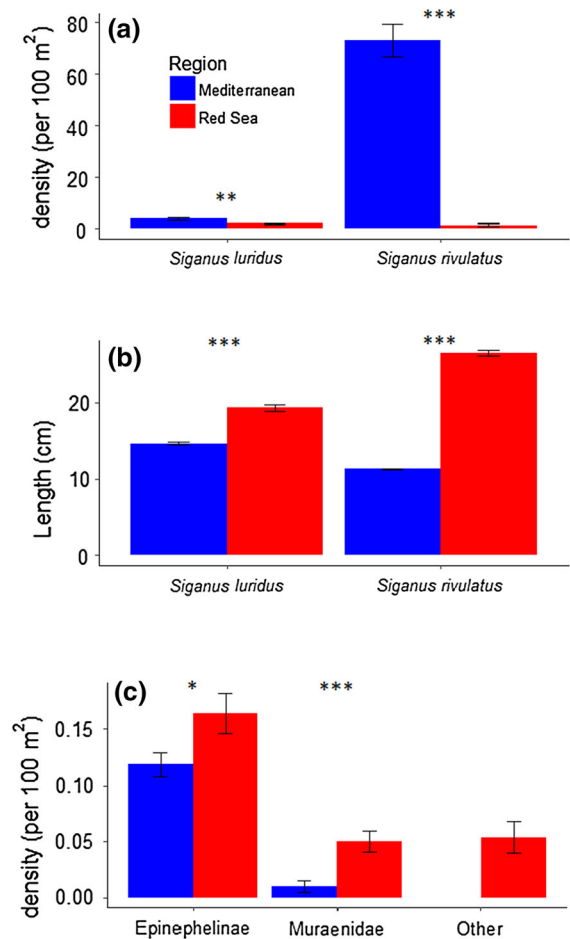
Calculating point locations of tracked fish (i.e., coordinates) requires transmitters to be detected by > 2 overlapping receivers. Nevertheless, detections by fewer receivers provide information on the presence of tagged fish within the array's perimeter. This was used to validate the extent of spatial utilizations and rule out long distance movements beyond the array's coverage (Supplementary material Fig. 1).

All statistical analyses were performed using R ver. 3.2.3 (R Core Team 2015).

## Results

The density of *S. rivulatus* is overwhelmingly higher in the Mediterranean compared to the Red Sea site (mean per 100 m<sup>2</sup> ± SE: 73 ± 6 and 1.3 ± 0.6, respectively; Welch Two Sample *t*-test, *t* = 11.15, *df* = 627.86, *P*-value < 0.001). Predator density was estimated by a combined abundance of large piscivores (> 20 cm) which is significantly lower in the Mediterranean compared to the Red Sea site (1.23 ± 0.11 and 0.48 ± 0.04, respectively; Welch Two Sample *t*-test, *t* = - 6.1222, *df* = 328.66, *P*-value < 0.001; Fig. 1; Supplemental material Table 1). Body size of *S. rivulatus* also differed significantly between sites, with smaller individuals in the Mediterranean compared to the Red Sea site (mean total length ± SE: 11.3 ± 0.01 and 26.5 ± 0.18; Welch Two Sample *t*-test, *t* = - 83.877, *df* = 335.46, *P*-value < 0.0001; Fig. 2).

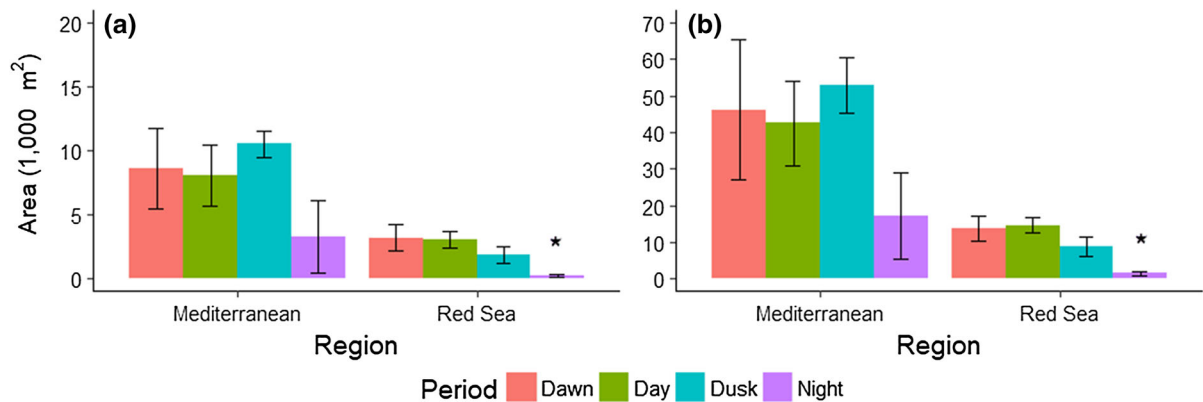
Core areas (KUD<sub>50%</sub>) utilized by *S. rivulatus* differed by up to an order of magnitude between individuals, ranging from 1145 ± 61 m<sup>2</sup> to 11,948 ± 564 m<sup>2</sup> (mean, SD). Similarly, overall home ranges (defined by KUD<sub>95%</sub>) ranged from 7112 ± 561 m<sup>2</sup> to 69,112 ± 5923 m<sup>2</sup>. In both regions, nocturnal KUDs were smaller compared to daytime and crepuscular periods in core areas and overall home ranges, as expected for a diurnal species, although the difference was significant in the Red Sea (KUD<sub>50%</sub>: Kruskal–Wallis;  $\chi^2$  = 9.98, *df* = 3, *P*-value < 0.05; KUD<sub>95%</sub>:  $\chi^2$  = 10.5, *df* = 3, *P*-value <



