Long-duration remote underwater videos reveal that grazing by fishes is highly variable through time and dominated by non-indigenous species

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RESEARCH ARTICLE

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Abstract

In the marine environment, fish contribute to key ecological processes such as controlling food-webs through top-down impacts, especially on algae. To date, the assessment of fish grazing activity has mostly been performed using short-term (<1 h) censuses by divers or remote cameras which do not allow estimating the variability of grazing rate within and between days. However, understanding the temporal variation of fish activity and hence contribution of species to ecosystem functioning is of particular interest in the context of biological invasion. Here, using long-duration remote underwater cameras, we recorded fish abundance and grazing events over three consecutive days in October 2019 in a shallow Mediterranean ecosystem from northern Crete. This novel approach allowed us to assess temporal variation of abundance and grazing activity of the two native (*Sarpa salpa* and *Sparisoma cretense*) and the two non-indigenous fish species (*Siganus rivulatus* and *Siganus luridus*). Non-indigenous *Siganus rivulatus* was the most common species in the studied coastal habitat, followed by the two native species while the non-indigenous *Siganus luridus* was scarce. Overall, the non-indigenous *S. rivulatus* and the native *S. salpa* are responsible for more than 90% of the recorded grazing activity with similar bite rates between the two species. More than 70% of the grazing activity arose in grazing pulses in the afternoon, supporting the diel feeding hypothesis according to which feeding is greater in the afternoon when nutritive quality of macrophytes is the highest. In addition, some of the highest peaks in grazing activity were driven by a few individuals. Hence, surveys of only abundance could not provide accurate estimates of herbivory. Last, *Siganus rivulatus* presence did not significantly affect grazing activity of the native *Sarpa salpa*. Our results demonstrate that long-duration remote underwater videos are a useful tool to accurately assess the contribution of fishes to ecosystem functioning.

Introduction

The Mediterranean Sea is a threatened hotspot of biodiversity (Coll et al., 2010). Despite representing only 0.32% of the world's oceans volume, it hosts at least 4% of all known marine species (Bianchi & Morri, 2000) including 63 endemic fish species (Psomadakis et al., 2012). Mediterranean biodiversity is concentrated in coastal ecosystems that host more than 350 fish species (Coll et al., 2010). Although most Mediterranean coastal ecosystems host diverse and abundant macrophytes, including seagrass and macroalgae, there were only two herbivorous fish species: *Sarpa salpa* and *Sparisoma cretense*, before the opening of the Suez Canal. These native herbivorous species control biomass and diversity of macrophyte communities through grazing. For instance,
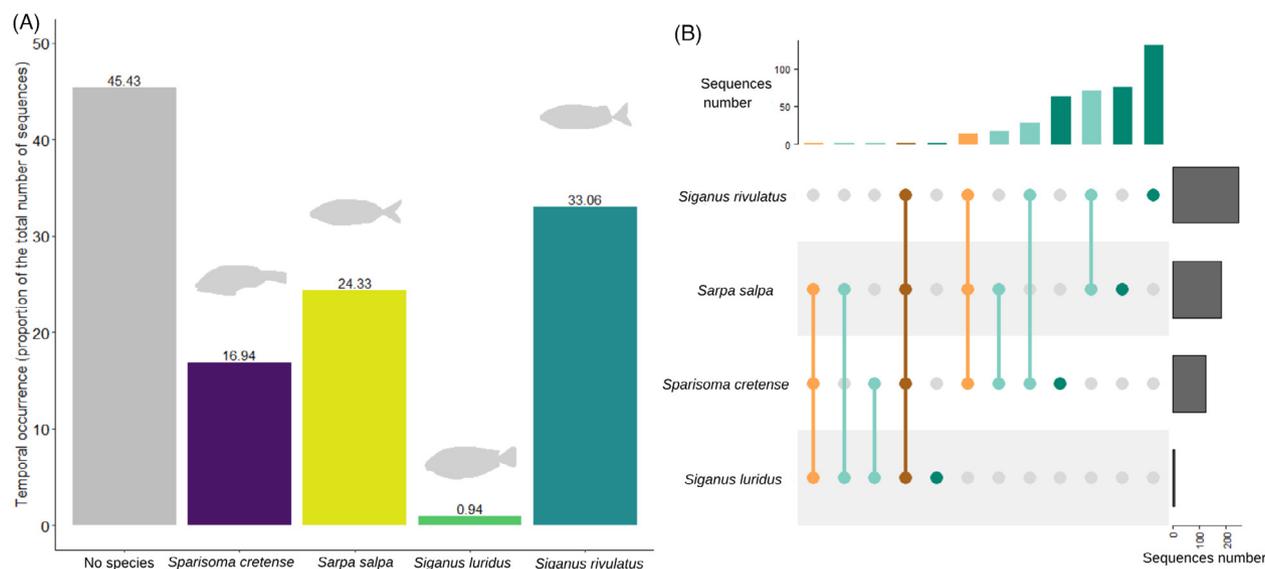
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Figure 1. Occurrence and co-occurrence of the four herbivorous fish species on the 744 annotated sequences. (A) proportion of annotated sequences (1min40s) on which no fish or one of the four herbivorous species was detected. As several fishes can be detected in the same sequence, the sum of the proportions exceeds 100%; (B) the number of annotated sequences on which each species, pairs of species, triplets of species, and quadruplet of species were present ordered with increasing number of sequences. Lines colours reflect the number of species in a studied combination (dark green for one species, blue for two species, orange for three species and brown for four species).

Cystoseira spp. depth distribution is largely shaped by *S. salpa* herbivory, with a high dominance in spatial refuges with low herbivory (Vergés et al., 2014).