**Fig. 2** Data from visual fish surveys along the fringing reef in the Red Sea site (*n* = 247, Brokovich 2001) and the Israeli Mediterranean coastline (*n* = 618, Frid and Yahel 2015), showing: **a** density (per 100 m<sup>2</sup>) of invasive rabbitfishes, **b** body size (TL) of invasive rabbitfishes (a and b, respectively) and **c** density of piscivores larger than 20 cm from depths between 0 and 30 m. Error bars represent the standard error. \*, \*\*, \*\*\*Represent significant differences between regions (*P*-value < 0.05, < 0.01, and < 0.001, respectively). **a** Rabbitfish densities, **b** Rabbitfish size and **c** Predator densities

0.05) but not in the Mediterranean (KUD<sub>50%</sub>-Kruskal–Wallis;  $\chi^2$  = 3.1061, *df* = 3, *P*-value = 0.3756; KUD<sub>95%</sub>- $\chi^2$  = 3.4697, *df* = 3, *P*-value = 0.3247; Fig. 3).

Comparison of daytime home range sizes (excluding nocturnal locations) between regions showed no significant differences at lower utilization levels (50–70%), but at higher utilization levels (80–95%) home range size in the Mediterranean was significantly larger compared to the Red Sea (*P*-value <



**Fig. 3** Mean ( $\pm$  SE) size of utilized core areas (a) and overall home ranges (b) in the Red Sea and Mediterranean ( $n = 5$  and  $n = 3$ , respectively) according to period of day. \*Represent

significant differences ( $P$ -value  $< 0.05$ ). Home range sizes were calculated for each period of day, across the study duration

0.05), and overall home range size was more than double in the Mediterranean (Fig. 4). Variation in size of cumulative home range showed a discernible difference between regions (Fig. 4). While Red Sea individuals maintained a constant home range size throughout their respective tracking periods, Mediterranean individuals showed intermittent increases in cumulative home range size over time (Fig. 4).

The consistent home range size of Red Sea individuals can also be seen in the measures of site fidelity, where we find that distances between consecutive COAs (mean  $\pm$  SE) are significantly longer in the Mediterranean ( $39 \pm 7$  m) than in the Red Sea ( $8.6 \pm 1$  m) (mixed effect model,  $F_{(1,7)} = 21.59$ ,  $n = 92$ ,  $P$ -value = 0.03; where every observation is a calculated distance between a pair of COAs, Fig. 5). The time elapsed between nights for which we had data was not found to have a significant effect on distance between COAs (Table 2).