Coastal Mediterranean ecosystems have been increasingly affected by climate change, fishing, pollution and habitat destruction, which synergistically led to a marked alteration of its unique biodiversity (Coll et al., 2010). In addition, coastal Mediterranean ecosystems are hotspots of non-indigenous species (Rilov & Galil, 2009), with about 90 new exotic fish species that established during the twentieth century (Streftaris et al., 2005). Most of the exotic species that have successfully colonized the Mediterranean Sea (Rilov & Galil, 2009) came from the Red Sea through the Suez Canal opened in 1869 under the supervision of Ferdinand de Lesseps. Among the so-called 'lessepsian species', the two tropical herbivorous species, *Siganus rivulatus* and *Siganus luridus* were some of the first colonizers in 1927 and 1956, respectively (Ben-Tuvia, 1964). Since then, they have been expanding northward to the Levantine basin and the Aegean Sea and westward to the Strait of Sicily (Azzurro et al., 2017). In the coastal ecosystems of the Levantine basin (Israel, Lebanon, Turkey), the two rabbitfish species represent more than 80% of the total herbivorous species biomass, while native *S. salpa* is now scarce (Bariche et al., 2004; Sala et al., 2011). In these invaded regions, overgrazing of macroalgae by *Siganus* has also led to a remarkable habitat shift from well-developed algal assemblages to barren rocky substrates (Sala et al., 2011; Vergés et al., 2014). This removal of algal canopy by non-indigenous rabbitfishes eventually leads to the reduction of species richness of fish and of benthic invertebrates and to the reduction in total fish biomass (Vergés et al., 2014).

In many regions from Aegean, Ionian and Sicilian Seas the native and non-indigenous herbivorous fishes co-occur and macrophytes are abundant (Bariche et al., 2004; Vergés et al., 2014). In those ecosystems, little is still known about the contribution of each species to macrophyte removal. It is of particular interest to compare abundance and behaviour of native and non-indigenous species including the temporal variability of grazing activity and the interactions between species.

Assessment of fish abundance and grazing activity has so far mostly been performed with underwater visual census using scuba diving (Brock, 1954). However, diver presence through sound (Radford et al., 2005) and visual stimuli (Dickens et al., 2011) could bias estimates of species abundance and species behaviour (Dickens et al., 2011; Emslie et al., 2018). While such mobile and short-term (<2 h) surveys have allowed assessing the grazing rate at the individual level, they did not assess the variability of the grazing rate within and between days in a given micro-habitat (e.g. Fox & Bellwood, 2007; Robinson et al., 2020). Yet, understanding these temporal variations is a key challenge to apprehend ecosystem functioning. In fact, the variation in mobile species

presence at a given location impacts the nutrient fluxes occurring in this given location. More specifically, as fishes are mobile and gregarious, their local abundance (Birt et al., 2012; Myers et al., 2016) and grazing behaviour could vary within and between days as could the timing activity between species (Scott et al., 2021; Tomas et al., 2005; White et al., 2002). While some video-based surveys of herbivory were conducted over multiple days and at various times within each day, we still know little about the between-days and within-days variabilities of grazing activity by herbivorous fishes. Using a long duration recording approach is thus essential to study these within and between day variations in a given micro-habitat. So far, assessing grazing activity of fishes using long-duration remote underwater recordings has been done only in tropical ecosystems and rivers (Fox & Bellwood, 2008; Nunes et al., 2020; Tebbett et al., 2020).

We investigated the contribution of the native and non-indigenous herbivorous fishes to grazing on coastal macroalgae using a long-duration remote recording approach in a coastal ecosystem from Crete (Aegean Sea, Eastern Mediterranean) where the four fish species co-occur. We specifically address the following questions: (i) How does the abundance of native and non-indigenous species vary within a day and between days? (ii) How does the grazing activity vary between species within a day and between days? (iii) Can fish abundance be used as a proxy of herbivory pressure? and (iv) Does the presence of non-indigenous fishes affect the grazing behaviour of native fishes?

Materials and Methods

Sampling methods

The study was carried out in Kokkini Hani (35.3308° lat; 25.25770° long) in northern Crete during three consecutive days in October 2019 (Fig. S1). The studied habitat was located 100 m off the shoreline, shallow (2 m depth) and dominated by sandy and rocky substrate covered by *Posidonia oceanica* patches, turf and macroalgae, respectively. Remote underwater camera systems consisted of two GoPro Hero 5 (GoPro Inc., USA) cameras positioned in opposite directions and within an acrylic cylindrical housing (diameter: 10.2 cm, length 30 cm; BlueRobotics, Torrance CA, USA). Each camera was connected to a 10,000 mAh battery allowing a recording in high-definition video (1920 by 1080 pixels at 25 frames per second) for more than 12 hours. Each housing was mounted on a 20 cm high tripod. Two systems were placed 25 metres apart and video recordings from the four cameras were synchronized. Systems were deployed by divers just before sunrise (7:00) and picked up just

before sunset (18:40). Immediately after the start of each recording, a 1m² quadrat was placed in front of each camera for 30 seconds and subsequently removed to avoid disturbance to fish behaviour. Since the cameras were static, this brief quadrat deployment at the beginning of the video recording was sufficient to monitor fish over this standardized area (Longo et al., 2014) by marking the quadrat shape on the computer interface. The four recording drops were representative of the local benthic composition and were mostly covered by a mixture of epilithic algal matrix (<2 cm tall brown, green and red algae) and of taller individuals of red and brown algae. They were close to *Posidonia oceanica* patches (<2m²). Meteorological and hydrological conditions were constant for three consecutive days of video recording (Table S3). Only videos recorded 60 minutes after the departure of divers and 10 minutes before their return on monitored drops (i.e. from 8:00:00 to 18:30:00) were retained for subsequent analysis, to remove the direct impact of divers on the recorded behaviour. Overall, we recorded 140 hours of high-definition videos.

Measuring abundance of herbivorous fishes and their grazing activity on videos

As annotating all individuals and their grazing behaviour is demanding (up to more than 10 minutes of annotation for each minute of video), we decided to assess the abundance and the grazing activity by the four herbivorous species (*Sarpa salpa*, *Sparisoma cretense*, *Siganus rivulatus*, *Siganus luridus*) on evenly spaced samples of each day-long video. Annotations of fish were thus done on sequences of 100 seconds every 10 minutes (*i.e.* six sequences of 1min40s per hour for a total of 10 minutes of annotation per hour) yielding 62 annotated sequences per day and per recording drop (equivalent to 103 minutes of annotations per day and per recording drop) for a total of 744 sequences over the 3 days and four drops.

For each of the video sequences, frames were extracted at a one frame per second rate, yielding 100 frames per sequence. For each frame, all individuals of the four studied species present in the 1 m² studied area were assigned into two behaviour types: 'swimming' was considered as the default behaviour and 'grazing' was annotated only when the mouth was in contact with turf or algae (Fig. S2). When the mouth was not visible, the behaviour was defined as swimming to prevent overestimation of the grazing rate.

Presence time was computed as the number of frames (hence seconds) in which a species was present within a 100-seconds sequence. The abundance of each species in each 100-seconds sequence was calculated as the maximum number of individuals observed within a single

frame (thereafter referred to as *maxN*) (Ellis & DeMartini, 1995; Willis & Babcock, 2000).

The allocation of grazing time for each species was calculated as the number of frames where the species is recorded grazing divided by the total number of frames where the species is present within a day and a drop.

The grazing activity for each species was computed as the total number of bites (*i.e.* an individual annotated as grazing in a frame) within a given time sequence. Then, the contribution of each species to the total herbivory over a given unit of time (from sequence to day) was computed as the proportion of total number of bites over the given unit of time made by each species.

To infer the potential grazed pressure for each species, individuals of the four species of interest were sampled in adjacent habitats of the studied ecosystem using gillnets: 28 individuals of juvenile *Sarpa salpa* (standard length between 7.5 and 12 cm) as only juveniles were seen on videos, seven individuals of juvenile and subadult *Sparisoma cretense* (7 cm to 16 cm), 28 individuals of adult *Siganus rivulatus* (12 to 16 cm) and eight juvenile individuals of *Siganus luridus* (7.5 to 12 cm). Mouth width, gape size and fish body length were measured as in Villéger et al., 2010. Mouth area was computed as an ellipse (mouth area = mouth width × gape size ×) for each individual and then average values were computed for each species. The potential grazed pressure was eventually computed as the product of the mouth area of each species times the bites number per unit of time.

Statistical analyses

For each species, we tested whether grazing rate was correlated with presence time and *maxN* per sequence using Spearman's rank correlation test on sequences where each species occurred. We then compared grazing time allocation and grazing activity between species using Kruskal–Wallis and associated Dunn tests. The difference of grazing activity of *S. salpa* and *S. cretense* when individuals were co-occurring with *Siganus* or without *Siganus* presence was assessed using Wilcoxon tests. Lastly, we tested for difference in the timing of grazing activity between species using a generalized mixed model with random effects and zero inflation correction:

$$bites\ number \tilde{\ } species\ identity : sequence\ number +$$
$$(1|system\ identity/drop\ identity)$$
$$+ (1 + sequence\ number|day)$$

We thus tested for the effects of species and of time (sequence number being seen as an ordinal variable) on bite numbers while controlling for the variation in drops (within camera systems) and the repartition of sequence number across days. The model was computed using the *glmmTMB* package and then the associated Nakagawa's R^2 (Nakagawa, 2012) was computed using the *performance* package.

All data were analysed using R 4.0.5 and analysis are available on Github (https://github.com/CmlMagneville/Herbivory_BioInv_Paper).

Results

Occurrence of the four species

Herbivorous fishes were present in 54.3% of the 744 annotated 100-second sequences, and in only 11.6% of the total 1,252 minutes (*i.e.* 20 hours) of video analysed (Fig. 1). Overall, the non-indigenous *S. rivulatus* was the most frequently present species (79 min), followed by the native *S. salpa* and *S. cretense* (55 min and 28 min respectively), while the non-indigenous *S. luridus* was present for only one minute. All individuals of the native *S. salpa* observed on videos were juvenile although a school of adults of *S. salpa* were spotted nearby while snorkelling (personal observations). Both juvenile and sub-adults of the other native species *S. cretense* were recorded. All individuals of the non-indigenous *S. luridus* and *S. rivulatus* recorded were adults, although few juveniles of siganids were observed in the surveyed site and other sites around Heraklion for the weeks before the survey (personal observations).

The four species occurred alone on 36.4% of the 744 sequences and 7.8% of the 75,144 annotated frames (Fig. S3). The native *S. salpa* and the non-indigenous *S. rivulatus* co-occurred in 11.7% of the 744 sequences representing 0.98% of the annotated frames. This co-occurrence represents 23.3% of frames where *S. salpa* was seen and 15.5% of frames where *S. rivulatus* was seen. The two natives and *S. rivulatus* co-occurred in less than 3% of sequences and less than 1% of the analysed time (i.e. <20 seconds).