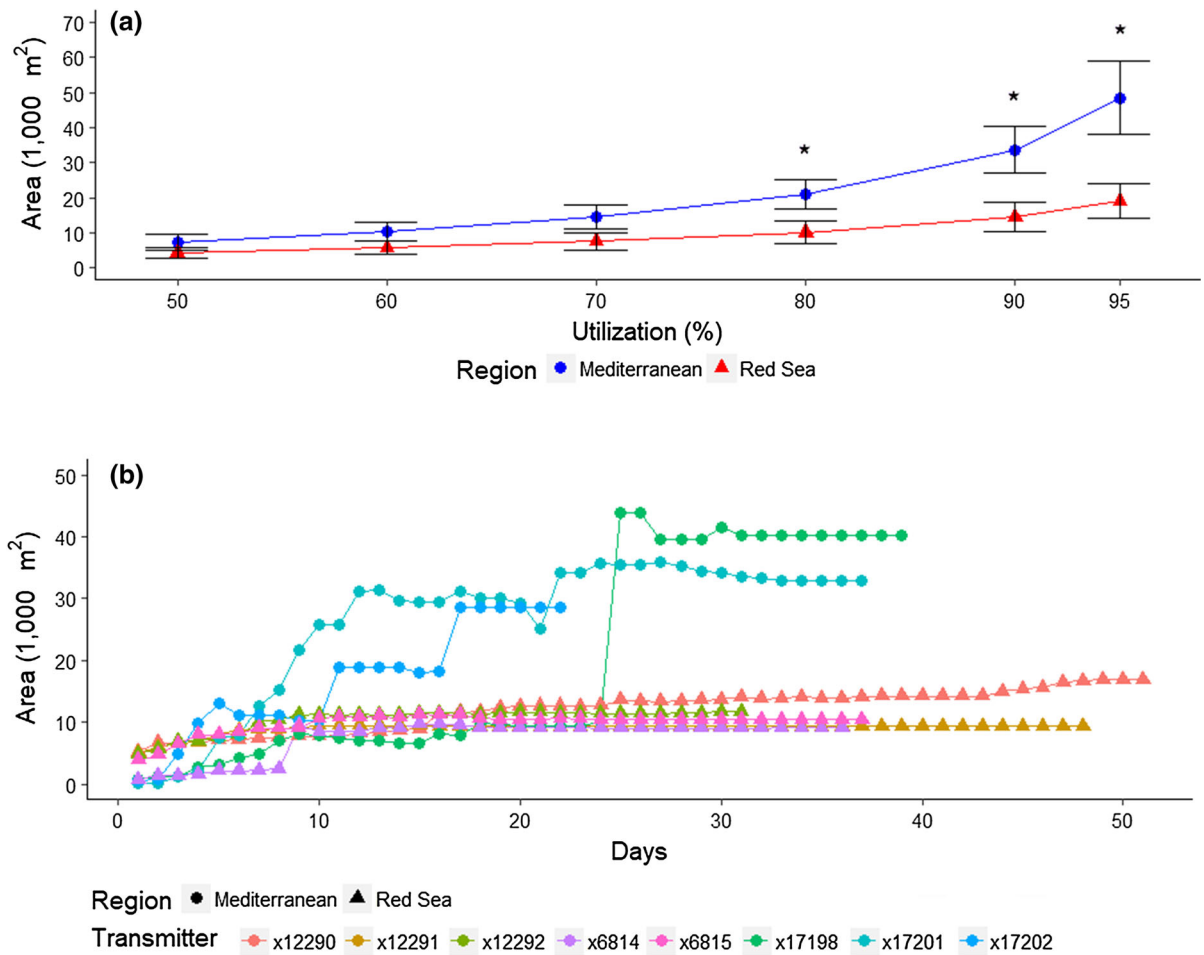
## Discussion

Animals are predicted to display behavioral changes when introduced to novel and unfamiliar landscapes, however there have been very few attempts to demonstrate such changes with invasives in the field (but see Knowlton and Graham 2010; Smith et al. 2018). Identifying unique behavioral patterns in the invaded range may illuminate processes that facilitate the spread and exacerbate the impact by invasive species (Holway and Suarez 1999). Moreover,

biological invasions present an excellent opportunity to study behavioral plasticity between populations that inhabit drastically different environments in their native and invaded range. We found that the movement patterns of *S. rivulatus* at a Mediterranean site differed substantially from those at a Red Sea site, including significantly larger overall home ranges and lower nocturnal site fidelity. This means that at the Red Sea site, individual *S. rivulatus* tend to remain within a given area, whereas in the Mediterranean site they move to different areas every several days. This inference is strengthened by the comparison of daily home range sizes separately, which shows no significant difference between regions (Supplementary material Fig. 2). These results may suggest that in the larger Mediterranean *S. rivulatus* individuals have substantially larger spatial footprints, particularly lower site fidelity, which leads to larger cumulative home ranges over time; potentially contributing to both their impact and their ability to expand their distribution in the invaded range. In this work, we employed continuous tracking of fish in the wild, at high spatial and temporal resolutions (mean tracking duration of 37 days, tag transmission frequency  $1 \times 30 \text{ s}^{-1}$ , Supplementary material Table 2). These data provide a window to understand fine scales movement patterns that may allow improved inferences on the behavior of coastal marine fishes.