Distribution of grazing activity among the four herbivorous species

Time allocated to grazing between days and drops was highly variable for each species, ranging from 0 up to nearly 40% of the total presence time (Fig. S4). Time allocation was significantly different among species (Kruskal–Wallis, *P*-value <0.001, Chi-Squared = 27.946, df = 3) with *S. salpa* and *S. rivulatus* having significantly higher time allocation for grazing (16.6% and 15.4% respectively) than *S. luridus* and *S. cretense* (1.06% and 5.40% respectively).

Grazing activity was highly variable among days and drops (Fig. 2). Overall, the most active grazers were *S. salpa* and *S. rivulatus* that each contributed to more than 45% of the bites recorded daily in the 1 m² quadrats. On the other hand, bites by *S. cretense* and *S. luridus* represented on average 8.86% and 0.2% of the daily bite number respectively.

The native *S. salpa* grazed on 38.8% of the 129 sequences in which it occurred without *S. rivulatus*, while it grazed on 67.4% of the 46 sequences in which the two species co-occurred. Taking abundance into account, grazing by *S. salpa* or by *S. cretense* was not significantly affected by the presence of *S. rivulatus* when maximal abundance was of one, 2–5 or 6–10 individuals (Wilcoxon test; *P*-value >0.15) (Fig. 3; Fig. S5).

Comparing grazing activity and abundance

Abundance per sequence was different for all pairs of species (Kruskal–Wallis's test, *P*-value <0.05; associated Dunn's test, Supplementary Table S1) with a mean number per sequence of 0.62 individuals for *S. rivulatus*, 0.47 for *S. salpa*, 0.34 for *S. cretense* and 0.01 for *S. luridus*. Among sequences with continuous presence of a given species (called time-occurrence), only one individual was

present in >60% of cases for each of the four species (Fig. S6). Groups of at least 10 individuals were spotted in 1.70% of *S. cretense* time-occurrence and less than 1 percent for *S. salpa* and *S. rivulatus* time-occurrence.

Correlation between abundance (maxN) and bite number was significant only for *S. salpa* and *S. rivulatus* with Spearman's correlation coefficients lower than 0.45 (Fig. 4 and Table S2). Correlation between presence time and grazing activity was significant for all species except *S. luridus* (Fig. S5) with correlation coefficients higher than 0.50.

Temporal variation of grazing activity and interspecific variation of grazing

Grazing activity significantly differed between species and across time (Table 1). If grazing was a homogeneous process, each of the 186 sequences would gather 0.67% of total recorded activity (red dotted line on Fig. 5). Sequences with no bite represent 37.63% of all sequences and the sequence with the highest number of bites recorded accounted for 9.55% of total grazing activity. The five highest grazing pulses cumulatively contributed to 23.66% of the total measured herbivory, as much as the 72 lowest grazing events combined. Overall, more than 55% of the total grazing
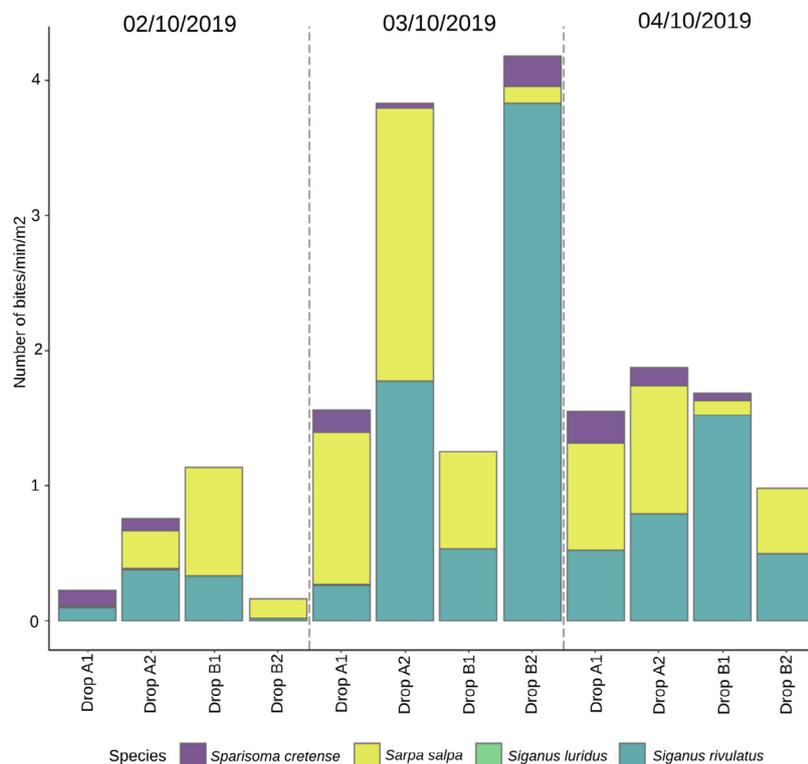