Substrate-associated coral reef fishes, such as rabbitfishes, are generally considered to have small home ranges (Sale 1978). For example, the damselfish *Pomacentrus flavicauda* utilizes areas as small as  $2 \text{ m}^2$

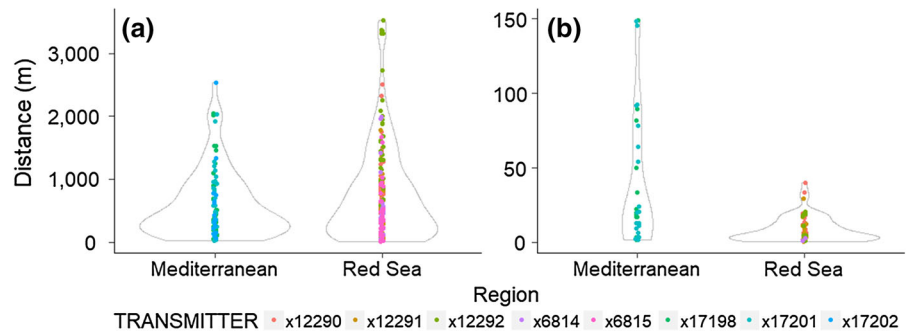




**Fig. 4** **a** Comparison of utilization distributions (mean  $\pm$  SE) of *Siganus rivulatus* in the Red Sea (red) and the Mediterranean (blue). Utilization represents the probability of locating individuals within an area of the corresponding size. \*Represent significant differences between regions (two sample *t*-test, *P*-value  $< 0.05$ ). Night locations were omitted when estimating

home range sizes. **b** Cumulative overall home range (95% minimum convex polygons) of *S. rivulatus* in the Red Sea and the Mediterranean. Each point represents the overall home range calculated by positions recorded from the first day of tracking (days = 0)

**Fig. 5** Violin plots showing the frequency of 'distances' in each of the two regions. **a** Distance traveled per day (**a**), and distances between nocturnal centers of activity (COA) (**b**). Outlined densities are based on a Gaussian smoothing kernel



**Table 2** Summary of linear mixed model for distance between nocturnal centers of activity (COAs), fish = 6, observations = 92

Effect	Coefficient	df	F	P-value
Region	− 30.763 (Red Sea)	2.37	21.59	0.03
Interval	0.963	84.13	0.4	0.51

(Low 1971), the white goatfish (*Mulloidichthys flavolineatus*) utilize areas up to 11,500 m<sup>2</sup> (Holland et al. 1993) and rivulatus parrotfish (*Scarus rivulatus*) use areas of 22,000 m<sup>2</sup> (Welsh and Bellwood 2012a). Overall home range size of Red Sea individuals tracked in this study was (mean ± SE) 18,982 ± 5000 m<sup>2</sup>. This is similar to the only home range estimations for rabbitfishes to date which are found to range between 17,000 m<sup>2</sup> to 46,000 m<sup>2</sup> for *S. doliatus* (Fox and Bellwood 2011) and 10,900 m<sup>2</sup> to 22,800 m<sup>2</sup> for *S. doliatus* (Brandl and Bellwood 2013). Though rabbitfish species show interspecific variation in foraging behaviors and home range sizes, the observed home range of *S. rivulatus* in the Red Sea falls within the observed range for this genus. Comparing home range sizes according to periods of day showed that in both regions *S. rivulatus* was strictly diurnal (active at dawn, day, and dusk). This confirms the species diurnal activity patterns at the study sites in both the native and invaded ranges.

Movement patterns of fish at the Mediterranean site indicate that individuals undergo home range relocation, which stands in contrast to the restricted and consistent home range over time at the Red Sea site (Fig. 4). Moreover, nocturnal site fidelity is significantly lower in the Mediterranean site compared to the Red Sea site. However, we find very similar daily home ranges and traveling distances between the Red Sea and Mediterranean individuals. This home range relocation (Robertson 1988), unlike migration, means that individuals do not return to their previous home range. Home range relocation is considered to be rare in coral reef fishes (Kramer and Chapman 1999; Robertson 1988; Sale 1978) and has only few and anecdotal instances of it occurring in the Mediterranean (*Diplodus sargus*, Abecasis et al. 2015). Thus, it is hard to assess, at this stage, if home range relocation is typical of other Mediterranean sites and other species.