Figure 2. Distribution of bite rate across the four species per day and per drop.
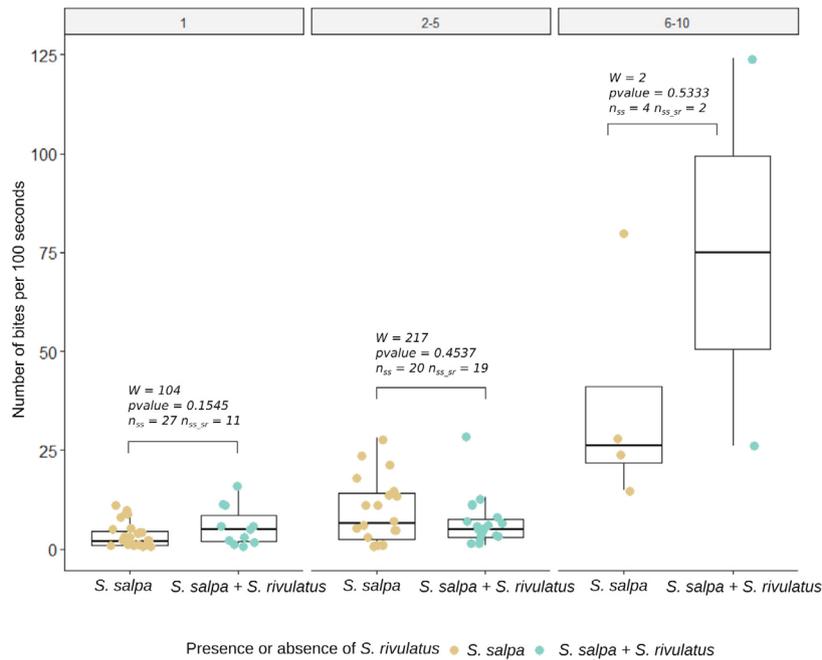
Figure 3. Variation of *S. salpa* grazing rate (bites number in a 1min40s sequence) according to the maximal number of *S. salpa* individuals seen in a sequence (1, 2–5, 6–10) (maxN) depending on whether *S. rivulatus* was present or absent. Only sequences where *S. salpa* was grazing were kept.
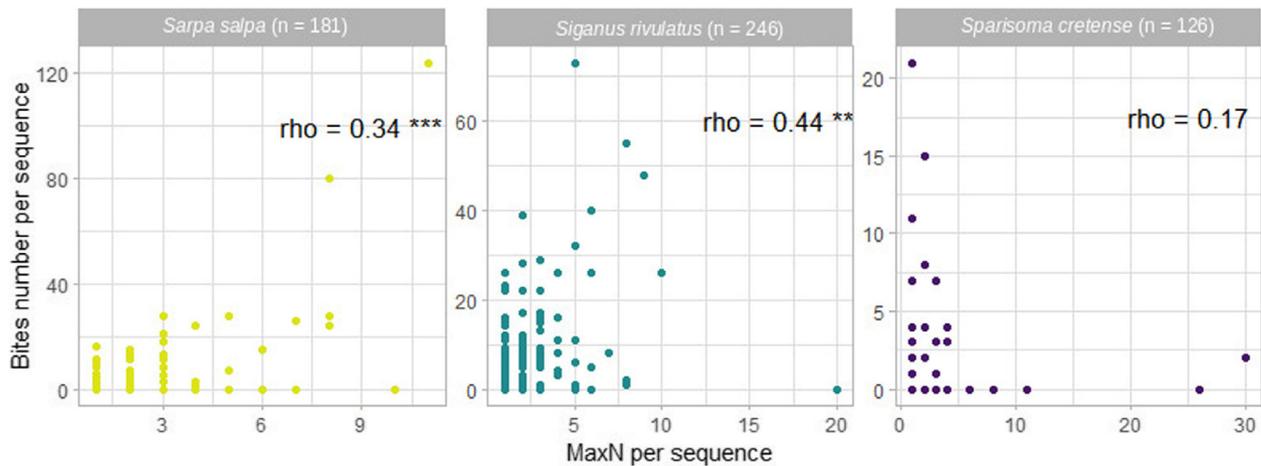

Figure 4. Correlation between maximal number of individuals and bites number in 1min40s sequences.

activity recorded over the 3 days occurred on a single day (03 October 2019) (Fig. 5).

Grazing activity of both *Sarpa salpa* and *Siganus rivulatus* was variable between days with more than half of their activity done on 03 October 2019 (Fig. 6). The afternoon timespan between 13:10:00 and 18:10:00 gathered most of the grazing activity of *S. salpa* and *S. rivulatus*. *Siganus rivulatus* individuals are present on 60.82% of sequences

($N = 97$) showing no grazing activity for this species and *S. salpa* individuals are present on 41.38% of sequences ($N = 116$) showing no grazing activity for this species.

The non-indigenous *S. rivulatus* had a mean mouth area of 4.48 ($\pm$ 0.70) cm^2 while the other species had a smaller mouth area of 2.62 ($\pm$ 0.99) cm^2 for *S. cretense*, 1.87 ($\pm$ 0.22) cm^2 for *S. luridus* and 1.84 ($\pm$ 0.15) cm^2 for *S. salpa*. Overall, *S. rivulatus* had the highest

Table 1. Effect of each variable used in the GLMM testing for the effects of fish species and time (using sequence number as an ordinal variable) and their interaction on grazing activity.

	Chi-Square	p-value ($\alpha = 0.05$)	Degree of freedom
Species identity	69.018	**<0.0001**	3
Sequence number	5.106	**0.0239**	1
Species:sequence number	2.905	0.406	3

contribution to algae removal with peaks in the afternoon, especially on 03 October 2019 (Fig. 7).

Discussion

Daylong recording by remote underwater cameras in a shallow coastal ecosystem from the Eastern Mediterranean Sea revealed that grazing activity by native and non-indigenous fishes is highly variable between species, both between and within day.

Overall, the non-indigenous *S. rivulatus* had the highest algal removal, with a three times higher impact than the native *S. salpa*. These findings corroborate those found in the other sites from the Eastern Mediterranean where *S. rivulatus* presence is in fact responsible for a decrease of 65% of canopy algae abundance (Vergés et al., 2014). However, the presence of *S. rivulatus* does not prevent *S. salpa* grazing and the two species are often seen grazing and swimming in mixed schools (first time reporting such schools to our knowledge). Thus, the decreasing abundance of the native *S. salpa* in the part of the Eastern Mediterranean Sea where *S. rivulatus* is abundant, is likely not due to direct negative behavioural interactions.

Siganus luridus was scarcely recorded confirming its preference for deeper water than the three other species (Bariche et al., 2014). It would thus be informative to test if in habitats where *S. luridus* is predominant, the grazing activity is higher than what we measured or if the non-indigenous *S. luridus* compete with the other non-indigenous species *S. rivulatus*. Moreover, despite observations of numerous post-larvae individuals in July 2019, there was an unusually low abundance of young-of-the-
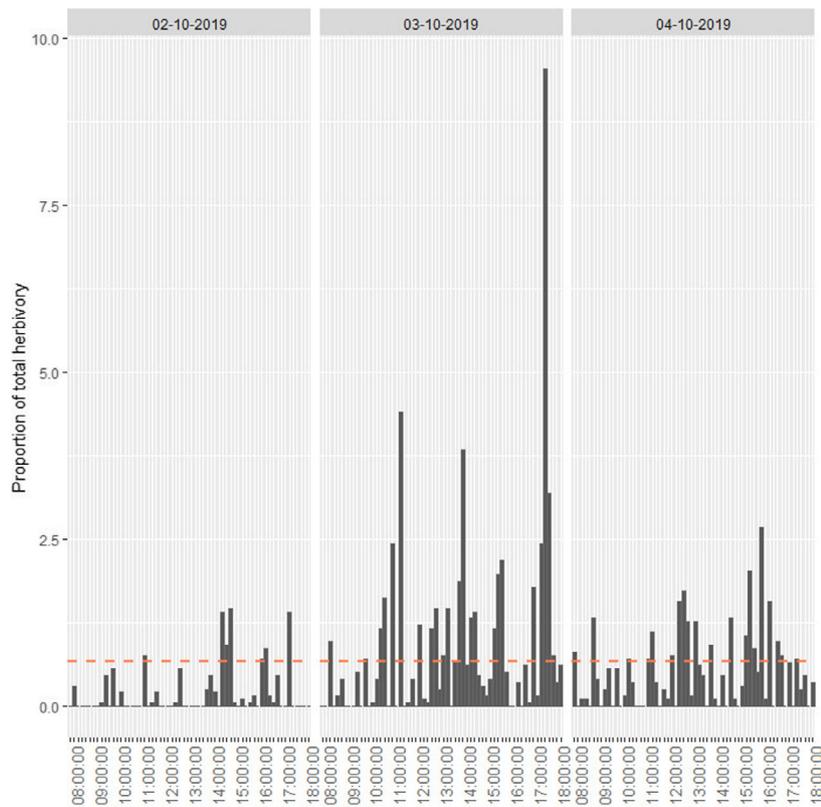

Figure 5. Variation of the grazing activity based on the proportion of total grazing realized per sequence (1min40s) throughout the three sampling days with the four 1m²-drops pooled. Red dotted line shows the proportion of herbivory per sequence expected if the herbivory is temporally uniform.
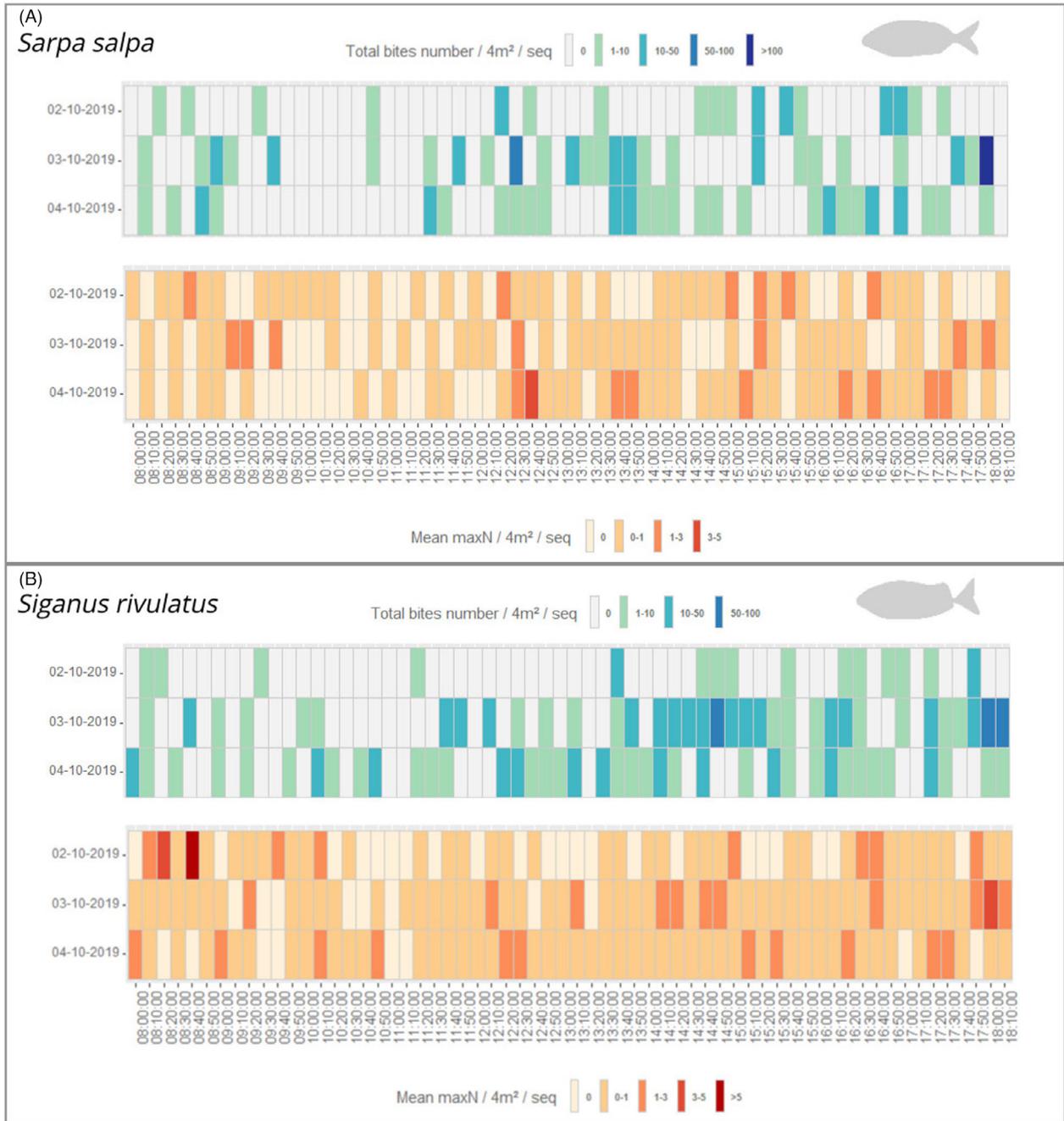
Figure 6. Heatmaps of grazing activity (top maps for A and B) and abundance intensity (bottom maps for A and B) for *S. salpa* (A) and *S. rivulatus* (B). Values are the average number of fish and bite rate over the four 1 m²-drops. The pooled *maxN* per 100 seconds was computed using the mean of *maxN* across the four drops for a given sequence.