Variation in resource density has been shown to influence movement patterns of reef fishes, but the spatial response to this effect may be complex. For example, Jud and Layman (2012) found that non-indigenous lionfishes (*Pterois* spp.) in Florida displayed small overall home ranges and very high site fidelity, while they experienced high prey resource density. Their suggested mechanism was that novel predators can easily exploit naive prey in a fixed position without actively foraging (Sih et al. 2010). However, rabbitfish, being herbivores, would be able to maintain a consistent home range only if the algae within the utilized area recovered at a sufficient rate (Berger-Tal and Bar-David 2015; Possingham 1989). This does not appear to be the case in the Mediterranean, where rabbitfishes are very abundant (Fig. 2) and have been shown to exhaust the resources over large areas (Sala et al. 2011), which would likely necessitate moving to new patches. Thus, in the Mediterranean, intense grazing of macroalgae by rabbitfishes, brought about by their high densities (Vergés et al. 2014), may drive home range relocation as resources are exploited faster than they can be replenished.

Predation risk has been postulated to restrict the distribution and home range size of reef fishes (e.g., Beukers and Jones 1998; Hixon 1991; Kramer and Chapman 1999; Sale 1993; Turgeon et al. 2010; Welsh and Bellwood 2012b). As movement generally increases the risk of predation by exposing fishes to predators (Turgeon et al. 2010 and references therein), individuals are more likely to utilize a smaller area and display a higher degree of site fidelity when predation risk is high. On coral reefs such as the Red Sea fishes are subjected to high predation risk (Beukers and Jones 1998; Hixon and Beets 1993; Hixon and Jones 2005), while in the Mediterranean, predator density is lower (Bariche et al. 2004; Fig. 2). We suggest that less constrained movement patterns, resulting in larger home ranges and lower site fidelity of *S. rivulatus* in the Mediterranean may be, in part, also facilitated by lower predation risk.

Raw detection data for all fish (Supplementary material Table 2) showed that in the Red Sea site receivers adequately covered the entire range of movement by tagged individuals, and fish transmitters were consistently detected by at least three receivers. Thus, Red Sea individuals have undoubtedly remained within the array. However, the raw detection data in

the Mediterranean site show gaps in the presence of rabbitfish with the array (Supplementary material Table 2). This means that overall home range sizes in the Mediterranean site are most likely underestimated. Thus, the observed differences in site fidelity and home range size between the Red Sea and Mediterranean sites may in fact be larger than estimated in this study.

Our study was limited to a single site within each region, and includes a limited number of individuals (five in the Red Sea, and three in the Mediterranean). Hence, it is difficult to generalize the results to the entire the Red Sea and Mediterranean. However, we have conducted this study at two site that are representative of the typical seascape and fish assemblage structure in areas occupied by rabbitfishes in the Eastern Mediterranean and the Red Sea. Additional studies are required in order to make broader inferences on the behavior of rabbitfish at larger geographic scales, and to examine behavioral variation within regions. Differences in home range size and site fidelity may provide some indication of phenotypic plasticity in the behavior of *S. rivulatus*. Given the genetic similarity between populations of *S. rivulatus* in the native Red Sea and the invaded Mediterranean (Bonhomme et al. 2003; Hassan et al. 2003), we consider it unlikely that the variation in behavior between regions is driven by a genetic component. The outcome of this behavioral change is that the impact by *S. rivulatus* is not confined to recruitment or settlement sites, but can increase as a result of post-recruit movements by adults. The marked increase in habitat utilization patterns by *S. rivulatus* in the invaded range is a likely contributor to the devastating ecological impact rabbitfishes are having in the Mediterranean.

## Conclusions

While immense ecological and conservation work have been invested in studying the distribution of marine invasive species, spatial patterns at the individual level have largely been overlooked. This work found considerable differences in site fidelity of *S. rivulatus* between sites in its native and invaded range, with fish in the Red Sea site maintaining a constant home range size, while fish in the Mediterranean site frequently relocated their home ranges. This dynamic

utilization distribution, if indeed indicative of patterns within the larger Mediterranean, could potentially increase secondary dispersal and the impact of over-grazing by adult *S. rivulatus*. The variation in *S. rivulatus* behavior between sites in the native and invaded ranges mirror shifts in their realized climatic niche (Parravicini et al. 2015). Information on home range and movement may be used to improve predictive models of species distribution and range expansion (Lima and Zollner 1996; Rhodes et al. 2005). The observed differences in space use between sites in the native and invaded ranges underscores the potential importance of behavior at the individual level for biological invasions, and should be investigated further at larger scales.

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## Compliance with ethical standards

**Ethics declaration** The research presented in this thesis was conducted according to the ethical guidelines, specified by the Veterinarian Service Center, Sackler Faculty of Medicine, Tel Aviv University. The proposed research methodology received permission from the experimentation ethics review committee (under permit approval #L-15-043). Fish from the coral reef of Eilat were collected with permission from the Israeli Nature and Parks Authority (INPA) (under permit approval #2013/40106, #2014/40245).

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