year Siganus *spp.* Therefore, future studies should measure how the grazing activity of each herbivorous species varies across larger temporal scales, especially between years.

Grazing activity was highly variable between days, with more than half of the bites recorded over only one third of total time. Environmental conditions (seawater and air temperature, wind and wave regime, currents) were similar over the three sampling days, so this variation can be attributed to fish behaviour. These temporal and spatial variabilities can be due to several parameters such as the benthic composition (Robinson et al., 2020), the nutritive quality of algae (White et al., 2002) or the fear of predators. In fact, *S. rivulatus* reduces its food consumption
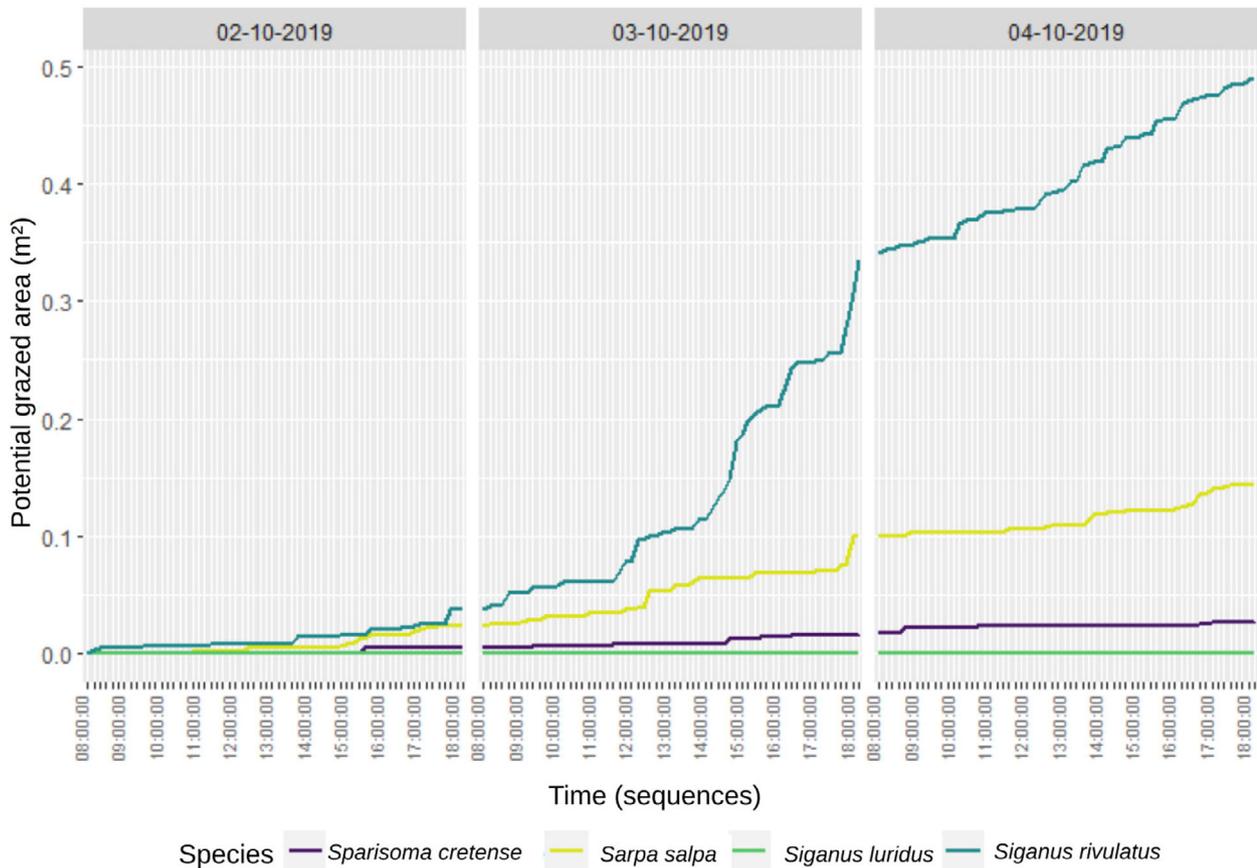
Figure 7. Cumulative potential area grazed across three days (total area across four plots of 1m^2 observed 1/6th of the time (412 minutes per day)).

when exposed to chemical cues from a recently killed conspecific (Shapiro Goldberg et al., 2021). Some predators such as *Seriola dumerili* and *Octopus vulgaris* were spotted on the surveyed site, during day and night, respectively, although we did not observe predation on fishes. In this study, we investigated the grazing activity on three sampling days in a single season. It would thus be informative to increase the temporal scope of this study by sampling on a higher number of days and on different seasons to see if the observed diel patterns are consistent with our results.

While the two main herbivorous species were present throughout the daytime in the surveyed site, 71% of the combined grazing activity of *S. salpa* and *S. rivulatus* occurred during the afternoon. In the marine environment, some circadian biological rhythms have already been documented such as the day–night change in fish species richness, abundance and identity (Azzurro et al., 2013; Harvey et al., 2012; Myers et al., 2016) but diel variation in fish activities (such as grazing) remains understudied (Harvey et al., 2012). Our results support the diel feeding hypothesis suggested by Taborsky and

Limberger (1980) and tested by only a few studies (Horn et al., 1990; Polunin & Klumpp, 1989; White et al., 2002; Zoufal & Taborsky, 1991). This hypothesis suggests a greater feeding activity in the afternoon linked with a higher algal nutritional value at this moment of the day (White et al., 2002). This pattern has already been documented for more than 20 herbivorous marine species (White et al., 2002). Moreover, as both *S. salpa* and *S. rivulatus* feed until dusk and then migrate away from feeding habitats to resting sites (Jadot et al., 2006; Pickholtz et al., 2018), they are likely to translocate nutrients from the feeding sites to night-resting sites (Bray et al., 1981; Meyer & Schultz, 1985). It would be enlightening to test whether diel grazing temporal variation is comparable among different habitats of a given ecosystem (i.e. algal beds, turf algae, seagrass meadows) as their nutritional value can vary differently across day's hours.

Overall, grazing activity by fishes was performed mostly in pulses. In fact, the five strongest events were equivalent in terms of bites number to the sum of the 72 weakest events, showing that the majority of herbivory is done by a few big grazing events. During a pulse, the grazing

activity is mainly done by a single species, thus recording only one of the grazing pulses does not give a global picture of grazing activity. Such pulses of grazing activity have already been documented in terrestrial and subtidal environments (Armitage et al., 2013; Gibson et al., 2021) on time periods larger than a day such as a year. The within- and between-day large variability of herbivory calls for comprehensive surveys to be able to accurately measure the cumulated role of each species to this key function.

Importantly, we found no significant correlation between the number of individuals present at a given time and their total grazing activity. In fact, we recorded a large number of individuals with no grazing activity, and at different times few individuals with high *per capita* grazing rates. Hence, abundance of a species at a given time is not a good proxy for its feeding activity and thus herbivory could not be inferred only from fish counts, as already reported for coral reefs (Bejarano et al., 2017; Fox & Bellwood, 2008).

Long-duration remote cameras recording for all daylight time over several days allow accurate estimates of abundance and algae removal. However, very few studies have used these approaches (Fox & Bellwood, 2008; Longo et al., 2019; Nunes et al., 2020; Tebbett et al., 2020). Indeed, while remote underwater cameras are neither challenging to set up (e.g. by two divers) nor highly expensive (~500 USD per camera), analysing hundreds of hours of videos is a time-consuming process. The development of deep-learning algorithms to identify fish individuals and species as well as their behaviour (Ditria et al., 2020) could tackle this resource bottleneck and contribute to ease the use of long-duration remote underwater videos in marine ecology.

Acknowledgements

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure 1. Map of the study site with sampling site highlighted as the blue dot.

Figure 2. Annotation of fish behaviours. Only individuals that were passing through the quadrat were annotated, thus standardising the measures into a 1m² surface. A swimming individual was considered to be in the quadrat as long as a part of its body was in the quadrat. However, a grazing individual was considered to be in the quadrat only if its mouth was into the quadrat. An individual was considered to be grazing if the annotator saw its mouth in contact with the substrate and its body inclined. Examples with bounding boxes around fish swimming and bounding boxes around mouth of fish grazing.

Figure 3. Occurrence and co-occurrence of the four herbivorous species on the 74 144 annotated seconds: the number of seconds on which each species, pair of species, triplet of species, quadruplet of species in seen ordered with increasing number of sequences, lines colors reflect the number of species in a studied combination (dark green for one species, blue for two species, orange for three species and brown for four species).

Figure 4. Comparison of the allocation of grazing time based on the proportion of time where each species was grazing. Each dot represents data for a given 1m² drop and a given day (three sampling days and four drops pooled).

Figure 5. Variation of *S. cretense* grazing rate (bites number in a 1min40s sequence) according to the maximal number of *S. cretense* individuals seen in a sequence (2 < maxN < 5) depending on whether *S. rivulatus* was present or absent. maxN = 1 and maxN > 5 were not considered as only one event gathered *S. cretense* and *S. rivulatus* when maxN = 1 and there was no event with maxN > 5 gathering *S. cretense* and *S. rivulatus*. Only sequences where *S. cretense* was grazing were kept.

Figure 6. Log transformed maximal number of individuals per time-occurrence (i.e. a sequence of frames with continuous presence of a given species) number of occurrences per species is shown on top.

Figure 7. Correlation between bites number and duration of presence (*i.e.* number of frames where a given species was seen within a sequence) in sequences where each species occurs.

Table 1. Pairwise Wilcoxon's tests to test differences between *maxN* values of sequences across species.

Table 2. Values of maxN and bites number for *S. luridus*.

Table 3. Environmental conditions of the three sampling days.